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Effects of natural enemies, competition, and host plant quality on introduced birch leafminers (Hymenoptera: Tenthredinidae)

by

Scott Cameron Digweed ©

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

Department of Entomology

Edmonton, Alberta
Spring, 1995

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Effects of natural enemies, competition, and host plant quality on introduced birch leafminers (Hymenoptera: Tenthredinidae)** submitted by Scott Cameron Digweed in partial fulfillment of the requirements for the degree of Master of Science.

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Date: 11 April 1995

To Maurya,

for love, togetherness, and the sharing of dreams

Abstract

The ecology of introduced birch-leafmining sawflies (Hymenoptera: Tenthredinidae) was studied to contribute to a pest management plan for urban birches in western Canada, and to test hypotheses about the ecological interactions that develop around introduced species.

Three species of introduced birch leafminers were found throughout Alberta, but only *Fenusa pusilla* (Lepeletier) and *Profenusa thomsoni* (Konow) were abundant. *Fenusa pusilla* adults first emerged in mid-May, and were capable of up to three generations per year, whereas *P. thomsoni* adults emerged as a single generation in June. Both species were more abundant and were active earlier at an urban than at a rural location.

Native natural enemies consumed introduced birch leafminers. Light larval mortality was caused by generalist larval parasitoids (Hymenoptera: Eulophidae), but *Lathrolestes luteolator* (Gravenhorst) (Hymenoptera: Ichneumonidae) and predatory arthropods may have significantly impacted populations. Life table analyses revealed that birch leafminer mortality was generally highest in early instars and on urban trees.

Birch leafminers participated in several competitive interactions. Intraspecific competition occurred in both birch leafminer species, reducing weights of larval *F. pusilla*, but reducing survivorship of larval *P. thomsoni*. Despite reduced larval survivorship, females of *P. thomsoni* did not avoid ovipositing on small or crowded leaves. Interspecific competition was suggested in that outbreaks of the native birch skeletonizer, *Bucculatrix canadensisella* Chambers, and early-season leaf damage by *F. pusilla*, seemed to decrease survival of larval *P. thomsoni*.

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I am very grateful to the generous homeowners in the Edmonton area who allowed me to enclose, clip, trap, or otherwise aesthetically impair their birch trees during the course of this study. I can only hope that this thesis will contribute in some way to the continued enjoyment of birches in Edmonton.

Lastly, I thank Maurya, Didi, and Oliver for their friendship and love.

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1. Introduction

1.1 The study of introduced pest insects

Insects are persistent and conspicuous pests of trees in North America. Indigenous and introduced pest species cause huge losses of marketable timber each year, despite massive pest control programs (Moody and Amirault 1992). In urban habitats, insect infestations make ornamental trees unsightly and weak (Barbosa and Wagner 1989). Chemical insecticides have been the main source of insect control, especially in agricultural and urban forest settings (Barbosa and Wagner 1989). In recent years, insecticides have become less popular and less effective because of problems concerning rapid selection for pest resistance, adverse effects on beneficial organisms (i.e. pollinators and natural enemies), phytotoxicity, and high economic and environmental costs (van den Bosch et al. 1982; Barbosa and Wagner 1989, DeBach and Rosen 1991; LaSalle 1993).

Successful biological control lacks most of the problems associated with chemical insecticides (Caltagirone 1981; Hulme 1988). Classical biological control, the inoculative release of exotic predators or parasitoids against a pest insect, is the most commonly employed biological control strategy (van den Bosch et al. 1982; Greathead 1986; DeBach and Rosen 1991), and has been successfully implemented in some systems (Caltagirone 1981; van den Bosch 1982; Barbosa and Wagner 1989). However, the level of pest suppression achieved can be greatly affected by differences between ecosystems in the region of origin and the region of introduction (Pschorn-Walcher 1977; van den Bosch et al. 1982). Thus, detailed study of the biologies of introduced pests, indigenous competitors, indigenous natural enemies, and exotic natural enemies (for potential introduction) are crucial to successful pest management programs (Nealis 1991).

Traditionally, the study of introduced pests has been "top-down", with research programs being designed around one or more suppressive techniques (Coulson and Witter 1984). The resulting data may be deficient in at least two ways. First, failure to examine "non-essential" aspects of the pest's biology may result in missed management opportunities that could complement or wholly supplant proposed control strategies. For example, failure to define trophic links in the pest's community before implementing management procedures can result in reductions or local extinctions of effective natural enemies, thus destabilizing the pest's population dynamics (Nealis 1991; LaSalle 1993). Second, the data collected may be of limited value outside the specified control program, reducing the generality, scope, and efficiency of the research effort. Expanded scope and minor changes in design may result in more general contributions to ecological knowledge.

To avoid these problems, a "bottom-up" approach can be used, such as collecting life history and general ecological data on an introduced pest and its community before deciding on control procedures. Detailed life history data form a foundation from which potential management strategies can be explored. These data help define the distribution and variability of the pest population (i.e. the extent and persistence of the problem), and can indicate developmental stages that are potentially vulnerable to management tactics. Life table studies can identify new relationships developing between the introduced pest and native host plants, natural enemies, or competitors (Strong et al. 1984; Cornell and Hawkins 1993). Such relationships should be considered prior to attempting pest suppression, so that biological diversity and community stability are maintained (LaSalle 1993).

Basic and detailed studies of introduced pests can also contribute more broadly to general ecological understanding. For example, biological control studies have provided evidence (see Debach and Rosen 1991) supporting the development of ecological theories of predator and parasitoid dynamics (e.g., Nicholson and Bailey 1935; Hassell and Varley 1969; Free et al. 1977; Beddington et al. 1978; Hassell 1978; Hassell 1986; May and Hassell 1988). The recent wave of interest in host-parasitoid interactions (Waage and Greathead 1986; LaSalle 1993; Godfray 1994; Hawkins 1994) has arisen largely from primary research in biological control (Eggleton and Belshaw 1992). Several other sub-disciplines of community ecology have benefitted from applied research, such as the study of insect-plant relationships (e.g., Baranchikov et al. 1991; Bernays 1990, 1991, 1992; Menken et al. 1992; Bernays and Chapman 1994), the role of competition in structuring communities (Lawton and Strong 1981; Strong et al. 1984;

Denno et al. 1995), and higher-order interactions (as defined by Billick and Case 1994; see references in Strong et al. 1984). Not surprisingly, discoveries and general syntheses in these areas feed useful information back into applied entomological research. For example, biological control efforts have benefitted greatly from pure ecological research examining host-parasitoid and predator-prey systems (Beirne 1963; Southwood 1977; Greathead 1986; references in Eggleton and Belshaw 1992). This sort of cooperative development can occur only if studies of pest systems begin from a basis of sound and detailed biological data, from which management options and ecological theory can be developed and explored.

1.2 The study system: birch-leafmining sawflies

This thesis focuses on leafmining insects feeding on birch (*Betula* spp.), an important tree taxon in northern forests worldwide (Hosie 1990). Although the Palearctic leafmining fauna on birch is diverse (Godfray 1984), there are few abundant, native Nearctic leafminers on birch (Lindquist and Thomson 1970; Ives and Wong 1988), and no birch-leafmining sawflies are native to the Nearctic (Smith 1971). However, five species of birch-leafmining sawflies have been accidentally introduced into North America from Europe this century (Smith 1971; Goulet 1992). Three of these are found in Alberta (Drouin and Wong 1984): *Heterarthrus nemoratus* (Fallen), *Fenusa pusilla* (Lepeletier) and *Profenusa thomsoni* (Konow). *Fenusa pusilla* and *P. thomsoni* are consistently abundant and pestiferous in Alberta (Drouin and Wong 1984).

All five sawfly species feed within birch leaves as larvae, causing damage in the form of blotch-shaped mines (Smith 1971). Thus, all can cause significant browning of birch leaves, which does not kill trees (Friend 1933) but presumably affects tree growth, especially when damage is caused early in the season (DeClerck and Shorthouse 1985). Infested birches are aesthetically displeasing, and are susceptible to attack by more serious pests such as the bronze birch borer, *Agrilus anxius* Gory (Coleoptera: Buprestidae) (Conklin 1969; Coulson and Witter 1984). The main economic effect of birch leafminer damage is probably on sales of ornamental birch, since birch timber is generally used only in small quantities to produce specialty items (Jasper Millworks Ltd. and Woodland Resource Services Ltd. 1987; Canadian Forest Service 1994).

The life histories of both *F. pusilla* and *P. thomsoni* have been examined in eastern North America, but *F. pusilla* has received more attention because it is more abundant there. Major studies of *F. pusilla* have been done in Connecticut (Friend 1931, 1933) and Québec (Cheng and LeRoux 1965, 1966a, 1966b, 1968, 1969, 1970). More limited studies have been conducted in Newfoundland (Jones and Raske 1976) and northern Ontario (DeClerck 1984; Kentner 1994). Aside from the study of Drouin and Wong (1984), very little is known about the biology of this species in Alberta.

Less is known about *P. thomsoni*, because it is rare in Europe (Liston 1981; Shaw 1981) and parts of Canada (DeClerck and Shorthouse 1985). Martin (1960) found it locally abundant in northern Ontario, and along with Watson (1959), described its life history and mortality factors. Drouin and Wong (1984) found *P. thomsoni* to be abundant in Alberta, and described its basic biology.

Chemical insecticides have been the method of choice for control of birch leafminers. Initially, contact insecticides were applied to leaves to kill eggs and larvae (Friend 1931, 1933; Shread 1952), but more recently, systemic insecticides have been used effectively against larvae (Shread 1966; Cheng and LeRoux 1968). However, the problems associated with chemical pesticides (discussed above) probably apply to this system as well, and thus effective alternatives have become desirable.

The solid foundation of work on *F. pusilla* in eastern North America has made possible several attempts at biological control. A long-term cooperative project involving Forestry Canada and the Commonwealth Institute for Biological Control (CIBC) determined that European populations of *F. pusilla* are controlled by an extensive parasitoid complex, and recommended several parasitoid species for introduction into North America. The two most promising candidates were the ichneumonids *Lathrolestes nigricollis* (Thomson) (Ctenopelmatinae) and *Grypocentrus albipes* Ruthe (Tryphoninae). Both parasitoid species have been introduced from central Europe into Newfoundland (Raske and Jones 1975), Québec (Guèvremont and Quednau 1977), and several middle-Atlantic states

(Fuester et al. 1984). Recent evidence suggests that *L. nigricollis* is established in Newfoundland, Québec, southern Ontario, and many eastern states (Fuester et al. 1984; Quednau 1984; Van Driesche 1989; Barron 1994) and causes parasitism rates of 20-72% (Van Driesche 1989). Introductions of *G. albipes* have been less successful (Raske and Jones 1975; Fuester et al. 1984; Van Driesche 1989), and it is unclear if any viable populations of *G. albipes* presently exist in North America. Neither parasitoid has yet been recorded in western North America.

Biological control efforts against *P. thomsoni* have not been pursued, because this species is rare in Europe, apparently lacks specialist parasitoids (Eichorn and Pschorn-Walcher 1973; Schönrogge and Altenhofer 1992), and is not generally pestiferous in eastern North America (Martineau 1984; but see Martin 1960). However, *P. thomsoni* causes significant damage in Alberta (Drouin and Wong 1984), providing impetus for the discovery and introduction of effective parasitoids.

There is a need for an integrated pest management plan for birch leafminers in Alberta. At present, many homeowners and municipalities attempt to control both *P. thomsoni* and *F. pusilla* using systemic insecticides (such as Cygon 2e®). This strategy is often ineffective and may have negative ecological consequences. Development of an effective pest management plan requires increased knowledge about the distribution and abundances of these leafminers in western Canada, and about how their populations are affected by predators, parasitoids, competitive interactions, and variation in host plant quality.

1.3 Objectives of this thesis

The overall objectives of this work are to determine the life histories of birch-leafmining sawflies in Alberta, and to understand their interactions within the community on *Betula* spp. Drouin and Wong (1984) discovered some significant differences between birch leafminer communities in Alberta and eastern Canada. For example, the most abundant species in Alberta is usually *P. thomsoni*, but in eastern North America it is *F. pusilla*. In addition, *F. pusilla* has fewer generations per year in Alberta. This thesis will build on previous work and contribute to the development of a pest management program for birch leafminers in Alberta. In addition, this work will provide more general ecological data about community-level interactions involving leafminers.

In Chapter 2, the abundances, provincial distributions, and phenologies of birch leafminers in Alberta are discussed. The native birch folivore guild on birch is also described, and the potential for its members to compete with birch leafminers for leaf resources is examined. In Chapter 3, the natural enemy community attacking birch leafminers is described, and life table analyses of birch leafminer mortality are presented.

Leaf resources can become limiting at relatively low densities of birch leafminer larve, because they are restricted to one leaf for their entire larval life. In Chapter 4, the probability, magnitude, and consequences of intraspecific competition for both *F. pusilla* and *P. thomsoni* are discussed. Also examined are interspecific competition between *F. pusilla* and *P. thomsoni*, and between *P. thomsoni* and the native birch skeletonizer, *Bucculatrix canadensisella* Chambers (Lepidoptera: Lyonetiidae). Lastly, host plant effects on birch leafminers at several spatial scales are discussed, and their role in competitive interactions is examined.

Chapter 5 is a discussion of the contribution of life history data and an understanding of community-level interactions to general ecological knowledge and to a pest management program for birch leafminers in Alberta. I propose directions for additional research that would further both the pest management and ecological research objectives of this thesis.

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2. Distribution, phenology, and potential competitors of birch leafminers (Hymenoptera: Tenthredinidae) in Alberta

2.1 Synopsis

Three species of exotic birch-leafmining sawflies were found in Alberta: *Fenusa pusilla* (Lepeletier), *Profenusa thomsoni* (Konow) and *Heterarthrus nemoratus* (Fallen). Only the first two were abundant. Birch leafminers were found at all sites surveyed in central and southern Alberta, and appeared to be expanding their ranges in the north. *Fenusa pusilla* adults began emerging in mid-May, and there were from one to three generations per year, depending on the site and year. *Profenusa thomsoni* began attacking trees from early to late June, and there was only one generation per year. Both species were more abundant and were active approximately 2 weeks earlier at an urban than at a rural location. *Fenusa pusilla* and *P. thomsoni* are unlikely to compete directly for leaf resources, since they were quite separate spatially and temporally on birch trees. However, potential exists for intraspecific competition within both species, as well as for interspecific competition between *P. thomsoni* and the native birch skeletonizer, *Bucculatrix canadensisella* Chambers (Lepidoptera: Lyonetiidae).

2.2 Introduction

At least five species of birch-leafmining sawflies from the tenthredinid tribes Fenusini and Heterarthrini were introduced into eastern North America from Europe since 1920 (Britton 1924, 1925; Dowden 1941; Martin 1960; Lindquist and Thomson 1970; Smith 1971; Nystrom and Evans 1989; Goulet 1992). *Messa nana* Klug and *Scolioneura betuleti* (Klug) are recent introductions and remain confined to eastern Canada (Lindquist and Thomson 1970; DeClerck and Shorthouse 1985; Nystrom and Evans 1989), whereas *Heterarthrus nemoratus* (Fallen), *Fenusa pusilla* (Lepeletier) and *Profenusa thomsoni* (Konow) spread to Alberta before 1970 (Drouin and Wong 1984; H. Cerezke, pers. comm.). This study focuses on *F. pusilla* and *P. thomsoni* because they have become significant pests of birch in Alberta.

Life history studies have been carried out in eastern North America for both *F. pusilla* and *P. thomsoni*. *Fenusa pusilla* females emerge in early spring, mate or reproduce parthenogenetically (Friend 1933), and oviposit in the mesophyll of young birch leaves (DeClerck and Shorthouse 1985). The first four larval instars feed within a growing blotch mine. Fifth instar larvae do not feed, but emerge from their mines, drop to the ground, burrow into the soil, and construct soil pupal cells using a mucilaginous secretion (Cheng and LeRoux 1965). Adults emerge later in the year or the following spring. *Fenusa pusilla* has one to three generations per year in Europe (Eichorn and Pschorn-Walcher 1973), three or four per year in Québec (Cheng and LeRoux 1965), and one or two per year in Alberta (Drouin and Wong 1984).

Profenusa thomsoni adults emerge in mid-summer and oviposit in leaves without mating; only females are known (Martin 1960; Togashi 1981). Five instars are spent in the blotch mine, and sixth-instar larvae emerge from the leaf, fall to the ground, and burrow into the soil to overwinter. One generation per year occurs in Europe and eastern North America, where *P. thomsoni* is rare (Martin 1960; Eichorn and Pschorn-Walcher 1973; Martineau 1984; Schönrogge and Altenhofer 1992). One generation per year also occurs in Alberta, but population sizes tend to be larger than in Europe or eastern North America (Drouin and Wong 1984).

Many leafmining insects are confined to one leaf for their entire larval lifespan, and thus are probably susceptible to intra- or interspecific competition for leaf resources, especially as their habitats deteriorate (Faeth 1991). Leafminers that do not compete use little leaf area (Faeth 1985) or are maintained at low levels by natural enemies (Faeth and Simberloff 1981). *Fenusa pusilla* and *P. thomsoni* use relatively large leaf areas to complete development (Friend 1933; Martin 1960) and do not seem well regulated by natural enemies in Alberta (Drouin and Wong 1984). Thus, intra- and interspecific competition may be prominent regulating forces in populations of these two species in Alberta.

It is also possible that *F. pusilla* and *P. thomsoni* compete with members of the native leaf-feeding community on birch, such as the birch skeletonizer, *Bucculatrix canadensisella* Chambers (Lepidoptera: Lyonetiidae). Adults of this moth emerge in mid-summer and oviposit on leaf surfaces (Friend 1927). The first two larval instars feed in a small serpentine mine, and the last three instars feed externally on leaf tissue between veins (Friend 1927). In late summer, fifth instar larvae drop to the ground and spin pupal cases in the litter, in which they overwinter. Extensive outbreaks of *B. canadensisella* do occur (Blais and Pilon 1968; Patterson et al. 1973), and populations have recently been high in parts of Alberta (Cerezke and Gates 1992; Cerezke and Brandt 1993).

More detailed life history information is needed about birch leafminers in Alberta to increase the effectiveness of management efforts. Adult and larval leafminers were sampled during 1992-1994 to establish species distributions, phenologies, and differences between urban and rural populations. In addition, I sought patterns suggestive of competition both within and between birch leafminer species. Lastly, the arthropod community on birch was sampled for *B. canadensisella* and other herbivores potentially competitive with birch leafminers.

2.3 Materials and Methods

The distribution and abundance of birch leafminers were assessed through a survey of native birch species (*Betula papyrifera* Marshall, *B. neoalaskana* Sargent, *B. glandulosa* A. Michaux, and *B. occidentalis* Hooker), introduced species (*B. pubescens* Ehrhart and *B. pendula* Roth), and probable hybrids of these. Sites were surveyed in the first week of September in one or more of the years 1992-1994, although some sites were surveyed in July or August as well. One mature tree having representative damage was examined at each site. The information collected from each tree included: 1) tree height and species; 2) site location and characteristics; 3) tree infestation index (a visual estimate of percent leaves infested with birch leafminer, ranked on a six-point scale: 1= 0%; 2= <5%; 3= 6-25%; 4= 25-50%; 5= 51-75%; 6= >75%); 4) leaf infestation index (a visual estimate of the average percent leaf area damaged by mining on infested leaves, ranked 1-6, with same categories as above); 5) species of leafminers present; and 6) damage caused by other herbivores. Fifty-five sites were surveyed in Alberta (Figure 2-1), and two sites were surveyed in the southern Northwest Territories (Hay River and Fort Simpson; not shown on Figure 2-1).

Birch leafminer life history was studied on six (1992) or five (1993) mature birch trees from urban settings in Edmonton (53°31'N, 113°31'W), and from a natural forest at the George Lake Field Station, approximately 80 kilometres northwest of Edmonton (ca. 53°57'N, 114°06'W). During 1994, activity of adult birch leafminers was monitored on five trees on the University of Alberta campus, Edmonton. All urban trees occurred in mown lawn habitats, and had not been chemically treated for at least three years. Statistical comparisons of response variables among locations, years, and birch leafminer species were made using PROC GLM in SAS (SAS Institute 1988). Non-normal data were transformed prior to analysis using square-root or logarithmic transformations (Zar 1984), or Blom's normal rank scores (SAS Institute 1988).

In 1992, pyramidal emergence traps were used to sample adult emergence from the soil (modified from Martin [1977]). Two sides were wooden and two were of fine mesh ("no-see-um" style irregular weave; no opening larger than 0.1 mm²). Insects were captured in a clear, ventilated plastic bottle inverted at the top of the trap. A clear plastic funnel was glued into the lid of the bottle to minimize escapes back down to the soil. Two traps were placed randomly within the dripline under each tree, one located permanently, and one moved to a new, random location each week to ensure capture of possible multiple generations of *F. pusilla* adults. Trap bottles were replaced two (George Lake) or three (Edmonton) times per week, and all birch leafminer adults were enumerated.

In 1993, sticky traps were used instead of emergence traps. They were 9.0 cm diameter translucent white plastic lids, one side of which was smeared with Darina AX axle grease (see Kalcounis et al. 1992). Traps were hung from branches approximately 2.0 m above the ground and changed once per week; adults of birch leafminers and of *B. canadensisella* were enumerated. In 1994, 10.0 x 15.0 cm commercial yellow sticky traps (Phero Tech Inc., Delta, B.C.) were placed on trees on the University of Alberta campus in Edmonton, to monitor weekly activity of birch leafminer adults. Since different methods were used to trap adults in different years, it was impossible to partition catch variation into trap and year effects. However, it is assumed that trapping methods do not differ in effectiveness between birch leafminer species, and so relative abundances of the species will be used to indicate between-year differences in catch.

To describe the phenology of larval birch leafminers and of larval *B. canadensisella*, leaf samples were collected from trees in Edmonton and at George Lake in 1992 and 1993. One branch having at least 15 leaves was collected from each of the upper, middle, and lower portions of the crown of each tree once per week. Branches were selected to contain a maximum number of leafminer larvae, and so did not provide accurate estimates of population sizes or of relative distributions of larvae at different levels in the tree crown. Population estimates (e.g., section 2.4.1) were projected by standardizing values as "larvae per leaf", using only those leaves from weeks in which larvae were found (i.e. leaves having the potential to be larval habitat). The following data were collected for all leaves: leaf age (young or mature); percent damaged (by birch leafminers, *B. canadensisella*, or others, estimated using 11 percentage classes [0%, 10%, 20%, ..., 100%]); number, species, and stage of leafminer eggs and larvae; number of parasitized leafminer eggs and larvae; number of dead leafminer eggs and larvae; number of *B. canadensisella* mines; and number of other folivorous larvae. Leaf area was estimated in 1993 by using leaf length (base to tip along the midrib) and width (at the widest point, usually near the base), in the following regression equation: area = 0.637 (length x width) - 70.784 (r^2=0.948, n=50 leaves, 10 from each of 5 sites). Actual areas for the 50 leaves used to generate the regression equation were determined by tracing them onto graph paper, and counting the number of 1.0 mm squares within the perimeter of the tracing.

The potential for intraspecific competition within *F. pusilla* and *P. thomsoni* was estimated by calculating the leaf area used for development by individual larvae in Edmonton in 1993. The area used was estimated by multiplying the total leaf area by the proportion of the leaf damaged by mining. The only leaves included in this analysis were non-saturated leaves (<100% mined upon completion of larval feeding) containing only larvae that completed their development.

To estimate the relative abundances of potential competitors of birch leafminers, sweep net samples were collected once per week in 1992 from the lower and middle crown of each tree using a 25.0 cm diameter net. Two passes were made with the net, after which all arthropods were removed with forceps, placed in alcohol, and subsequently identified.

All phenological abundance patterns were initially plotted on both Julian- and degree-day axes, but are presented only on Julian axes here. Degree-days were calculated using the modified sine wave method of Allen (1976) with a threshold of 5°C. This threshold was chosen because it is commonly used for insects (Pruess 1983), and because the use of different thresholds did not greatly affect the fit of theoretical development curve models to empirical data for either *F. pusilla* or *P. thomsoni* (see Figure 2-7). Degree-days were accumulated starting from 1 April, since on average only 4.4 degree-days accumulate from 1 January to 31 March at a 5°C threshold (Environment Canada 1994). Meteorological data used were provided by Environment Canada from the Edmonton Municipal Airport and from Sion (located approximately 4 kilometres south of George Lake).

To test the sensitivity of degree-day models to variation in developmental parameters, theoretical development curves were generated for immature stages of both *F. pusilla* and *P. thomsoni* based on empirical abundance data from Edmonton in 1993. These data were used because accurate estimates of live egg abundances were obtained only in 1993, and insufficient sample sizes of immature stages were obtained from George Lake. Degree-day accumulations were calculated at thresholds ranging from 1 to 12°C using the modified sine wave method of Allen (1976). Subsequently, crude visual estimates were made of the timing (in degree-days, for each threshold 1 to 12°C) of the maximum abundance of each instar from the empirical data. These twelve sets of estimates were then placed in the model of Dennis et al. (1986), which uses iterative nonlinear regression techniques to generate parameters describing theoretical phenological curves for each immature stage. Calculations were performed using PROC NLIN within SAS (SAS Institute 1988), and resulting R^2 values were used to assess the fit of theoretical parameter estimates to empirical data at each of the twelve developmental thresholds. The theoretical parameters from the threshold having the highest R^2 were then used to generate curves showing the proportion of the insect population in each developmental stage over a range of degree-days.

2.4 Results

2.4.1 Species abundances and distributions. The most abundant species of birch leafminer at the Edmonton and George Lake study sites was *P. thomsoni* (Figure 2-2), although differences in abundance between *P. thomsoni* and *F. pusilla* were only significant in 1992 and 1994 (Table 2-1). Sex ratios of *F. pusilla* varied between years in Edmonton (proportion of females: 1992, 0.459 [emergence traps]; 1993, 0.280 [white sticky traps]; 1994, 0.512 [yellow sticky traps]), but sex ratio differences may be confounded with those resulting from the different trap types used. Sex ratios were not calculated at George Lake, since only males were captured, probably as a result of very low captures (1992, n=5; 1993, n=5). No adults and only six larvae of *H. nemoratus* were collected at Edmonton and George Lake between 1992 and 1994. *Messa nana* and *Scolioneura betuleti* were not collected in central Alberta.

Relative abundances of adult *F. pusilla* and *P. thomsoni* were similar in Edmonton and at George Lake in both 1992 and 1993 (Figure 2-2; see interaction terms in Tables 2-1A and B). In addition, adults were more abundant in Edmonton (mean catch per tree ± SE: 14.6 ± 4.1) than at George Lake (1.1 ± 4.1) in 1993 (Table 2-1B). This trend of greater abundance on urban trees is similar to that from the provincial survey of birch leafminer damage. The mean rank for the leaf infestation index was marginally greater for urban trees (mean ± SE: 3.63 ± 0.24) than for rural trees (2.81 ± 0.24) (2-sample t-Test, 2-tailed, p=0.132, df=63). However, there was little difference between tree infestation index ranks for urban (3.09 ± 0.37) and rural (2.91 ± 0.21) trees from the survey (p=0.714).

Although leaf sampling was not designed to quantify population levels, I assume here that it reflected trends in the field. There were significantly more *P. thomsoni* larvae per leaf in samples collected in 1992 (mean ± SE: 0.515 ± 0.035) than in 1993 (0.131 ± 0.038), and from Edmonton (0.382 ± 0.037) than from George Lake (0.265 ± 0.037) (Table 2-2B). The number of *F. pusilla* larvae per leaf was also greater in Edmonton (0.185 ± 0.056) than at George Lake (0.095 ± 0.056), but the difference was not statistically significant (Table 2-2A). The actual differences in larval leafminer abundance between locations are probably greater than indicated by these data, since leaves containing larvae were actively sought, and these were much harder to find at George Lake than in Edmonton.

Birch leafminers were found at most sites surveyed throughout Alberta (Figure 2-1). *Profenusa thomsoni* was the most abundant species found, and *H. nemoratus* was usually absent. However, *H. nemoratus* was more abundant near Slave Lake and Lac la Biche (also reported in Cerezke and Brandt 1993). Both *F. pusilla* and *P. thomsoni* were abundant in Calgary, but at Waterton Lakes National Park, only *F. pusilla* was detected. Other southern sites surveyed casually (e.g., Sand Point, Idaho and Chiliwack, British Columbia) had only *F. pusilla* as well.

In the north, a few larvae of *F. pusilla*, but none of *P. thomsoni*, were found at two sites mid-way between Peace River and High Level (Figure 2-1). However, in the town of High Level, both *F. pusilla* and *P. thomsoni* occurred on young ornamental birches in the schoolyard. Since neither species was found at naturally-forested sites within 50 km of this town, sawflies were probably imported with the trees. No birch-leafmining sawflies were found at rural sites north of High Level in 1992 or 1993, although in 1994, *P. thomsoni* were detected in the city of Yellowknife (62°30'N, 114°29'W) (D. Langor, pers. comm.).

Both *F. pusilla* and *P. thomsoni* were found on all birch species examined. Surprisingly, larvae were able to develop successfully even in the small leaves of bog birch, *B. glandulosa* (see Wilkinson 1990 for leaf illustrations). In addition, larvae of *F. pusilla* were collected from leaves of introduced *Betula jacquemontii* Spach (native to the Kashmir [Mitchell and Wilkinson 1982]) and "Purple Rain" birch (a *Betula* variety having purple leaves), both recently planted at a nursery north of Edmonton.

2.4.2 Phenology. First generation *F. pusilla* adults consistently became active in mid-May in Edmonton (approximately 220 degree-days), and persisted until mid- to late June (approximately 600 degree-days; Figure 2-3A). Activity was delayed by about 2 weeks at George Lake (Figure 2-3B). This delay apparently was not due to air temperature differences between the two sites, since plotting phenologies on degree-day axes did not eliminate the difference.

The presence and size of subsequent *F. pusilla* generations varied among years in Edmonton. In 1992, some trees had a small second emergence in late July (Figure 2-3A). There was only one generation in 1993, but in 1994, a large second generation began in mid-July, and a smaller third generation occurred in mid-August (Figure 2-3A). More generations occurred in years having higher degree-day accumulations in July and August; highest was 1994 (774 degree-days, 3 generations), followed by 1992 (694 degree-days, two generations) and 1993 (658 degree-days, one generation). Variation in the number of generations was also observed among sites within years. For example, in 1992, one generation of *F. pusilla* was detected on large trees at George Lake (Figure 2-3B), two generations occurred on large trees in Edmonton (Figure 2-3A), and three distinct generations were incidentally noted on young trees at a nursery just north of Edmonton.

Larvae of *F. pusilla* were first seen in the field in early June (approximately 350 degree-days) and persisted until late July (approximately 1000 degree-days) (Figure 2-4A). Again, activity at George Lake was delayed about 2 weeks relative to that in Edmonton (Figure 2-4B), and this delay was not explainable by differences in degree-day accumulation. In 1992, a small second generation of larvae, corresponding to that of the adults, was evident in Edmonton, peaking on August 7 (Figure 2-4A). In 1993, a bimodal distribution of larvae occurred in Edmonton in the early summer (Figure 2-4A), but it seems unlikely that this represents two distinct generations given that only one generation of adults was observed (Figure 2-3A) and the degree-day accumulation was lower in 1993 (June: 291; July: 333) than in 1992 (June: 349; July: 356). Thus, a "real" larval second generation in 1993 would have occurred much later than the second peak in larval abundance observed in mid-July, 1993 (Figure 2-4A).

Profenusa thomsoni adults became active in Edmonton from early to late June (between approximately 400 and 550 degree-days), and persisted until early August (approximately 1000 degree-days) (Figure 2-5A). Similar to *F. pusilla*, activity was delayed by 1-2 weeks at George Lake (Figure 2-5B), but unlike *F. pusilla*, there was only one generation per year. Plotting activity on a degree-day scale reduced, but did not remove, the variation in timing of adult activity between years and sites.

Larval *P. thomsoni* formed a discreet single generation in both years sampled. In Edmonton, larvae were first seen in the first week of July (approximately 700 degree-days) and were mostly finished development by late August (approximately 1200 degree-days) (Figure 2-6A). Larval activity commenced roughly 2 weeks later at George Lake, and in 1993, sampling was stopped before the peak of larval abundance was reached (Figure 2-6B). At both Edmonton and George Lake, some larvae were still feeding within yellowing leaves as temperatures cooled in late September. Such late-occurring larvae probably died within the senescing leaves.

Theoretical development curves were generated for both *F. pusilla* and *P. thomsoni* in Edmonton using 5°C as a threshold, since commercially-available degree-day data use this threshold (e.g., Environment Canada Monthly Meteorological Summaries), and the R^2 values hardly differed when thresholds between 1 and 12°C were used to generate theoretical parameters (Figure 2-7). Model predictions corresponded well with timings of activity observed in the field, although the model consistently fit the *P. thomsoni* data better than those of *F. pusilla* (note lower R^2 values for *F. pusilla* in Figure 2-7). *Fenusa pusilla* larvae were predicted to be present shortly before 400 degree-days, and to have mostly emerged from their leaves by 1000 degree-days (Figure 2-8). Only the putative first generation for *F. pusilla* is shown, since the empirical data for 1993, on which the theoretical curves were based, included only a single generation (Figure 2-4A). Just as larval *F. pusilla* were predicted to begin emerging from leaves at around 800 degree-days, first instar larvae of *P. thomsoni* were predicted to become increasingly abundant (Figure 2-8). By 1300 degree-days, corresponding roughly to early September, *P. thomsoni* larvae were predicted to have mostly finished larval development.

2.4.3 Potential for competition and biology of *B. canadensisella*. Very few leaves possessed mines of both *F. pusilla* and *P. thomsoni* (calculated as a percentage of larva-bearing leaves; Edmonton: 1992, 0.23%; 1993, 1.28%; George Lake: 1992, 0.05%; 1993, 0.07%). Thus, there is little possibility of direct competition for leaf resources occurring between these species.

However, there is potential for intraspecific competition within each of *F. pusilla* and *P. thomsoni*. This is evident in the mean amount of leaf area required per larva to complete development, which was significantly higher for *P. thomsoni* than for *F. pusilla* (Table 2-3; mean ± SE: *F. pusilla*, 146 ± 13 mm^2; *P. thomsoni*, 276 ± 13 mm^2). Using the estimated area required for development, 17.8% and 13% of the larval populations of *F. pusilla* and *P. thomsoni*, respectively, had a less than optimal food supply available to them in 1993, and therefore may have been susceptible to intraspecific competition. The likelihood of competition cannot be evaluated in 1992 because leaf areas were not measured, but it was probably even greater than in 1993 for *P. thomsoni* larvae, which were significantly more abundant in 1992 than in 1993 (see section 2.4.1 and Table 2-2B).

Native leafminers were extremely rare on birch in 1992 and 1993 in Edmonton (14 mines from 12317 leaves sampled) and at George Lake (17 mines from 11902 leaves sampled). Similarly, sweep net sampling in 1992 revealed few herbivores likely to compete with birch leafminers in Alberta. Possible candidates include members of the hemipteran families Miridae, Acanthosomatidae, and Lygaeidae, the homopteran families Aphididae, Cicadellidae, and Psyllidae, as well as the lepidopteran, *Bucculatrix canadensisella* (Table 2-4). Similar taxa have been found to affect birch in eastern North America (Conklin 1969). The hemipterans and homopterans were not examined further, since they either fed on birch seeds or did not reduce the leaf area available for birch leafminers.

Adults of *B. canadensisella* were active from the end of May until the end of July in 1993, and peak activity was slightly delayed at George Lake relative to Edmonton (Figure 2-9). Only one generation of larvae was observed; they were present from early July to early August as miners, and from late July on as free-feeding skeletonizers (Figure 2-10). Few free-feeding larvae were found after mid-August in sweep net samples taken in Edmonton in 1992 (total catches: 1-14 August, 77 larvae; 15-31 August, 11 larvae), but larvae persisted into late August at George Lake (1-14 August, 89 larvae; 15-31 August, 44 larvae). There was no visual difference between larval phenologies at Edmonton and George Lake, but larval activity seemed protracted at both sites in 1993 relative to 1992 (Figure 2-

10). This may have resulted from cooler temperatures experienced during 1993 (Environment Canada 1992, 1993).

Geographic variation occurred in population levels of *B. canadensisella*. More adults were captured per sticky trap at George Lake (mean ± SE: 69.0 ± 18.6) than in Edmonton (45.6 ± 18.6) in 1993, but this difference was not statistically significant (ANOVA on square-root-transformed data, MS[Location]=6.01, F=0.88, p=0.376, df=1,8). The number of occupied *B. canadensisella* mines per leaf was higher at George Lake (mean ± SE: 1.74 ± 0.24) than in Edmonton (0.78 ± 0.24), and in 1992 (1.84 ± 0.23) than 1993 (0.67 ± 0.23) (Table 2-2C). This comparison is more valid than that for larvae of either leafminer species, since leaves were selected at random with respect to *B. canadensisella* mines. Although most *P. thomsoni* development was finished by the time skeletonization began in Edmonton (compare Figures 2-6A and 2-10A), large populations of free-feeding *B. canadensisella* at George Lake coincided with *P. thomsoni* larval activity (compare Figures 2-6B and 2-10B). It is therefore possible that these two species compete for leaf resources.

2.5 Discussion

2.5.1 Species abundances and distributions. *Fenusa pusilla* had lower abundances relative to *P. thomsoni* in Alberta than in Europe and eastern North America, where it is the most prevalent species (Cheng and LeRoux 1965; Eichorn and Pschorn-Walcher 1973; Fuester et al. 1984; Pezzolesi and Hager 1994). These regional differences in abundance may be related to the ages of trees sampled, and to the fact that *F. pusilla* oviposits only in young leaves on long shoots (see DeClerck and Shorthouse 1985). Long-shoot leaves are not abundant after initial leaf flush (Cheng and LeRoux 1965), especially in mature native paper birch (Friend 1933; personal observation). My casual observations indicate that most leaves suitable for oviposition are presently used by *F. pusilla*, and Chichester (1994) found that the number of *F. pusilla* adults emerging from the soil is positively correlated with the number of exploitable leaves present. Since younger trees produce more long-shoot growth (personal observation), the relative abundances of birch leafminer species probably differ on trees of different ages. Studies of *F. pusilla* in eastern Canada tended to use young trees (e.g., Cheng and LeRoux 1965), which may have given an inflated perception of *F. pusilla* damage there. Recent work indicates that *Messa nana* and *P. thomsoni* are the most important exotic birch leafminers in New Brunswick, and that some of this damage was probably previously attributed to *F. pusilla* (G. Smith, pers. comm.).

Sex ratios found here for *F. pusilla* are consistent with those noted in other studies. Although Friend (1933) reported a female-biased sex ratio of 0.60, both Daviault (1937) and Cheng and LeRoux (1965) found a more even sex ratio approaching 0.50. These values are similar to those encountered in Edmonton in 1992 and 1994, and also from laboratory rearings of individual *F. pusilla* larvae from 1993 (29 males to 31 females). The low proportion of females collected on white sticky traps in 1993 may have resulted from avoidance behaviour, since the sawflies did not seem particularly attracted to these traps relative to the yellow traps used in 1994. I attribute the lack of females captured at George Lake to the extremely small overall catches of *F. pusilla* from this location (1992, n=5; 1993, n=5).

A high relative abundance of *P. thomsoni* appears unique to the Nearctic. *Profenusa thomsoni* is rare in Europe (Eichorn and Pschorn-Walcher 1973; Pschorn-Walcher and Altenhofer 1989; Schönrogge and Altenhofer 1992), but it can outbreak in northern Ontario (Martin 1960), and is the most important birch leafminer species in Alberta (Figure 2-2). It may be that *P. thomsoni* is effectively controlled by predators and parasitoids in Europe; generalist chalcidoid parasitism rates can reach 27.5%, even on sparse populations (Schönrogge and Altenhofer 1992). Although *P. thomsoni* occurs in Asia (Togashi 1981), its abundance relative to other birch leafminers there is unknown.

It has been suggested that *P. thomsoni* may be a native of North America (Schönrogge and Altenhofer 1992) because a possible specialist parasitoid of *P. thomsoni* has been found in northern Ontario, but not in Europe (*Lathrolestes* sp., Martin 1960; see also Pschorn-Walcher and Altenhofer 1989). However, I argue that *P. thomsoni* is introduced, because distribution patterns observed in northern Alberta (Figure 2-1) and the Northwest Territories suggest that birch leafminers are still expanding their ranges in western Canada with the aid of trade in infested ornamental birches. In addition, birch leafminer damage was first noted in eastern

Canada after 1925 (Cheng and LeRoux 1965), and in Alberta only by the 1970's (Drouin and Wong 1984).

Heterarthrus nemoratus abundances were low throughout the surveyed area except at Slave Lake and Lac la Biche in 1992. This may have been due to habitat specificity, since these sites were near bogs, and *H. nemoratus* is abundant in boggy habitats elsewhere (Dowden 1941; Eichorn and Pschorn-Walcher 1973). *Heterarthrus nemoratus* can be common in eastern North America (Dowden 1941; Hall 1992), but is generally rare in Europe (Eichorn and Pschorn-Walcher 1973). Drouin and Wong (1984) found it common in Edmonton in 1978 and 1979, second in abundance to *F. pusilla*. The great decrease in Alberta populations of this species over the past 15 years may have resulted from competition with larger populations of *P. thomsoni*. Both of these species consume mature leaves in late summer (Drouin and Wong 1984), making competition likely if population densities are high enough. A second reason for the rarity of *H. nemoratus* may be the fact that it overwinters in leaves (Dowden 1941), unlike *F. pusilla* and *P. thomsoni*, which overwinter in the soil. Raking of leaves in urban habitats may have gradually decreased *H. nemoratus* populations over the past 15 years.

Neither *Messa nana* nor *Scolioneura betuleti* were found in Alberta, but they are expected to arrive eventually through active dispersal or on imported nursery stock. *Messa nana* has recently spread to New Brunswick, where it is becoming the most damaging birch leafminer species (G. Smith, pers. comm.). It has been common in northern Ontario for some time (DeClerck and Shorthouse 1985). *Scolioneura betuleti* was first collected in Canada in 1983 in Newmarket, Ontario (Nystrom and Evans 1989), and is now found in the Ottawa region as well (Moody 1988). Both species are widespread in northern Europe (Viramo 1969), and therefore should be able to exploit birch throughout Canada.

2.5.2 Phenology. Drouin and Wong (1984) did not observe more than two generations of *F. pusilla* per year in Alberta, but my study shows significant among-year variation in voltinism, and establishes that three generations per year are possible (Figure 2-3). It is unlikely that *F. pusilla* is capable of four generations in Alberta, because the timing of the third activity period for adults in Alberta (mid- to late August) is similar to that of the fourth and last activity period in Québec (Cheng and LeRoux 1965).

Variation in voltinism of *F. pusilla* among years and sites is probably related to variation in the prevalence of immature long-shoot leaves later in the summer. In 1993, very little new long-shoot growth was observed after June, and no subsequent generations of *F. pusilla* were seen. In 1994, many new long-shoot leaves were seen on sampled trees in late July, and three generations of *F. pusilla* were observed. Similarly, the variation in number of generations observed among locations in 1992 corresponded well with the availability of young long-shoot leaves later in the summer. Nursery trees had a perpetual supply of new long-shoot leaves, and had three generations of *F. pusilla*, whereas mature trees at George Lake lacked new leaves after June, and experienced no subsequent *F. pusilla* activity. Chichester (1994) found that both *F. pusilla* and *F. dohrnii* (Tischbein), the alder leafminer, are able to regulate diapause such that the number of adults emerging per generation is proportional to the quantity of acceptable foliage available. However, it is not yet clear how prepupae of *F. pusilla* in the soil assess the availability of later-occurring, immature long-shoot leaves. Perhaps prepupae monitor soil temperatures or accumulated degree-days, and emerge later in the summer if temperatures have been sufficient to promote further long-shoot growth. Alternatively, the propensity to emerge later in the summer may be determined in the first generation *F. pusilla* larvae while they are feeding; perhaps faster larval development times or hormonal cues from the host plant are used by larvae to prevent diapause behaviour in the subsequent soil-dwelling prepupal stage.

As in other studies (Martin 1960; Drouin and Wong 1984), *P. thomsoni* was found to have one generation per year. Timing of adult activity in Sault Ste. Marie (Martin 1960) was similar to that observed at George Lake (i.e. mid-July to early August). The earlier emergence timing seen in Edmonton relative to Sault Ste. Marie (roughly 2-3 weeks) may be the result of strong selective pressure for earlier emerging adults in Edmonton. Larvae produced by later-emerging females are more likely to be killed by an early frost, or trapped in senescing leaves. Alternatively, extra heat retained by the urban environment in Edmonton, in combination with the exposed habitats occupied by most urban birches, may have promoted earlier emergence of adult *P. thomsoni* in Edmonton relative to Sault Ste. Marie.

The among-year variation in initiation of *P. thomsoni* adult activity (Figure 2-5) is puzzling. Plotting activity on a degree-day axis did not reduce this variation; however, calculation of degree-days using air temperatures may have been unsuitable because *P. thomsoni* overwinters in the soil. In addition, it is not known when *P. thomsoni* dormancy stops and development begins. For this reason, selection of an arbitrary date (e.g., 1 April) for the start of degree-day accumulation can be a major source of error (Pruess 1983). Thus, it cannot be ruled out that temperature-dependent differences in timing of development caused this among-year variation.

Theoretical development curves agreed well with empirical phenological data, and suggest that precise temporal niche partitioning occurs between larvae of *F. pusilla* and *P. thomsoni* (Figure 2-8). This may be an artifact retained from the evolution of these species in Europe. The genus *Betula* has 50 leafmining insect species associated with it in Britain, the largest number of all native trees there (Godfray 1984). Members of such a large guild should display a high degree of niche partitioning, such that interspecific competition is minimized (e.g., Pleasants 1980). The five species of leafmining sawflies that occur on birch in Europe occupy quite different spatio-temporal niches (Eichorn and Pschorn-Walcher 1973), and similar niche partitioning is evident in lepidopteran leafminers on birch in Europe (*Stigmella* spp.; see Boomsma et al. 1987). In contrast, North American birch have a much smaller leafminer fauna (16 species recorded in Ontario; Lindquist and Thomson 1970), thus perhaps reducing selective pressure for resource partitioning and negating the strict niche constraints imposed on *F. pusilla* and *P. thomsoni* in Europe. However, introduced birch leafminers seem to retain life history traits in North America which have evolved in Europe (DeClerck and Shorthouse 1985), and this is further supported by the theoretical development curves generated here.

2.5.3 Urban-rural differences. Greater abundances of birch leafminers were consistently observed in Edmonton relative to George Lake. This was supported by a similar trend observed in the Alberta survey. The reasons for these differences are not clear, but Olkowski et al. (1978) found that the cedar aphid (*Cinara curvipes* Patch) in California may be more abundant in urban habitats due to different climatic condititions and a lack of parasitoids. Different levels of immature birch leafminer mortality may contribute to urban-rural differences in abundance, and are explored in Chapter 3.

Another possible reason for the decreased abundances at George Lake may be related to the abundance of *B. canadensisella*, which was much higher at George Lake than in Edmonton in 1992 and 1993. High densities of *B. canadensisella* result in severe birch defoliation (Friend 1927), which can decrease the quality of birch leaves (Niemelä and Tuomi 1993), and may negatively affect populations of both *F. pusilla* and *P. thomsoni*. In addition, *P. thomsoni* larvae are present at the same time as those of *B. canadensisella*, and therefore may compete directly with them for leaf resources.

Phenological differences between Edmonton and George Lake were expected to be resolved by placing the curves on degree-day axes based on air temperatures, but this was not the case. Degree-day estimates based on soil temperatures would probably have been more closely related to pre-emergence development. Soil at George Lake was sometimes still partially frozen in early May, but was completely thawed in the more exposed habitats under birch trees in Edmonton (personal observation). In addition, there may have been differences between these locations in the timing of cues used by birch leafminers to emerge. This is suggested by the fact that birch bud burst was observed to be slightly later at George Lake than in Edmonton.

2.5.4 Potential for competition. Species-specific differences in temporal and spatial resource use patterns indicate that there is little opportunity for direct interspecific competition between *F. pusilla* and *P. thomsoni*. However, intraspecific competition seems likely for at least some individuals. The value I calculated for the amount of leaf area used by *F. pusilla* falls midway between that of Jones and Raske (1976) (mean: 90 mm^2, n=10) and Friend (1933) (mean ± SE on unsaturated leaves: 194.8 ± 17.4, n=17). However, Martin (1960) found that *P. thomsoni* larvae required approximately 530 mm^2 to complete development, significantly more than was required in Alberta. His methods are not explicitly stated, so it is difficult to determine reasons for this discrepancy. My study suggests that intraspecific competition occurs in both species, and probably occurs at lower larval densities per leaf in *P. thomsoni* than in *F. pusilla*.

Sufficient evidence exists to suspect interspecific competition between *B. canadensisella* and *P. thomsoni*. The timing of activity of larval *B. canadensisella* in Alberta appears similar to that in eastern North America (Friend 1927; Blais and Pilon 1968), and overlaps significantly with that of larval *P. thomsoni*. This competition is expected to be variable in time and space, since population outbreaks of *B. canadensisella* only last 3-5 years (Blais and Pilon 1968) and appear relatively localized in Alberta (Cerezke and Gates 1992; Cerezke and Brandt 1993; Brandt 1994).

This study shows that populations of introduced birch leafminers are well-established in central Alberta, and that urban populations tend to be active earlier and more abundant than rural populations. Unlike eastern North America and Europe, the most damaging leafminer species in Alberta is *P. thomsoni*. Even though it has only one generation per year, it is able to build up large populations on mature trees because it feeds on mature leaves throughout the tree crown. Management strategies for urban birches would maximize efficiency by focusing on population-regulatory mechanisms of this birch leafminer species.

Table 2-1. Analyses of variance evaluating differences in catches of adult *F. pusilla* and *P. thomsoni* at Edmonton and George Lake, 1992-1994. A, 1992 (emergence traps, square-root-transformed); B, 1993 (white sticky traps, log-transformed); C, Edmonton only, 1994 (yellow sticky traps, square-root-transformed).

A.

Source	df	MS	F	p
Location	1	6.5	1.33	0.263
Species	1	103.3	21.12	0.0002
Location x Species	1	0.2	0.04	0.842
Error	20	4.9		

B.

Source	df	MS	F	p
Location	1	2.8	15.18	0.001
Species	1	0.2	0.92	0.351
Location x Species	1	0.03	0.18	0.680
Error	16	0.2		

C.

Source	df	MS	F	p
Species	1	250.3	5.44	0.048
Error	8	367.9		

Table 2-2. Analyses of variance evaluating differences in numbers of larvae per leaf between Edmonton and George Lake in 1992 and 1993. A, *F. pusilla*; B, *P. thomsoni*; C, occupied *B. canadensisella* mines. All data were transformed to Blom's normal rank scores (SAS Institute 1988) for analysis.

A.

Source	df	MS	F	p
Location	1	1.65	1.75	0.203
Year	1	0.03	0.03	0.854
Location x Year	1	0.67	0.71	0.409
Error	18	0.94		

B.

Source	df	MS	F	p
Location	1	2.14	7.80	0.012
Year	1	12.24	44.64	0.0001
Location x Year	1	0.42	1.53	0.233
Error	18	0.27		

C.

Source	df	MS	F	p
Location	1	5.24	13.29	0.002
Year	1	6.94	17.61	0.001
Location x Year	1	0.58	1.48	0.239
Error	18	0.39		

Table 2-3. Analysis of variance evaluating differences in leaf area used for development by larvae of *F. pusilla* and *P. thomsoni* in Edmonton in 1993. Only non-saturated habitats were included in analyses (i.e. leaves with <100% of their area damaged at time of completion of larval development). Data were log-transformed for analysis.

Source	df	MS	F	p	Error Term
Block	4	0.13	4.15	0.099	Block x Sp
Species	1	2.15	70.15	0.001	Block x Sp
Block x Species	4	0.03	1.09	0.365	Error
Error	132	0.03			

Table 2-4. Relative abundances of non-predatory insects obtained from sweep net samples, 1992. The "Other" category under "Order" includes members of the Neuroptera, Trichoptera, Ephemeroptera, Collembola, Hymenoptera Symphyta (other than birch leafminers), and the arachnid order Acari.

Order	Subordinal Taxon	Number of Individuals	
		George Lake	Edmonton
Coleoptera	Curculionidae	9	21
	Chrysomelidae	1	5
	Elateridae	-	1
	Lathridiidae	11	3
	Mordellidae	1	-
	Scirtidae	1	3
Diptera	Various	530	455
Hemiptera	Acanthosomatidae	2	81
	Lygaeidae	-	136
	Miridae	6	40
	Various nymphs	10	14
Homoptera	Aphididae	23	307
	Cercopidae	18	-
	Cicadellidae	89	80
	Delphacidae	1	1
	Membracidae	1	-
	Psyllidae	11	101
	Various nymphs	6	265
Hymenoptera Apocrita	Braconidae	35	61
	Ceraphronidae	1	1
	Chalcidoidea (various)	154	2050
	Chrysididae	-	2
	Cynipoidea (various)	-	2
	Diapriidae	3	-
	Dryinidae	1	5
	Embolemidae	-	1
	Eucoilidae	4	39
	Ichneumonidae	30	95
	Megaspilidae	4	4
	Mutillidae	-	2
	Platygastridae	15	4
	Scelionidae	9	14
	Sphecidae	-	2
Lepidoptera	*B. canadensisella* adults	69	64
	B. canadensisella larvae	160	91
	Various adults	9	41
	Various larvae	16	12
Psocoptera	Various	58	3
Thysanoptera	Thripidae	1	19
	Phlaeothripidae	-	16
	Aeolothripidae	-	5
Other	Various	50	34
Total		1339	4110

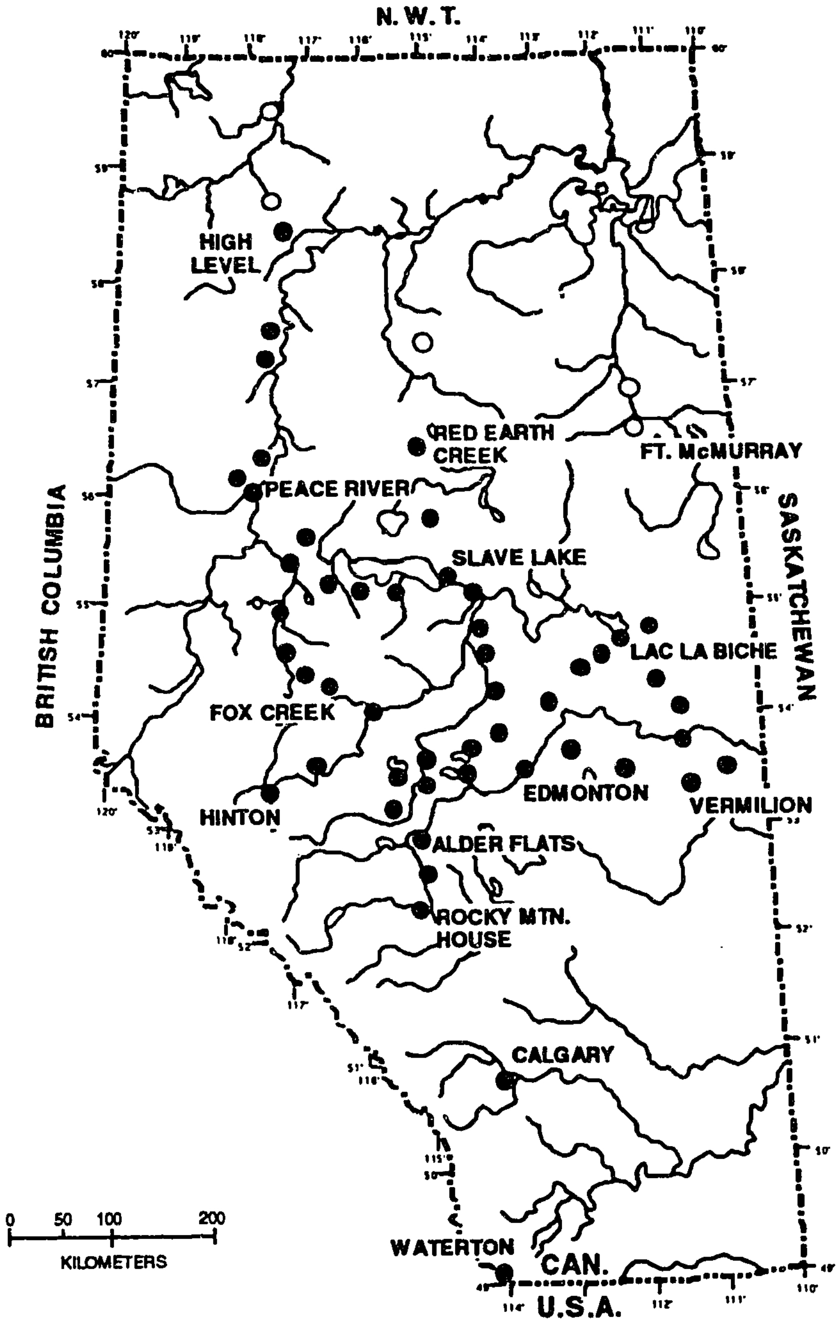

Figure 2-1. Area of Alberta surveyed for birch leafminers during 1992-1994 (55 sites). ● = positive collection; O = negative collection.

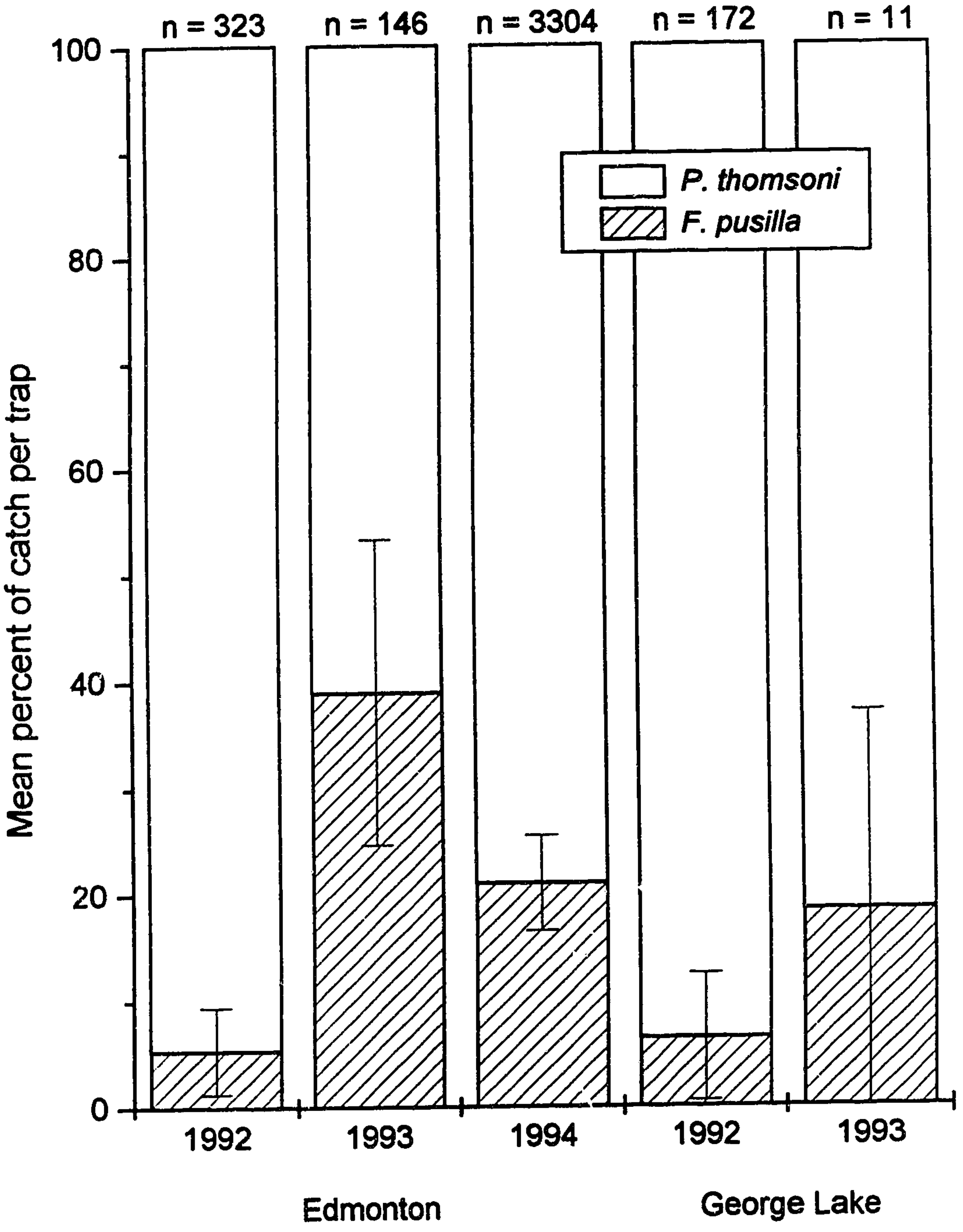

Figure 2-2. Mean (±SE) relative abundances of adult birch leafminers at Edmonton and George Lake, 1992 - 1994. Sampling methods: 1992: emergence traps; 1993: white sticky traps; 1994: yellow sticky traps.

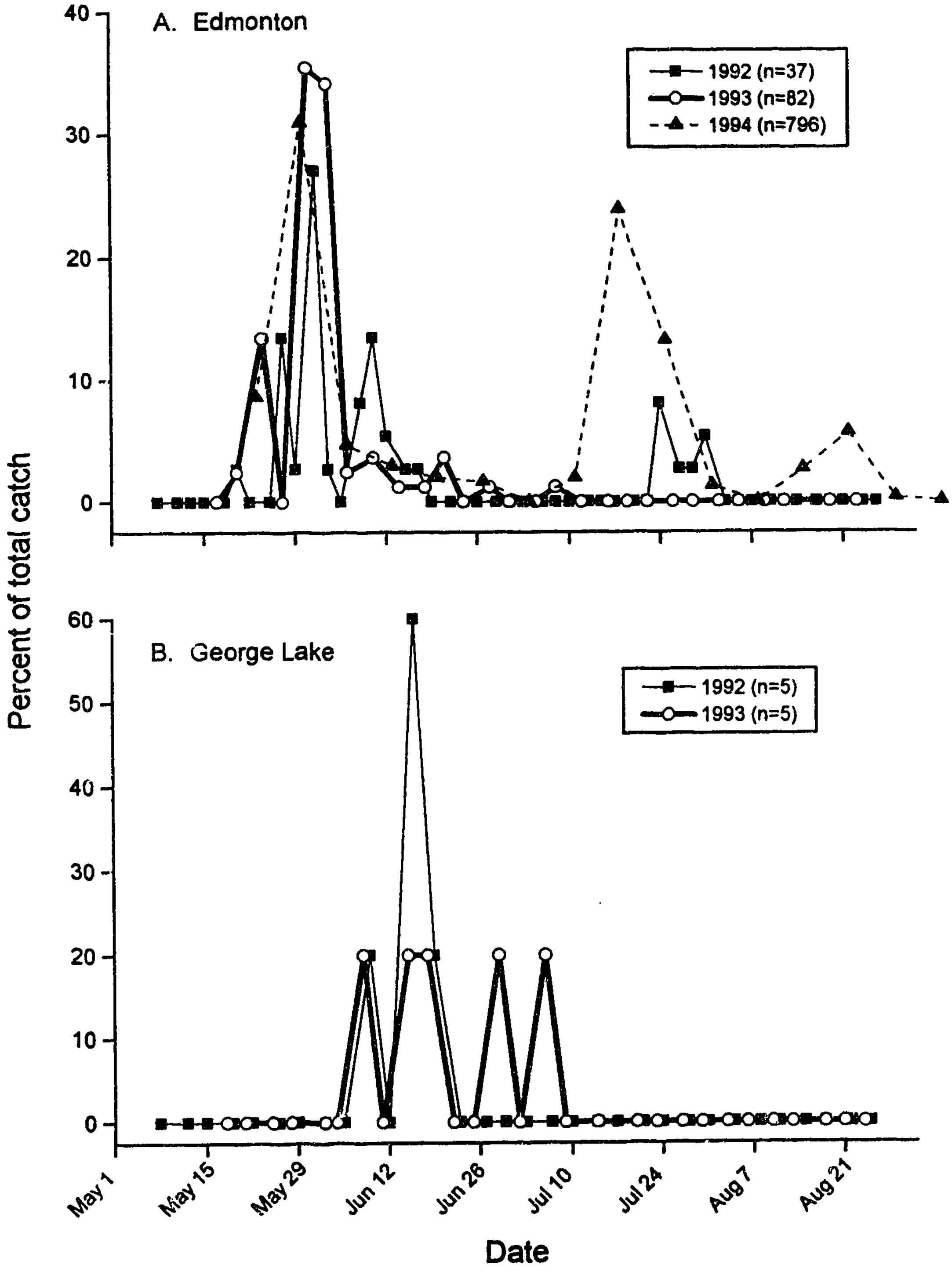

Figure 2-3. Activity of adult *F. pusilla* during 1992 - 1994 at Edmonton and George Lake, as determined by emergence traps (1992), white sticky traps (1993), and yellow sticky traps (1994).

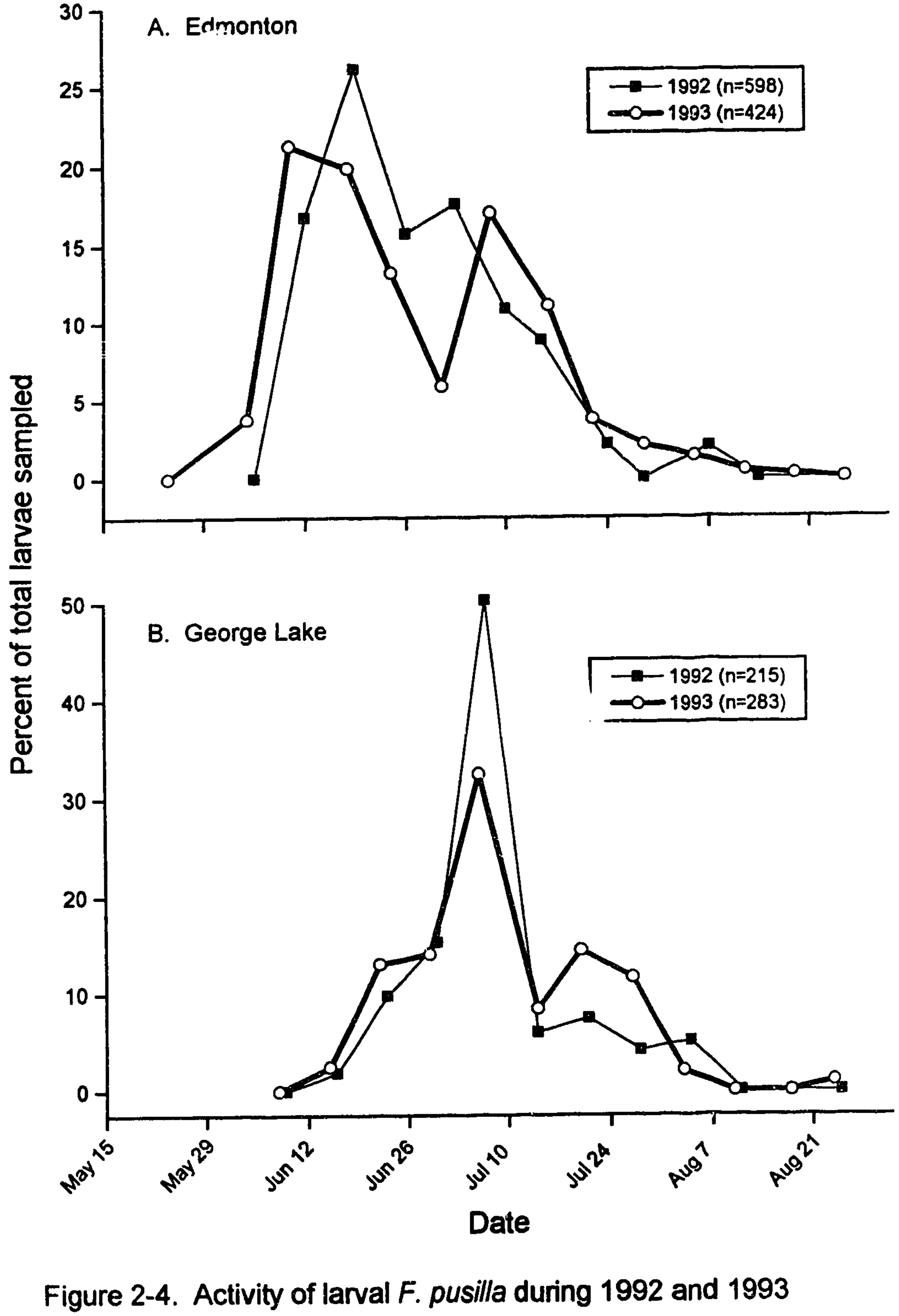

Figure 2-4. Activity of larval *F. pusilla* during 1992 and 1993 at Edmonton and George Lake as determined by leaf sampling.

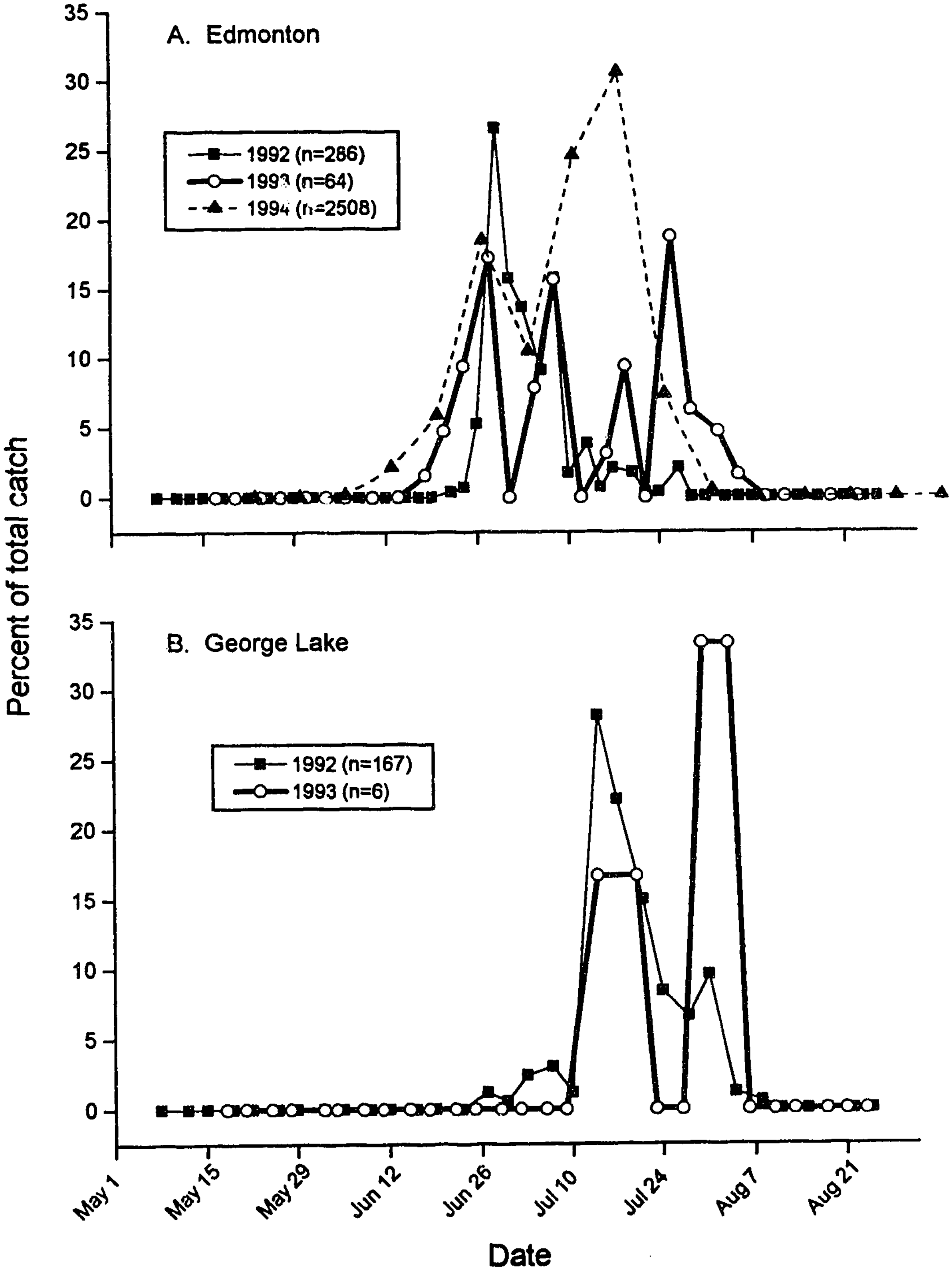

Figure 2-5. Activity of adult *P. thomsoni* during 1992 - 1994 at Edmonton and George Lake, as determined by emergence traps (1992), white sticky traps (1993), and yellow sticky traps (1994).

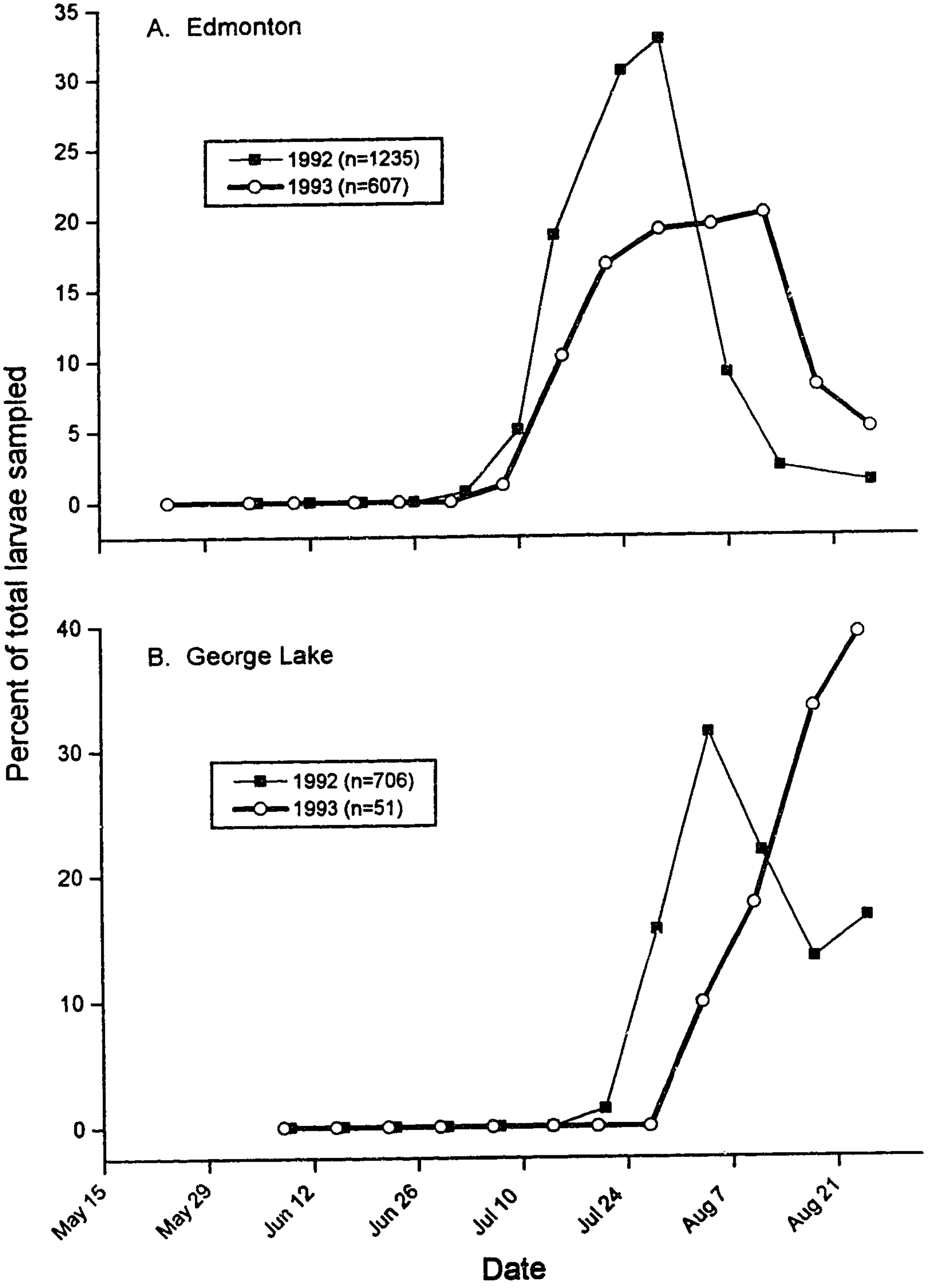

Figure 2-6. Activity of larval *P. thomsoni* during 1992 and 1993 at Edmonton and George Lake as determined by leaf sampling.

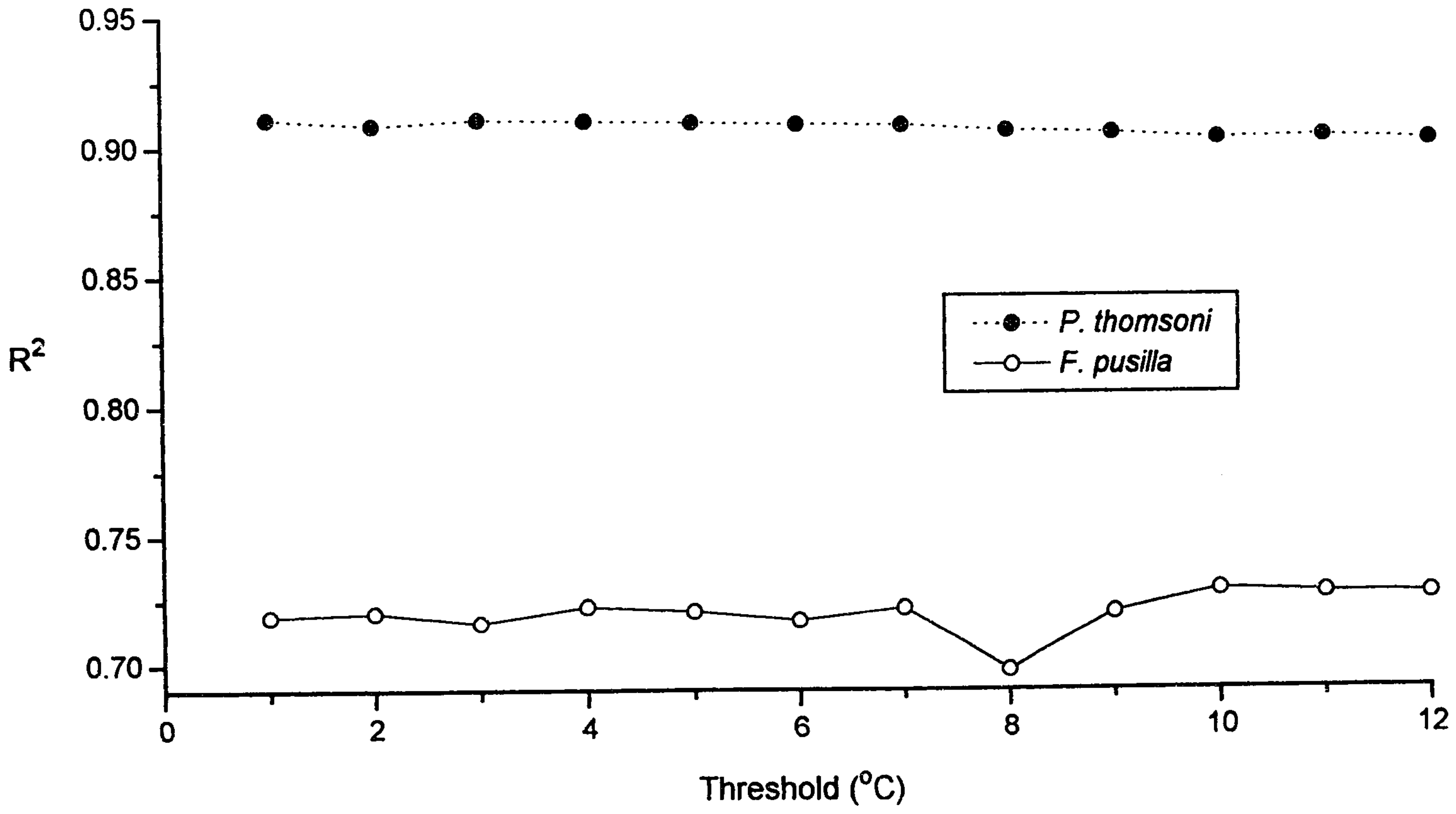

Figure 2-7. Values of R^2 from non-linear regressions fitting empirical data for larvae of *F. pusilla* and *P. thomsoni* to theoretical parameters describing larval phenology in Edmonton in 1993.

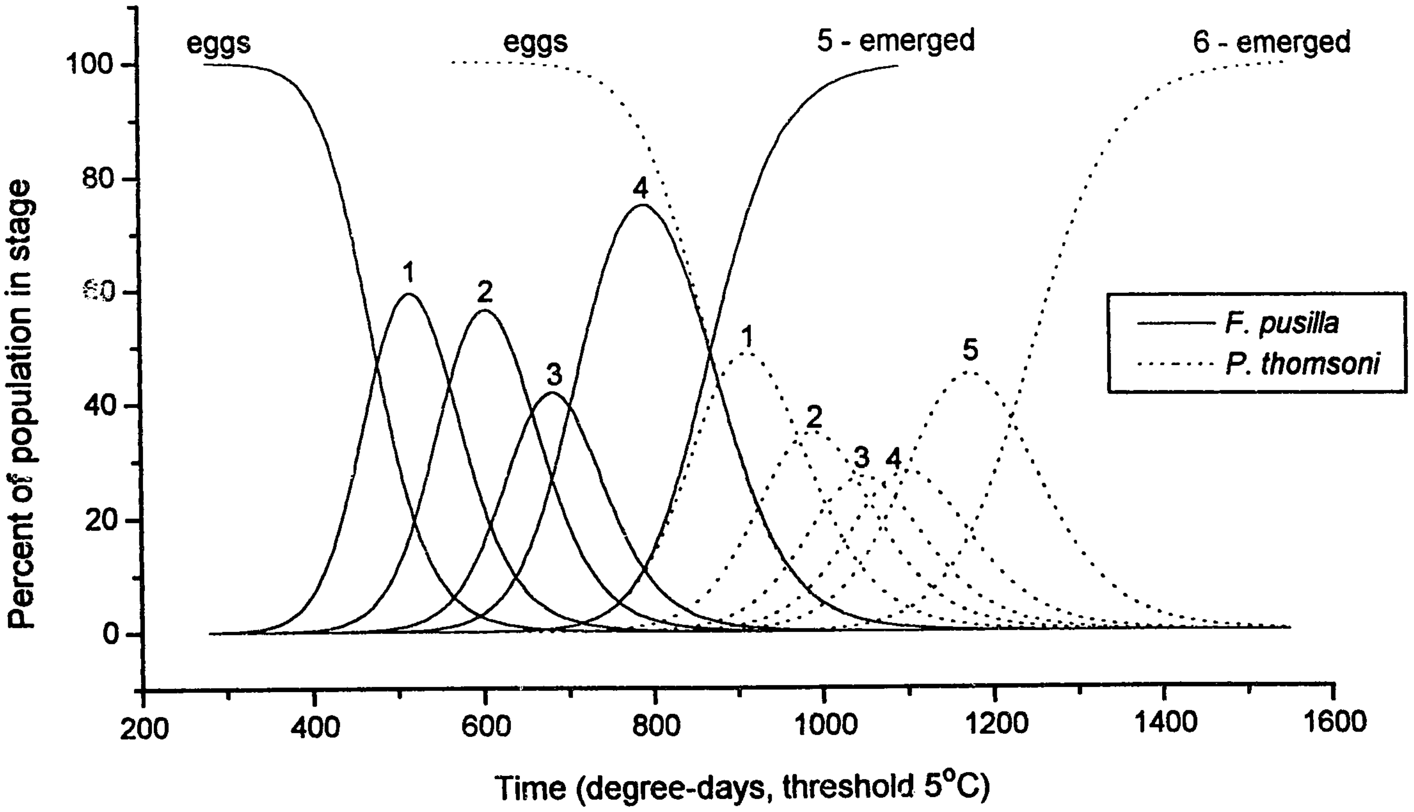

Figure 2-8. Theoretical proportions of *F. pusilla* and *P. thomsoni* populations in different pre-adult stages in Edmonton, 1993. Eggs were first seen in the field at 280 degree-days for *F. pusilla*, and 570 degree-days for *P. thomsoni.*

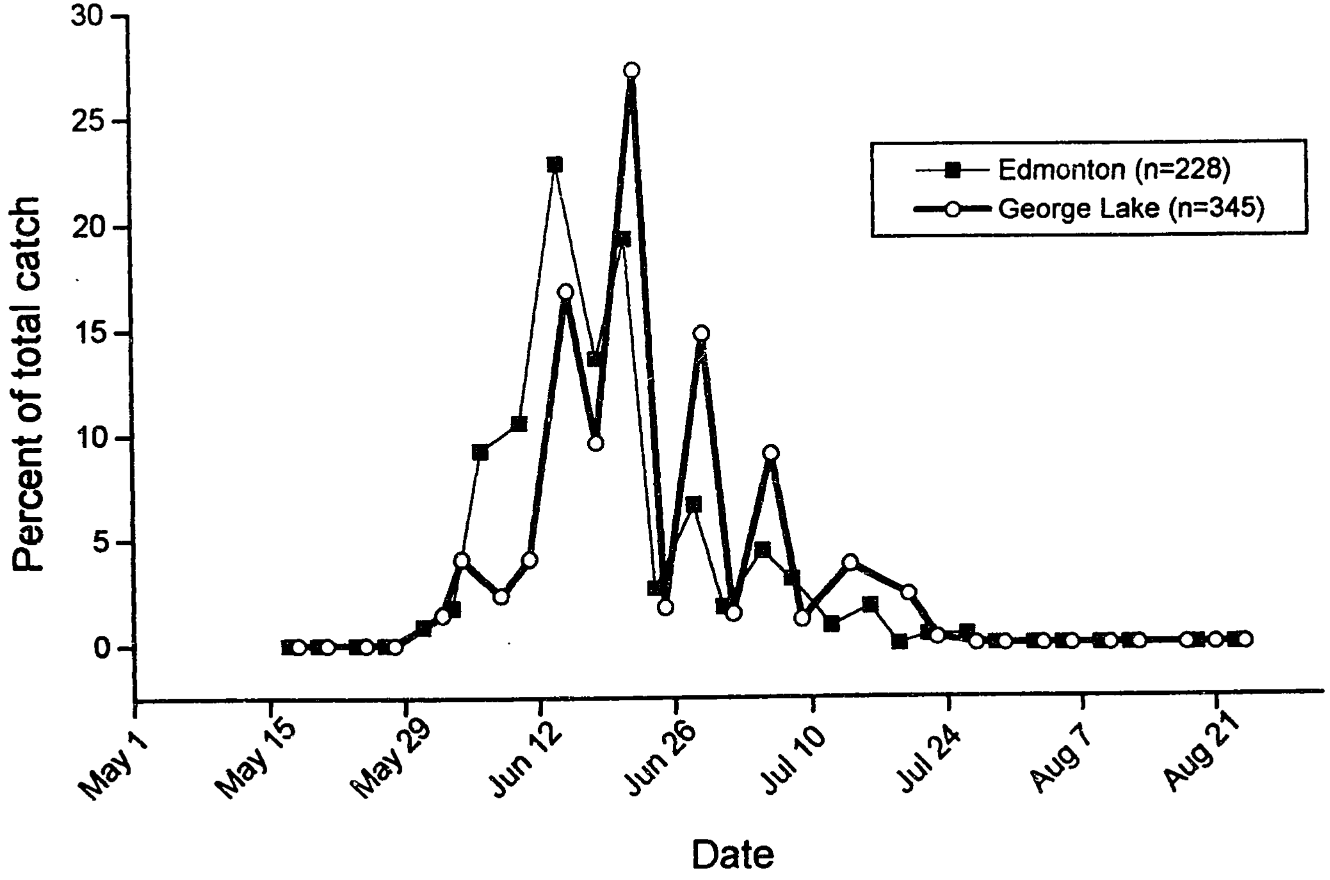

Figure 2-9. Activity of adult *B. canadensisella* as determined by white sticky traps at Edmonton and George Lake, 1993.

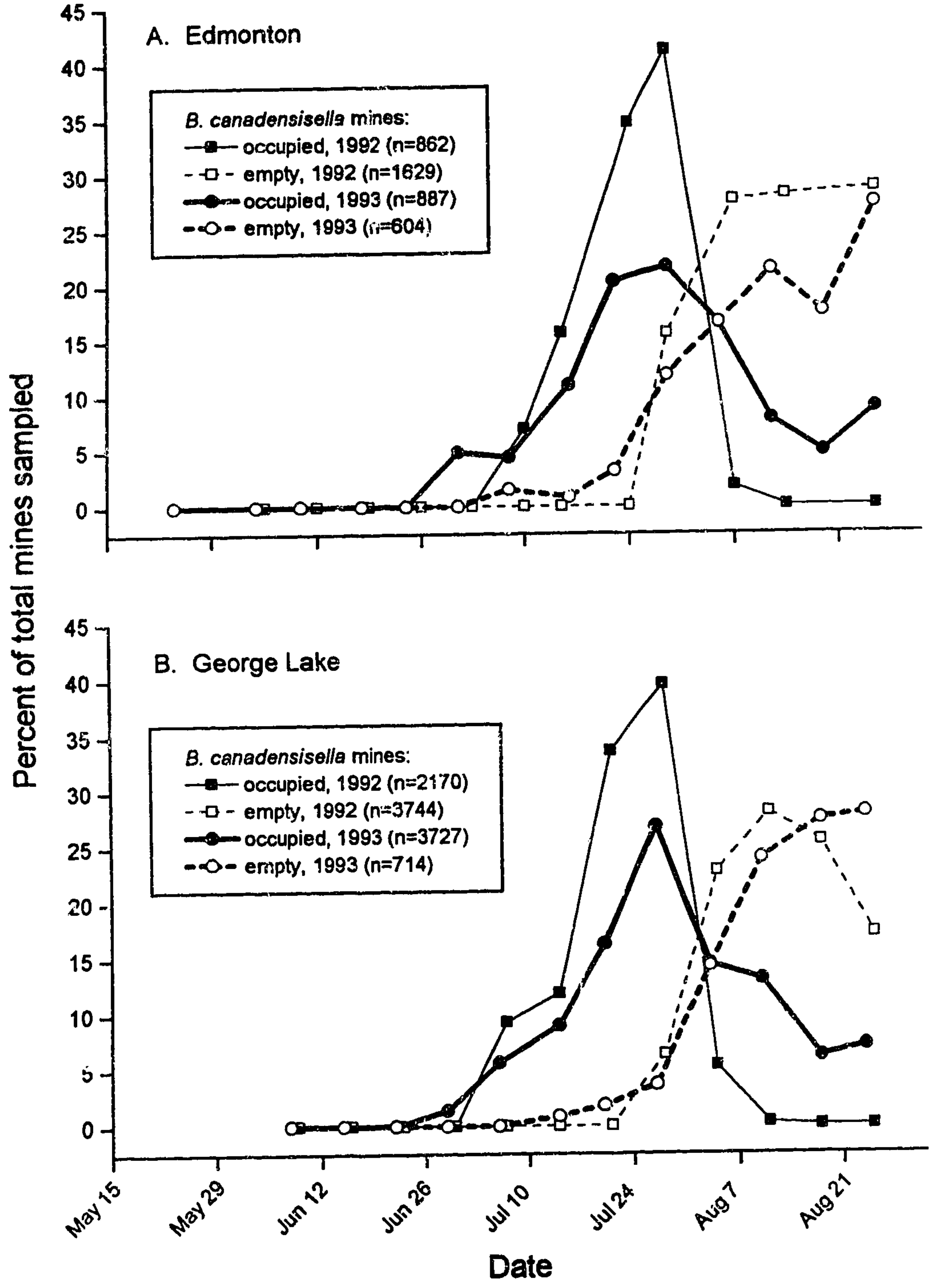

Figure 2-10. Activity of larval *B. canadensisella* during 1992 and 1993 at Edmonton and George Lake as determined by leaf samples. "Empty mines" reflect the abundance of free-feeding larvae.

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3. Birch leafminer mortality: impacts of natural enemies on introduced pests

3.1 Synopsis

Birch-leafmining sawfly larvae in Alberta suffered light mortality due to generalist parasitoids from the family Eulophidae (Hymenoptera: Chalcidoidea), and eggs of *Profenusa thomsoni* (Konow) were attacked by two species of *Trichogramma* (Chalcidoidea: Trichogrammatidae). A more specialized parasitoid, *Lathrolestes luteolator* (Gravenhorst) (Ichneumonidae: Ctenopelmatinae), was found attacking *P. thomsoni* larvae in increasing numbers between 1992 and 1994. Spiders, beetles, predatory bugs, thrips, ants, neuropterans, and predatory flies have the potential to prey on birch leafminer eggs and larvae. Individuals from several families within these groups were observed to do so.

Mortality levels varied between birch leafminer species, and tended to be higher in earlier instars, on urban trees, and in 1993. Experiments in 1993 revealed little predation of larval *Fenusa pusilla* (Lepeletier) when population densities were uniformly high, but in 1994 predators efficiently exploited branches having high densities of immature *P. thomsoni* within a matrix of low background birch leafminer density.

3.2 Introduction

Detailed knowledge of mortality factors in both the native and exotic environments of introduced pests can be used to build an effective management program. Five species of birch-leafmining sawflies have been introduced to North America this century (Martineau 1984; Nystrom and Evans 1989), and *Fenusa pusilla* (Lepeletier) and *Profenusa thomsoni* (Konow) have become significant pests of birches in western Canada (Drouin and Wong 1984; Chapter 2) In eastern North America, populations of *F. pusilla* and *P. thomsoni* were not greatly limited by parasitoids (Friend 1933; Martin 1960; Cheng and LeRoux 1969). The majority of these parasitoids were generalist species of eulophid chalcidoids, which commonly attack hosts occupying concealed habitats (Pschorn-Walcher and Altenhofer 1989). Notably absent were host-specific parasitoids from the ichneumonid genera *Lathrolestes* (Ctenopelmatinae) and *Grypocentrus* (Tryphoninae), although an individual of an undetermined *Lathrolestes* species has been reared from *P. thomsoni* in Ontario (Martin 1960).

In Europe, *F. pusilla* has a 17-species parasitoid complex, causing as much as 38-47% parasitism of larvae (Eichorn and Pschorn-Walcher 1973). The two most prevalent and specific parasitoids of *F. pusilla*, *Lathrolestes nigricollis* (Thomson) and *Grypocentrus albipes* Ruthe (Hymenoptera: Ichneumonidae), have been intentionally introduced from Europe into Newfoundland (Raske and Jones 1975), Québec (Guèvremont and Quednau 1977), and the Middle Atlantic States (Fuester et al. 1984). *Lathrolestes nigricollis* is established at several sites in eastern North America, and parasitism rates have reached 20-72% (Guèvremont and Quednau 1977; Fuester et al. 1984; Van Driesche 1989; Barron 1994). However, *G. albipes* does not appear to have become established in North America, despite repeated introductions (Raske and Jones 1975; Fuester et al. 1984; Van Driesche 1989). No parasitoid introductions have been made in western North America against *F. pusilla*.

Profenusa thomsoni is rare in Europe, and is atypical in that its parasitoid complex is scant and lacks specialists (Eichorn and Pschorn-Walcher 1973; Pschorn-Walcher and Altenhofer 1989; Schönrogge and Altenhofer 1992). However, this species can be abundant in eastern North America (Martin 1960; Pezzolesi and Hager 1994), and is the most common birch leafminer in Alberta (Chapter 2). These regional differences may be related to differences in natural enemy complexes. No parasitoids are known from Asia for either *F. pusilla* or *P. thomsoni*, even though both are widely distributed there (Smith 1981; Togashi 1981; A. Zinovjev, pers. comm.).

Less is known about impacts of predators on birch-leafmining sawflies. Spiders, ants, wasps, predatory bugs, larval chrysopids, and birds consume larvae and adults, but their relative impacts have not been determined (Friend 1933; Martin 1960; Cheng and LeRoux 1969). One exception is the study of Pezzolesi and Hager (1994), which suggested that ants are more effective predators of *F. pusilla* than of *P. thomsoni*, based on results from one site.

During 1992-1994, birch leafminer mortality was investigated in Alberta, to enumerate specific mortality agents and analyze their relative effects. Species lists of parasitoids and potential predators of birch leafminers were compiled, and life tables were constructed for immature stages collected from leaf samples in 1992 and 1993. Field experiments were used to differentiate bird and arthropod predation from non-predatory mortality of *F. pusilla* and *P. thomsoni.*

3.3 Materials and Methods

Idiobiont parasitoids (i.e. those which consume the host in the stage and location it is in when attacked [Askew and Shaw 1986]) of birch leafminers were investigated by rearing eggs and larvae collected in leaf samples from Edmonton and George Lake in 1992 and 1993. Collections were made weekly from each of six (1992) or five (1993) trees at Edmonton and George Lake. All birch leafminer eggs and larvae were enumerated from branches having at least 15 leaves collected from each of the upper, middle, and lower portions of the tree crown (for more details of sampling procedure, see Chapter 2). To ensure representation of as many parasitoid species as possible, additional collections were made by searching for leaves containing parasitized larvae in Edmonton (with the cooperation of Robin McQueen and Chris Saunders, City of Edmonton Pest Management Services), at George Lake, and at all sites where leaf samples were collected in a province-wide survey of birch leafminer populations (see Chapter 2 for details). Egg parasitoids and idiobiont larval parasitoids were reared in vials with moistened cotton, similar to the method used by Cheng and LeRoux (1969). To assay *F. pusilla* and *P. thomsoni* for koinobiont parasitoids (i.e. those which allow the host to live for a time, usually long enough to construct a pupal retreat [Askew and Shaw 1986]), larvae were reared to their final non-feeding instar in the laboratory in 1993, then were placed individually in vials of moistened soil to overwinter. Vials were held at ambient temperature in an insectary at the Northern Forestry Centre, Edmonton, until the first frost (early October). They were overwintered in an incubator at 4°C (no photoperiod), and were returned to the insectary with the onset of frost-free nights in late April, 1994. Emergence of adult leafminers and parasitoids within the vials was monitored twice per week throughout the summer of 1994.

Potential predators of birch leafminer eggs and larvae were collected in sweep net samples taken in Edmonton and at George Lake in 1992. Two passes were made with a 25.0 cm diameter net on each of six trees at both locations each week, and all arthropods were removed with forceps after each pass and placed in alcohol. Excepting Diptera, all predatory arthropods were identified to family, and those suspected of or observed feeding on birch leafminers were identified to the lowest possible taxonomic level.

Life tables were constructed according to Carey (1993), using stage-frequency data gathered from leaf samples collected in Edmonton and at George Lake in 1992 (six trees per location) and 1993 (five trees per location). No estimates of egg mortality were made in 1992, so this stage was omitted from the life tables for that year. The probability of death, q(x), for each instar was estimated by taking the mean of the proportion of insects found dead per tree per year. Since dead leafminer eggs and larvae persisted in the field long after they were initially killed, q(x) estimates were inflated, especially for early larval instars. To partially correct for this, I only included dead insects from sampling periods in which live insects of the same instar were also found on the branches sampled. Mortalities from life tables for both species were analyzed by comparing percent mortality (i.e. 100q[x]) using a repeated measures ANOVA model (SAS Institute 1988) with instar as the repeated measure. Degrees of freedom were reduced in analyses because any replicates with missing values could not be included in the repeated measures analysis (SAS Institute 1988). Differences in overall larval survivorship were examined using an ANOVA of the probabilities of larvae of *F. pusilla* and *P. thomsoni* living to the final instar (i.e. l[5] and l[6], respectively). Significant departures from normality in the data were corrected using the arcsine transformation (Zar 1984), or by using ranks.

Where possible, d(x), the proportion of the original cohort dying in stage x, was partitioned among different mortality causes or symptoms. For eggs, mortality was partitioned between parasitoids and dessication, as well as into several symptom classes having consistent visual characteristics (e.g., "brown", "crushed", "cut around"). Larval mortality was divided among idiobiont parasitoids and all other agents combined. No estimate of mortality caused by koinobiont parasitoids was included in the life tables.

Field experiments were conducted to partition mortality among bird predation, arthropod predation, and non-predatory agents. In 1993, mortality of *F. pusilla* was investigated at a nursery plantation of small (2-3 m high), native birch just north of Edmonton. On 6 June, 12 trees were selected randomly, and three branches having 10-15 leaves with representative levels of *F. pusilla* damage were selected on each tree. Branches were then assigned randomly to three treatments: all non-leafminers excluded (covered with bags made from fine drapery mesh), birds excluded (covered with bags made from plastic gutter guard, having holes roughly 0.7 cm in diameter), and open (no bag). At initiation of the experiment, all *F. pusilla* were present as eggs, first instar, or second instar larvae. After 10 days, branches were removed and examined in the laboratory for mortality of *F. pusilla* larvae.

In 1994, similar experiments were conducted to examine mortality of *P. thomsoni*. Five large (>4m tall) trees were selected randomly in Edmonton and at George Lake just after bud burst. On the south-facing half of each, three branches were selected (approximately 50 leaves per branch) and enclosed with fine mesh bags ("no-see-um" style mesh; irregular weave, no opening larger than 0.1 mm^2) to prevent exploitation of the leaves by other herbivores. Females of *P. thomsoni* which had not yet oviposited were collected using emergence traps (see Chapter 2 for design) from a stand of birch southwest of Edmonton. Between 8 and 16 July, the number of leaves per branch was counted again, and one female for every 10 leaves present was introduced into each bag. After oviposition, treatments were randomly assigned to the three branches on each tree: all non-leafminers excluded (covered with bags made from "no-see-um" style fine mesh), birds excluded (covered with bags made from plastic utility netting, having holes roughly 2.0 cm in diameter), and open (no bag). Each individual of *P. thomsoni* was assessed weekly to determine instar and whether it was still alive. Mortality of the egg stage was eliminated from analyses involving the five trees from Edmonton, since hot weather caused most of the eggs to hatch before treatments could be applied to the branches.

Results from both experiments were analyzed by comparing percent mortality using ANOVA. For the experiment involving *F. pusilla*, overall mortality percentages were analyzed, since instar-specific mortality data were not collected, but for the experiment involving *P. thomsoni*, 100q(x)s for each instar were analyzed similarly to the 1992 and 1993 life tables, using a repeated measures ANOVA model. Pre-planned orthogonal contrasts were also performed to compare fine-mesh-bagged branches with coarse-mesh-bagged and unbagged branches (i.e. comparing no predation with all predation), and to compare coarse-mesh-bagged branches with unbagged branches (i.e. comparing arthropod predation with bird + arthropod predation). Life tables were constructed for each treatment in the *P. thomsoni* mortality experiment, which allowed statistical comparison of overall larval survivorship (i.e. l[6]) among treatments and among years (1992, 1993, and 1994) using ANOVA and orthogonal treatment contrasts.

3.4 Results

3.4.1 Parasitoids. Two species of *Trichogramma* were found developing in the eggs of *P. thomsoni* (Table 3-1). Parasitized eggs were easily recognized in the field by their dark black color. Only one wasp developed in each *P. thomsoni* egg, and these parasitoids caused only a small proportion of the overall egg mortality observed in 1993 (Table 3-3). However, the distribution of egg parasitism was very patchy, and on some branches of some trees, most eggs of *P. thomsoni* were parasitized.

Fifteen species of idiobiont parasitoids were found exploiting birch leafminer larvae as hosts in central Alberta between 1991 and 1994 (Table 3-1). Most were ectoparasitic eulophids, but an endoparasitic eulophid (*Chrysocharis nitetis* [Walker]) and an ectoparasitic ichneumonid (*Scambus* [*Scambus*] sp.) also were found. Idiobiont parasitoids accounted for little larval mortality in either *F. pusilla* or *P. thomsoni* in 1992 and 1993 (Table 3-3).

Chrysocharis nitetis (Walker) was the only parasitoid reared from *H. nemoratus* (Table 3-1). It was effective at finding the rare *H. nemoratus* larvae, parasitizing 1 of the 5 larvae found at George Lake in 1992, and 3 of the 13 larvae found at various sites in a province-wide survey of birch leafminer populations conducted in 1992 (for details of survey, see Chapter 2). This parasitoid may help maintain *H. nemoratus* at low levels in Alberta.

Most of the eulophids were reared from *F. pusilla*, but representatives from each subfamily were also reared from *P. thomsoni* (Table 3-1). *Closterocerus trifasciatus* Westwood was observed to be hyperparasitic on other chalcidoids, in addition to parasitizing larvae of *F. pusilla* (Table 3-1). Most parasitoids were collected from Edmonton, probably because of greater effort. However, parasitism occurred throughout the province, even at sites where leafminers were rare (e.g., Moose Lake; Table 3-1). *Chrysonotomyia* sp., *Cirrospilus* sp. 2, *Zagrammosoma* sp., *Sympiesis* sp., *Pnigalio* spp. 2 and 3, *Minotetrasticus* sp. nr. *treron* and *Peckelachertus* sp. all appear to be previously undescribed, but most of these genera are in need of revision (J. Huber, pers. comm.). In addition, individuals of *Sympiesis* and *Pnigalio* can only be positively identified to species using females (J. Huber, pers. comm.), which were not obtained in all cases.

No koinobiont parasitoids were reared from *F. pusilla*, but the ctenopelmatine ichneumonid *Lathrolestes luteolator* (Gravenhorst) was found parasitizing larvae of *P. thomsoni*. After detection of this parasitoid by rearing, weekly samples collected from emergence traps in 1992 (see Chapter 2; two pyramidal traps placed under each of six trees in Edmonton and six trees at George Lake) and yellow sticky traps in 1994 (one 10.0 x 15.0 cm yellow card trap [Phero Tech Inc.] on each of five trees on the University of Alberta campus, Edmonton) were re-examined for *L. luteolator*. This species occurred at low levels in Edmonton and at George Lake in 1992, but population sizes seem to have increased greatly in Edmonton between 1992 and 1994 (Figure 3-1). However, this trend may be partially due to the different trapping methods used in the two years, since *L. luteolator* appeared more attracted to the yellow sticky traps than did *P. thomsoni*. Differential attraction of *L. luteolator* is supported by the finding that male *L. luteolator* constituted 89.7 ± 2.0% of the *L. luteolator* catch from sticky traps in 1994, but only 39.5% of the *L. luteolator* catch from emergence traps in 1992.

However, other observations suggest that the putative increase in the *L. luteolator* population between 1992 and 1994 (Figure 3-1) is real, and that these parasitoids may be suppressing *P. thomsoni* populations.

Lathrolestes luteolator emerged from 46.2% of cocoons (n=26) of laboratory-overwintered *P. thomsoni*; these *P. thomsoni* larvae were collected blindly with respect to *L. luteolator* parasitism from several mature birch at a nursery north of Edmonton in 1993 (collected as part of intraspecific competition experiments detailed in Chapter 4). This percentage does not include parasitized larvae in which parasitoids or hosts died prior to emergence, nor does it include sub-lethal effects of encapsulated parasitoids on overwintering hosts. In addition, decreasing abundances of *P. thomsoni* were noted in 1993 relative to 1992 (Chapter 2), and larvae were very rare at most sites in 1994 (personal observation).

3.4.2 Predators. Seventeen families of potentially-predacious arthropods were collected from birch in 1992 (Table 3-2). Most families were represented at both locations, although more species were detected in Edmonton (Table 3-2). The predominant potential predators at George Lake were spiders, whereas those in Edmonton were a mixture of spiders, Coleoptera, Hemiptera, and Thysanoptera (Table 3-2).

Members of several families were observed feeding on adults or larvae of birch leafminers. Except for the araneids and neuropterans, these predators were identified to genus or species (Table 3-2). Several araneids were observed feeding on adults captured in their webs, and philodromids were observed removing *P. thomsoni* larvae from their mines. Anthocorids were often found in or near mines, and probably feed on eggs as well as living and dead larvae. Phlaeothripid thysanopterans were also observed in abandoned mines, where they may have fed on dead larvae. *Formica* sp. ants were observed on several occassions to tear larval leafminers from mines, and to feed on living or dead adult leafminers on the ground.

Larval neuropterans were not abundant, but were consistently present. They were observed to stick their elongate mandibles through mine walls and into *P. thomsoni* larvae, feed for a time, and then carefully remove their mandibles. All that remained was a shrivelled leafminer larva bearing no obvious evidence of the predation event, similar to cadavers left behind by predatory Hemiptera.

Although Diptera were not retained from sweep net samples of potential predators, individuals of an empidid fly (*Platypalpus* sp.) were observed using their raptorial midlegs to capture adult *P. thomsoni* in flight. This fly was seen both in Edmonton and at George Lake, and was extremely common at a localized *P. thomsoni* outbreak southwest of Edmonton in 1993 and 1994.

3.4.3 Life tables. Larval mortality was generally highest in eggs and the first two larval instars of *F. pusilla*, and in eggs and the first three larval instars of *P. thomsoni*, at both locations in 1992 and 1993 (Table 3-3). There were large and statistically significant differences among q(x)s for different larval instars of both *F. pusilla* and *P. thomsoni* (Table 3-4, "Instar"). These differences varied less between years and locations for *F. pusilla* than for *P. thomsoni* (compare interactions which include "Instar" in Table 3-4). Mortality of *F. pusilla* eggs and first instar larvae was significantly higher in Edmonton than at George Lake (Table 3-4; compare q[x]s for *F. pusilla* on Table 3-3). For *P. thomsoni*, first instar larval mortality was significantly higher in 1993 than in 1992 (Table 3-4), and mortalities of second and third instar larvae were marginally higher at George Lake than in Edmonton (Table 3-4, p-values near α=0.05; compare q[x]s for *P. thomsoni* on Table 3-3).

Survivorship of immatures to the final larval instar varied significantly among trees, and was higher for *F. pusilla* than for *P. thomsoni* in 1993 (Table 3-5A; compare l[x] values for final larval instars in Table 3-3). With the inclusion of 1992 larval data in the analysis, the variation among trees remained significant, but species differences in survivorship disappeared (Table 3-5B). In addition, larval survivorship to the final instar was marginally higher at George Lake than in Edmonton (Table 3-5B, p-value near α=0.05; compare l[x] values for final larval instars in Table 3-3).

3.4.4 Mortality experiments. The experiment involving *F. pusilla* in 1993 revealed no significant differences in larval mortality among the three treatment levels (randomized complete block ANOVA, MS[Treatment]=4.560, F=0.24, p=0.788, df=2,22; see Table 3-6 for treatment means). However, a similar experiment involving *P. thomsoni* in 1994 showed much mortality attributable to predators. In general, mortality did not differ significantly between Edmonton and George Lake, and differed among trees only for first, fourth, and fifth instar larvae (Table 3-7). Differences among treatment levels were more consistent, and were observed for eggs and first, second, and fourth instar larvae, as well as for all instars combined (Table 3-7). The source of these differences was also consistent, with mortality on branches bagged with fine mesh bags always differing from that on open branches or on branches bagged with coarse mesh (Table 3-7, orthogonal contrasts). However, the directionality of this difference changed with immature stage: on branches bagged with fine mesh, percent mortality was significantly lower for eggs, first instar larvae, and second instar larvae, but was significantly higher for fourth instar larvae (Table 3-6). High mortality of young instars on exposed branches resulted from 'unknown causes', whereas high mortality of fourth instar larvae on fine-mesh-bagged branches resulted from resource exhaustion (Tables 3-9 and 3-10).

Similar trends were evident in analyses of survivorship of immature *P. thomsoni* to the final larval instar. With egg mortality included (George Lake data only), survivorship differed significantly among treatment levels, and was highest on branches bagged with fine mesh (Table 3-8A; compare l[x] values for instar 6 in Table 3-10). When comparing between locations (excluding egg mortality), survivorship to the final larval instar was higher in Edmonton (mean ± SE: 0.399 ± 0.032) than at George Lake (0.176 ± 0.032), and was still highest on branches bagged with fine mesh (fine mesh, 0.402 ± 0.040; coarse mesh, 0.261 ± 0.040; open, 0.199 ± 0.040) (Table 3-8B).

Survivorship of larval *P. thomsoni* to the final instar in this experiment can be compared with that calculated in life tables constructed using leaf sample data from 1992 and 1993. Survivorship varied significantly among years (ANOVA: MS=0.471, F=15.78, p=0.0001, df=2,26), but not between locations (MS=0.001, F=0.04, p=0.839, df=1,26). An overall decrease in survivorship accounted for the difference among years (mean ± SE: 1992, 0.606 ± 0.050; 1993, 0.495 ± 0.055; 1994, 0.199 ± 0.055). The interaction between year and location was also statistically significant (MS=0.294, F=9.87, p=0.0006). This resulted from a difference in trend between survivorship in Edmonton, which declined and then levelled off (mean ± SE: 1992, 0.689 ± 0.071; 1993, 0.307 ± 0.077; 1994, 0.323 ± 0.077), and survivorship at George Lake, which increased and then decreased (1992, 0.523 ± 0.071; 1993, 0.684 ± 0.077; 1994, 0.074 ± 0.077).

Life tables were constructed for all treatments of the experiment involving *P. thomsoni* at Edmonton and George Lake to compare different mortality causes. At George Lake, most eggs died showing symptoms of being crushed or internal browning, and relatively few were parasitized by *Trichogramma* species (Table 3-10). At both sites, most early instar mortality was due to unknown causes or to larvae being ripped from their mines, whereas most late instar mortality resulted from resource exhaustion, especially on branches bagged with fine mesh (Tables 3-9 and 3-10). Few eggs or larvae died as a result of early leaf fall (Tables 3-9 and 3-10).

3.5 Discussion

3.5.1 Patterns of mortality. The life table approach used here demonstrated that significant within-generation variation occurred in the amount of mortality, and also in the relative importances of mortality sources. In field experiments with *P. thomsoni*, early instar larvae tended to be hit hard by extrinsic mortality agents on exposed branches, whereas most mortality resulted from resource exhaustion on branches having natural enemies excluded (Tables 3-9 and 3-10). Few studies of insect population dynamics have combined experimental and life table approaches (but see Preszler and Price 1988; Stein et al. 1994), and thus most have been forced to infer causation from correlative relationships between mortality sources and population changes (Price 1987). This has lead to serious doubt over the regulatory effects of mortality agents identified in life table analyses (Price 1987). In addition, identified population-regulatory agents have been challenged when they do not have density-dependent consequences over several generations (Dempster 1983). However, density-dependence may still be having regulatory effects in such systems, but on a within-generation scale (Hassell 1985, 1987).

My study of *P. thomsoni* used a combined experimental and life table approach to remove certain mortality agents, and measure the within-generation effects of experimental treatments. The importance of within-generation effects is suggested by the fact that there were large differences in q(x)s among instars in all treatments of the experiment involving *P.*

thomsoni, as well as in the life tables generated from leaf samples collected in 1992 and 1993 ("Instar" in Tables 3-4, 3-5, and 3-7). Similar within-generation mortality differences were evident in Cheng and LeRoux' (1966) study of *F. pusilla*. Most of this mortality cannot yet be partitioned among causes. However, these life tables and the experiments performed with *P. thomsoni* in 1994 begin the process of attributing visual symptoms to specific mortality agents of birch leafminers, and of assessing the relative importances of these agents in urban and forest settings.

It is odd that significant predation was not detected in the experiment involving *F. pusilla*, but was an obvious effect on exposed branches in the *P. thomsoni* experiment (Tables 3-6 and 3-7). The main reason for this is likely that the trees used for the *F. pusilla* experiment in 1993 had much higher background densities of leafminers than most trees used in the *P. thomsoni* study of 1994. Thus, predators probably aggregated on the localized, high-density prey patches created on branches in the *P. thomsoni* experiment, and greatly decreased survivorship of exposed leafminers. Such aggregation behaviour is expected when natural enemies encounter high-quality habitats that yield high return per search effort (Hassell 1976; Heads and Lawton 1983). Thus, predators of birch leafminers may efficiently aggregate on and exploit isolated shoots or branches having high local leafminer densities, but they may search more randomly and be less effective population regulators when overall leafminer densities are high and the population is more evenly-distributed spatially. This may explain why predators have been ineffective at regulating birch leafminer populations that have been in outbreak in Edmonton for the past two decades (Drouin and Wong 1984; see also Chapter 2).

Aggregation of predators on branches with high leafminer densities may also explain why overall larval survival was lower in experimental *P. thomsoni* populations at George Lake than in Edmonton in 1994 (Table 3-8). Higher background densities of *P. thomsoni* were observed on trees in Edmonton than at George Lake. Therefore, treated branches at George Lake may have been more attractive prey patches than in Edmonton, and thus were more heavily exploited.

Different mortality factors predominated under different treatment conditions in the experiment involving *P. thomsoni*. On exposed branches, young leafminers suffered high mortality from unknown causes, which presumably included predation (Tables 3-9 and 3-10). On branches inside fine mesh bags, few young *P. thomsoni* died, resulting in high population densities of later instar larvae. These densities resulted in the high levels of mortality of fourth instar larvae attributable to resource exhaustion (Tables 3-9 and 3-10). Thus, in outbreak situations where predators may be less effective (i.e. higher overall larval densities and a less patchy larval distribution), competition among later instar larvae may become an important mortality factor in population regulation. This was also suggested by Martin (1960): "The most important larval mortality factor [for *P. thomsoni*] was undoubtably starvation in all but very light infestations."

Abiotic and microbial mortality agents may also have been important. For example, the fragile and exposed eggs of *P. thomsoni* may be susceptible to mechanical puncturing by adjacent leaves or twigs (resulting in the "crushed" symptom), since many eggs were found "crushed" even when protected from predators within fine mesh bags in experiments during 1994. Labonte and Lipovsky (1984) found many eggs of *Profenusa alumna* (MacGillivray) on oak were killed by wind whipping leaves against other leaves, or against twigs and branches. Some "crushed" eggs of *P. thomsoni* may also have been punctured by conspecific females while searching for oviposition sites. A further source of mortality may have been pathogens, which could have killed the "brown" *P. thomsoni* eggs, or the moribund, intact larvae that were sometimes observed in natural and experimental *P. thomsoni* populations. Moribund larvae may also have been paralyzed, but not oviposited on, by parasitoids (Van Driesche 1983).

Eggs of *F. pusilla* observed to be "cut around" may have been victims of host-plant-mediated mortality. The leaf region surrounding *F. pusilla* eggs becomes discolored soon after oviposition (Friend 1933), perhaps resulting from disruption of fluid movement, or from localized cytokinin production (DeClerck and Shorthouse 1985). Leaf cells near the egg appear to have abnormal chloroplasts, enlarged nuclei, and reduced starch content (DeClerck and Shorthouse 1985). The "cut around" symptom is characterized by much dead, hardened, and separated leaf tissue, resulting in a crescent-shaped cut in the leaf surrounding the *F. pusilla* egg. Aphids may have caused the "cut around" symptom, since they were often found associated with leaves bearing these eggs, and may have been attracted to feed on the altered leaf cells. Alternatively, this symptom may have been an extension of the birch response noted by DeClerck and Shorthouse (1985), which resulted in the cutting off of vascular supply to leaf cells near *F. pusilla* eggs. The "cut around" symptom was the most important mortality source for eggs of *F. pusilla* (Table 3-3), thus it is desirable to discover the cause.

Experiments demonstrated that early leaf fall and bird predation on larvae in the leaves were negligible mortality sources. In some leafminer species, early leaf fall can have a significant population-regulatory effect (Faeth et al. 1981; Potter 1985; Bultman and Faeth 1986), but in other species this is not the case (Pritchard and James 1984; Kahn and Cornell 1989). High background population levels of *F. pusilla* on experimental and nearby trees in 1993 were expected to attract many birds, given that Cheng and LeRoux (1970) observed birds opening mines in Québec. Birds were possibly frightened away by experimental bags, and thus avoided nearby unbagged branches. However, there was little evidence of mines opened by birds on non-experimental trees.

Differences in mortality between locations and years varied between species and among instars. Where differences were detected, higher mortality always occurred in 1993 relative to 1992 (Tables 3-3 and 3-4). It may be that higher mortality of leaf-feeding stages accounted for the higher abundances of *P. thomsoni* larvae observed in 1993 relative to 1992 (Chapter 2). Higher mortality of eggs and first instar larvae of *F. pusilla* in Edmonton (Table 3-3) may have been host-plant-related. These stages are found in immature long-shoot leaves, which may be more plastic in their ability to respond chemically to invasion by leafminers than are mature leaves. Trees in the two locations may differ in there ability to do this.

Location-specific differences in mortality were reflected in marginally higher overall survivorship of larval *P. thomsoni* at George Lake relative to Edmonton in life tables from 1992 and 1993 (Table 3-5B). If it is assumed that predators were partially responsible for the lower survivorship in Edmonton, then the urban predator assemblage, characterized by anthocorids and thrips (Table 3-2), may be more effective than the assemblage at George Lake, characterized by spiders. This is supported by the fact that few larval mines at either location in 1992 or 1993 were ripped, a damage pattern consistent with spider predation, but not with that of anthocorids or thrips. In addition, higher survivorship of larvae to the final instar occurred at George Lake even though q(2) and q(3) were marginally higher there than in Edmonton (Tables 3-3 and 3-4). This suggests that mortality was not only higher in Edmonton, but was also more evenly-distributed among instars. This pattern may reflect weaker prey size preferences in a more effective urban predator assemblage.

The lower overall survivorship of *P. thomsoni* larvae in Edmonton represented in life tables from 1992 and 1993 suggests a paradox, since birch leafminers were generally more abundant in Edmonton than at George Lake during that time (Chapter 2). It may be that very low leafminer densities and sparse, homogeneous distributions of larvae at George Lake in 1992 and 1993, combined with higher densities of the birch skeletonizer, *Bucculatrix canadensisella* Chambers (Chapter 2), resulted in less predator aggregation on leafminers, and therefore lower mortality rates. This is supported by the fact that lower overall survivorship occurred at George Lake relative to Edmonton in mortality experiments in 1994 (Tables 3-8, 3-9, and 3-10), probably as a result of increased predator aggregation on branches having high *P. thomsoni* densities at George Lake (see above). Thus, location-specific differences in effectiveness of natural enemies may vary with prey density and distribution. In 1992 and 1993, it appears that mortality of leaf-feeding stages contributed little to regulation of *P. thomsoni* populations at George Lake. It is possible that *P. thomsoni* at George Lake were regulated by ground-dwelling predators feeding on inactive stages in the soil. Cheng and LeRoux (1966) found significant mortality of prepupal and pupal stages of *F. pusilla*.

Overall larval survivorship varied considerably among trees in both 1992 and 1993 for both birch leafminer species (Table 3-5), and in the 1994 mortality experiment with *P. thomsoni* (Table 3-8). These differences may be an expression of direct effects of host plant quality on larvae, such as differences in leaf nutrition derived from variation in tree habitat quality or genetics (e.g., Marino et al. 1993). It is known that success of *F. pusilla* is reduced on trees from certain birch species (Fiori and Dolan 1984; Braker 1986; Fiori and Craig 1987) and that there is much variation in birch leaf quality among trees, ramets, branches, and shoots (Suomela and Ayres 1994; Suomela and Nilson 1994). Alternatively, among-tree differences may have resulted from differences in natural enemy communities, or from indirect effects (*sensu* Billick and Case 1994) in which host tree differences affect other organisms in the community, which in turn interact with leafminers and produce differential leafminer survivorship among trees.

Overall survivorship of larval *P. thomsoni* appears to have decreased from 1992 to 1994 (section 3.4.4). However, given that the data from 1994 may have been biased by predators responding to patches with artificially high *P. thomsoni* density, this trend should be viewed with caution. The apparent increase in survivorship at George Lake from 1992 to 1993 resulted from the fact that sampling in 1993 ceased before late instar *P. thomsoni* larvae had finished developing (Chapter 2), and so their mortality was not accurately estimated. However, populations of *P. thomsoni* were noted to decrease between 1992 and 1993 (Chapter 2), and even smaller populations were casually observed in 1994, suggesting that extrinsic mortality factors may have been exacting an increasing toll on *P. thomsoni* populations in Alberta during this period.

3.5.2 Mortality agents. This study shows that native natural enemies have effectively switched onto exotic birch-leafmining sawfly hosts, and have assembled in diverse guilds to exploit this resource. In addition, it appears that predators are more important agents of birch leafminer mortality than idiobiont parasitoids, even though diverse guilds of both have developed in Alberta. The guild of generalist chalcidoids parasitizing birch leafminers in Alberta is similar to that observed on *F. pusilla* in eastern North America (Friend 1933; Cheng and LeRoux 1969) and in Europe (Eichorn and Pschorn-Walcher 1973), but its members are not presently numerous enough to seriously impact leafminer populations (Table 3-3). Thus, displacement of native idiobionts should not be a concern if specialist parasitoids are introduced as biological control agents. However, similar idiobiont species sometimes cause significant parasitism on birch leafminers in Europe (Eichorn and Pschorn-Walcher 1973; Schönrogge and Altenhofer 1992), and thus may become important in Alberta as well. In addition, the koinobiont *L. luteolator* appears to be consuming an increasingly significant proportion of *P. thomsoni* (Figure 3-1), suggesting that detailed investigation of its impacts relative to other mortality agents would be fruitful.

Two unexpected new host-parasitoid associations were observed. First, *Trichogramma aurosum* was reared for the first time from eggs of *P. thomsoni*. It has not been previously recorded from North America, but in Russia it parasitizes sawfly eggs on birch (J. D. Pinto, pers. comm.). Both *F. pusilla* and *H. nemoratus* suffer parasitism by *T. minutum* Riley in eastern North America (Peck 1963; Cheng and LeRoux 1969) but do not in Alberta, or in Europe (Eichorn and Pschorn-Walcher 1973). Second, *Scambus* (*Scambus*) sp. has not been previously reared from *F. pusilla*, although two other species of *Scambus* have been reared from *H. nemoratus* (Dowden 1941; Krombein et al. 1979). No pimplines attack *F. pusilla* in Europe (Eichorn and Pschorn-Walcher 1973), but *Alophosternum foliicola* Cushman was reared from *F. pusilla* in Québec (Cheng and LeRoux 1969).

All of the remaining idiobionts reared were eulophid chalcidoids (Table 3-1). Most genera represented have members which parasitize leafmining hosts in the orders Lepidoptera, Coleoptera, Diptera, and Hymenoptera (Yoshimoto 1984; Goulet and Huber 1993), and many have members previously reared from birch leafminers. These species probably switched quickly onto birch-leafmining hosts as they arrived in western Canada. Four of the six identified species were Holarctic (Table 3-1), and parasitize birch leafminers throughout their ranges. *Chrysocharis nitetis* is a common parasitoid of almost all leafmining sawflies in Europe (Pschorn-Walcher and Altenhofer 1989), and was previously reared from both *F. pusilla* and *H. nemoratus* in North America (Dowden 1941; Cheng and LeRoux 1969; Yoshimoto 1973; Hansson 1985, 1987) and from *F. pusilla* in Europe (Eichorn and Pschorn-Walcher 1973). This parasitoid was introduced into North America as a biocontrol agent of *F. pusilla* (Fuester et al. 1984) before it was realized to have an Holarctic distribution (Hansson 1987). *Closterocerus trifasciatus* is commonly associated with leafmining sawflies, and also hyperparasitizes their braconid and chalcidoid parasitoids (Krombein et al. 1979; Pschorn-Walcher and Altenhofer 1989; Schönrogge and Altenhofer 1992). It has been reared from *F. pusilla*, *H. nemoratus* and their parasitoids in Europe (Boucek and Askew 1968; Eichorn and Pschorn-Walcher 1973), and from *H. nemoratus* in North America (as *C.*

sesquifasciatus; Dowden 1941). *Elachertus argissa* (Walker) has been reared from *F. pusilla* in Europe (Eichorn and Pschorn-Walcher 1973), but more commonly parasitizes lepidopteran larvae in concealed habitats (Schauff 1985). *Minotetrastichus frontalis* (Nees) is Holarctic in distribution and has been reared from *F. pusilla*, *H. nemoratus*, and many other leafmining sawflies (as *Tetrastichus xanthops* [Ratzeburg] or *T. ecus* [Walker]; Dowden 1941; Cheng and LeRoux 1969; Krombein et al. 1979; Pschorn-Walcher and Altenhofer 1989; Graham and LaSalle 1991; LaSalle 1994).

Of the two known Nearctic species identified, *Cirrospilus cinctithorax* (Girault) was the most common, and has been previously reared from *F. pusilla*, *H. nemoratus*, and the birch skeletonizer, *B. canadensisella* (Peck 1963; Cheng and LeRoux 1969; Krombein et al. 1979). High population levels of *B. canadensisella* in parts of Alberta (Chapter 4) may have provided a source population of *C. cinctithorax* for *F. pusilla*. *Pnigalio metacomet* (Crawford) was reared from *Fenusa ulmi* Sundevall in eastern North America (Miller 1970), but has not been previously reared from *F. pusilla*.

The remaining eulophid genera have members commonly reared from concealed hosts. Species of *Zagrammosoma* were previously reared from *F. pusilla*, and *Sympiesis* species from *F. pusilla* and *H. nemoratus* (Dowden 1941; Cheng and LeRoux 1969). The life histories of members of the genus *Peckelachertus* are virtually unknown, but they have been found to parasitize eggs of diprionid sawflies in North America (LaSalle 1994). Parasitoids from this genus have not been previously recorded attacking leafmining sawflies.

No koinobiont parasitoids of *F. pusilla* were discovered in Alberta, confirming that the Palearctic specialists *Lathrolestes nigricollis* and *Grypocentrus albipes* are not present. However, it was surprising to discover *L. luteolator* parasitizing *P. thomsoni*, since *P. thomsoni* is one of the few fenusine sawflies in Europe with no known specialist parasitoids from the genus *Lathrolestes* (Pschorn-Walcher and Altenhofer 1989; Schönrogge and Altenhofer 1992). It has been suggested that *P. thomsoni* may be native to the Nearctic (Schönrogge and Altenhofer 1992), since a *Lathrolestes* sp. was reared from *P. thomsoni* in Ontario (Martin 1960) but has not been reared from *P. thomsoni* in Europe. However, *P. thomsoni* was absent in Alberta before 1970 and is still expanding its range (Drouin and Wong 1984; Chapter 2), making it unlikely that it is native. In eastern North America, *L. luteolator* attacks the red oak leafminer, *Profenusa alumna*, and the pear slug, *Caliroa cerasi* L., on oak (Barron 1994). Barron (1994) suggests that *L. luteolator* switches from leafminers on oak onto *P. thomsoni* in western Canada, where oak is rare. However, *C. cerasi* can be abundant on ornamental hawthorn in Edmonton (C. Saunders, pers. comm.), and these populations may have provided the original western source of *L. luteolator.*

The predator assemblage recorded in Alberta is similar to that observed in eastern North America (Cheng and LeRoux 1966, 1969, 1970), and demonstrates that a diverse native assemblage of predators is available to switch onto exotic birch leafminers. Abundant generalist predators, such as empidid flies, spiders, and beetles, may switch easily onto abundant, new exotic prey, like the slow-moving adult birch leafminers. Kovalev (1966) reported that members of *Platypalpus* and related empidid genera effectively controlled populations of coccids, mites, and leafmining flies. Most of the collected spiders (Table 3-2) probably feed on adult birch leafminers to some degree, and those from the hunting families (Philodromidae, Salticidae, Gnaphosidae, and Clubionidae) may also take larvae. Spider predation has not been previously documented on birch leafminer adults or larvae, although Cheng and LeRoux (1969) hint that spider predation of *F. pusilla* larvae occurred in Québec.

Staphylinid beetles tend to be generalist predators (Borror et al. 1989), and may take birch leafminer larvae in the canopy. However, both staphylinid and carabid beetles are probably more important as ground-dwelling predators of late instar larvae, pupae, and teneral adults (Cheng and LeRoux 1966). Larval coccinellids were observed feeding on *F. pusilla* eggs in Québec (Cheng and LeRoux 1966), and may also do so in Alberta. Most of the adult coccinellids collected were probably feeding on the abundant aphids found on all birch examined in 1992 (see Chapter 2).

The anthocorids were the only hemipterans observed feeding on birch leafminers. Cheng and LeRoux (1966, 1969) recorded *Anthocoris musculus* (Say) as a predator of *F. pusilla* larvae, but only if the mine had been previously opened by another agent. The three collected species of *Anthocoris* have been previously recorded on birch in western Canada, usually feeding on homopterans (references in Kelton 1978).

Larval Chrysopidae are generalist predators, and have been recorded feeding on larval *F. pusilla* (Cheng and LeRoux 1966, 1970). Larvae of chrysopids and hemerobiids are efficient searchers, and generally eat a wide variety of slow-moving, soft-bodied prey (New 1975). One larval chrysopid can consume large numbers of small prey (Tauber 1987), so this group may have a significant effect on leafminer populations. Adults of both chrysopids and hemerobiids are partially or wholly predaceous (New 1975), and may also impact leafminer populations.

It is possible that the phlaeothripid *Haplothrips kurdjumovi* Karny feeds on birch leafminers (B. S. Heming, pers. comm.). Cheng and LeRoux (1966) reported predation of *F. pusilla* eggs by adult and larval thysanopterans. Ants are known to eat large numbers of final instar *F. pusilla* larvae that have fallen to the ground to burrow (Friend 1933; Cheng and LeRoux 1966, 1969, 1970). I observed *Formica* sp. ants ripping larvae from mines in the canopy; Cheng and LeRoux (1966) observed similar activities in Québec.

Several other predators may impact birch leafminer populations. The two predaceous mirids found (*Deraeocoris brevis* [Uhler] and *D. aphidiphagus* Knight) were rare, and feed on Homoptera (Kelton 1980). The two acanthosomatids (*Elasmuchas lateralis* Say and *Elasmostethus cruciatus* Say) were common in Edmonton, and may be partly predaceous (McPherson 1982), but I observed them feeding only on birch seeds. One group not collected but commonly observed was the vespoid wasps (*Vespula* spp.), known to rip open mines and prey on larval leafminers in eastern Canada (Cheng and LeRoux 1966, 1969). In addition, Cheng and LeRoux (1966, 1969) reported that birds consumed large numbers of *F. pusilla* larvae both from the mines and from the soil surface before larvae burrowed in. Bird predation of mine-inhabiting larvae was not observed in Alberta, but birds may consume larvae once they have fallen to the ground.

This study suggests there are differences between Alberta and Europe in mortality caused by natural enemies. This may be largely due to the fact that the European parasitoid guild, of *F. pusilla* at least, is much more effective (up to 38-47% parasitism; Eichorn and Pschorn-Walcher 1973) than that in Alberta. It has been argued that specialist parasitoids, particularly in the genus *Lathrolestes*, are crucial to the population regulation of fenusine leafminers (Pschorn-Walcher and Altenhofer 1989). This appears to be the case for *F. pusilla*, since population reductions have coincided with introductions of *Lathrolestes nigricollis* in eastern North America (Van Driesche 1989). It may also be the case for *P. thomsoni* in Alberta, which is experiencing a population decline concurrently with increasing *L. luteolator* parasitism (Chapter 2; Figure 3-1). However, causation cannot be inferred from these correlative relationships (Price 1987). Experimental investigation of the within-generation effects of individual mortality agents can be used to establish their relative impacts and overall regulatory effects on populations (Hassell 1985, 1987). Thus, further investigation of the stage-specific impacts of both canopy- and ground-dwelling predators, and of *Lathrolestes* species parasitoids, should be fruitful in revealing mechanisms of birch leafminer population regulation that can be compared with those operating in Europe. Such comparisons should be powerful tools in directing effective birch leafminer management programs.

Table 3-1. Parasitoids reared from birch leafminers in Alberta in 1991-1994. Data are my own combined with those of Robin McQueen and Chris Saunders, City of Edmonton Pest Management Services. All are idiobionts of larvae except *L. luteolator* (koinobiont of larvae) and the *Trichogramma* species (idionbionts of eggs).

Family	Subfamily (Tribe)	Species	# found	Host	Distribution	Location(s) Collected
Eulophidae	Entedoninae	*Chrysocharis nitetis* (Walker)	12	*F. pusilla, H. nemoratus*	Holarctic	Edmonton, Alder Flats, Slave Lake, Chip Lake
		Chrysonotomyia sp.	3	*F. pusilla, P. thomsoni*	-	Edmonton
		Closterocerus trifasciatus Westwood	12	*F. pusilla*	Holarctic	Edmonton
	Eulophinae (Elachertini)	*Cirrospilus cinctithorax* (Girault)	26	*F. pusilla*	Nearctic	Edmonton, George Lake, Alder Flats
		Cirrospilus sp. 2	3	*F. pusilla*	-	Edmonton, George Lake, Edson
		Elachertus argissa (Walker)	1	*F. pusilla*	Holarctic	Moose Lake
		Zagrammosoma sp.	1	*P. thomsoni*	-	Edmonton
	Eulophinae (Eulophini)	*Symplesis* sp.	3	*P. thomsoni*	-	Edmonton
		Pnigalio metacomet (Crawford)	12	*F. pusilla*	Nearctic	Edmonton, Edson
		Pnigalio sp. 2	2	*P. thomsoni*	-	Edmonton
		Pnigalio sp. 3	5	*F. pusilla, P. thomsoni*	-	Edmonton
	Tetrastichinae	*Minotetrastichus frontalis* (Nees)	8	*F. pusilla*	Holarctic	Edmonton
		Minotetrastichus sp. (near *bremn*)	10	*F. pusilla, P. thomsoni*	-	Edmonton
		Peckelachertus sp.	1	*F. pusilla*	-	Edmonton
Ichneumonidae	Pimplinae	*Scambus* (*Scambus*) sp.	7	*F. pusilla*	-	Edmonton, Hinton
	Ctenopelmatinae	*Lathrolestes luteolator* (Gravenhorst)	>100	*P. thomsoni*	Nearctic	Edmonton, George Lake
Trichogrammatidae	Trichogrammatinae	*Trichogramma aurosum* Sugon. & Sorok.	>20	*P. thomsoni*	Holarctic	Edmonton, George Lake
		Trichogramma sp. (near *pintoi*)	>20	*P. thomsoni*	-	Edmonton, George Lake

Table 3-2. Potential predators of birch leafminers sampled from birch trees by sweep netting in Edmonton and at George Lake, 1992. Familes designated with an asterisk (*) had members that were observed feeding on or closely associated with birch leafminers; these were further identified if possible.

Order		Family	George Lake		Edmonton		Genus or species
			# species	# individ.	# species	# individ.	
Araneae	*	Araneidae	11+	66	5	8	
		Tetragnathidae	1	2	-	-	
		Theridiidae	1	1	1	1	
	*	Philodromidae	2	14	2	19	*Philodromus rufus quartus* Dondale and Redner, *Philodromus* sp. (only immatures captured)
		Salticidae	1	10	1	3	
		Gnaphosidae	1	1	1	5	
		Clubionidae	2	4	1	1	
Coleoptera		Staphylinidae	1	2	1	1	
		Coccinellidae	2	12	9	31	
Hemiptera	*	Anthocoridae	-	-	3	40	*Anthocoris musculus* (Say), *A. melanocerus* Reuter, *A. antevolens* White
		Miridae	3	6	9	40	
		Acanthosomatidae	2	2	2	81	
Thysanoptera	*	Phlaeothripidae	-	-	1	16	*Haplothrips kurdjumovi* Karny
Hymenoptera	*	Formicidae	4	10	2	5	*Formica* sp., *Myrmica* sp., *Camponotus* sp.
Neuroptera	*	larval Hemerobiidae	-	-	1	1	
	*	larval Chrysopidae	1	2	3	3	
Total			33+	133	46+	279	

Table 3-3. Life table for eggs and larvae of *F. pusilla* and *P. thomsoni* from leaf samples, 1992 and 1993. No estimates of egg mortality were obtained in 1992. Mortality causes 1-4 d(x) for different instars in 1993: *F. pusilla* eggs: 1d(x)="cut around", 2d(x)=dessicated; *P. thomsoni* eggs: 1d(x)=brown, 2d(x)=crushed, 3d(x)=dessicated, 4d(x)=parasitized by *Trichogramma* sp.; larvae (both species): 1d(x)=dead, 2d(x)=parasitized by idiobionts.

Location	Species	Instar	1992			1993						
		(x)	q(x)	l(x)	d(x)	q(x)	l(x)	d(x)	1d(x)	2d(x)	3d(x)	4d(x)
Edmonton	*F. pusilla*	egg	-	-	-	0.278	1.000	0.278	0.181	0.097		
		1	0.116	1.000	0.116	0.378	0.722	0.273	0.273	0.000		
		2	0.299	0.884	0.264	0.198	0.449	0.089	0.086	0.003		
		3	0.033	0.620	0.020	0.075	0.360	0.027	0.027	0.000		
		4	0.062	0.599	0.037	0.044	0.333	0.015	0.014	0.000		
		5		0.562			0.319					
	P. thomsoni	egg	-	-	-	0.298	1.000	0.298	0.099	0.133	0.041	0.024
		1	0.091	1.000	0.091	0.428	0.702	0.300	0.299	0.001		
		2	0.070	0.909	0.064	0.393	0.402	0.158	0.156	0.002		
		3	0.089	0.845	0.075	0.123	0.244	0.030	0.027	0.003		
		4	0.059	0.770	0.046	0.031	0.214	0.007	0.004	0.002		
		5	0.046	0.724	0.033	0.011	0.207	0.002	0.002	0.000		
		6		0.690			0.205					
George Lake	*F. pusilla*	egg	-	-	-	0.085	1.000	0.085	0.052	0.032		
		1	0.047	1.000	0.047	0.053	0.915	0.049	0.049	0.000		
		2	0.175	0.953	0.167	0.256	0.866	0.222	0.213	0.009		
		3	0.009	0.786	0.007	0.035	0.645	0.023	0.020	0.003		
		4	0.006	0.779	0.005	0.022	0.622	0.013	0.013	0.001		
		5		0.774			0.608					
	P. thomsoni	egg	-	-	-	0.280	1.000	0.280	0.102	0.170	0.000	0.008
		1	0.114	1.000	0.114	0.193	0.720	0.139	0.139	0.000		
		2	0.208	0.886	0.184	0.167	0.581	0.097	0.097	0.000		
		3	0.227	0.702	0.160	0.133	0.484	0.065	0.065	0.000		
		4	0.040	0.542	0.022	0.000	0.419	0.000	0.000	0.000		
		5	0.060	0.520	0.031	0.000	0.419	0.000	0.000	0.000		
		6		0.489			0.419					

Table 3-4. Repeated measures analyses of variance on arcsine-transformed q(x) values for immature birch leafminers. Variation was partitioned between years (1992 and 1993) and locations (Edmonton and George Lake). "Eggs" were analyzed separately using ranks (*F. pusilla*) or untransformed data (*P. thomsoni*) from 1993.

Effect	Source	*F. pusilla*				*P. thomsoni*			
		df	MS	F	p	df	MS	F	p
eggs	Location	1,8	36.100	6.50	0.034	1,4	13.214	0.04	0.850
1st instar	Year	1,15	0.217	3.79	0.071	1,14	0.183	6.53	0.023
	Location	1,15	0.491	8.56	0.010	1,14	0.038	1.37	0.261
	Year x Location	1,15	0.128	2.23	0.156	1,14	0.106	3.79	0.072
2nd instar	Year	1,15	0.024	0.29	0.596	1,14	0.001	0.03	0.873
	Location	1,15	0.017	0.21	0.651	1,14	0.142	4.46	0.053
	Year x Location	1,15	0.025	0.31	0.584	1,14	0.492	15.42	0.002
3rd instar	Year	1,15	0.012	0.38	0.548	1,14	0.019	0.56	0.467
	Location	1,15	0.016	0.49	0.496	1,14	0.159	4.58	0.050
	Year x Location	1,15	0.000	0.00	0.973	1,14	0.008	0.24	0.630
4th instar	Year	1,15	0.001	0.05	0.829	1,14	0.045	2.21	0.159
	Location	1,15	0.049	1.70	0.212	1,14	0.018	0.88	0.365
	Year x Location	1,15	0.000	0.01	0.912	1,14	0.002	0.12	0.739
5th instar	Year					1,14	0.067	3.17	0.097
	Location					1,14	0.000	0.01	0.920
	Year x Location					1,14	0.004	0.17	0.687
Among instars	Year	1,15	0.053	0.63	0.440	1,14	0.001	0.02	0.893
	Location	1,15	0.348	4.13	0.060	1,14	0.021	0.44	0.518
	Year x Location	1,15	0.011	0.13	0.720	1,14	0.218	4.60	0.050
	Instar	3,45	0.457	11.88	0.0001	4,56	0.257	11.57	0.0001
	Instar x Year	3,45	0.067	1.75	0.171	4,56	0.079	3.54	0.012
	Instar x Location	3,45	0.075	1.95	0.135	4,56	0.084	3.79	0.009
	Instar x Year x Loc	3,45	0.047	1.23	0.308	4,56	0.099	4.44	0.003

Table 3-5. Analyses of variance evaluating the proportion of immatures surviving to final instar larvae for *F. pusilla* and *P. thomsoni* at two locations (Edmonton and George Lake). A, data from 1993 only, with egg mortality included; B, data from 1992 and 1993, with egg mortality excluded.

A.

Source	df	MS	F	p	Error Term
Location	1	0.418	3.30	0.107	Tree(Location)
Tree(Location)	8	0.127	10.15	0.002	Error
Species	1	0.083	6.66	0.033	Error
Location x Species	1	0.000	0.02	0.903	Error
Error	8	0.012			

B.

Source	df	MS	F	p	Error Term
Year	1	0.143	2.15	0.160	Tree(Year x Loc)
Location	1	0.283	4.25	0.054	Tree(Year x Loc)
Year x Location	1	0.211	3.16	0.092	Tree(Year x Loc)
Tree(Year x Loc)	18	0.067	2.44	0.033	Error
Species	1	0.067	2.45	0.135	Error
Year x Species	1	0.000	0.01	0.939	Error
Location x Species	1	0.035	1.29	0.272	Error
Year x Loc x Spec	1	0.191	7.02	0.016	Error
Error	18	0.027			

Table 3-6. Mean (±SE) percent mortality of immature *F. pusilla* and *P. thomsoni* from field experiments involving birch branches subjected to three bagging treatments. Stage-specific mortality was not recorded for *F. pusilla*. Means for *P. thomsoni* eggs are from George Lake only (five trees), and those for *P. thomsoni* larvae are from Edmonton and George Lake (5 trees per location).

Species	Instar	Treatment		
		Fine Mesh	Coarse Mesh	Open
F. pusilla	all	4.5 (±1.3)	5.7 (±1.3)	4.9 (±1.3)
P. thomsoni	egg	27.3 (±7.8)	60.4 (±7.8)	55.9 (±7.8)
	1	8.7 (±4.1)	35.9 (±4.1)	45.1 (±4.1)
	2	2.0 (±2.8)	7.8 (±2.8)	13.8 (±2.8)
	3	2.6 (±2.4)	8.6 (±2.4)	10.8 (±2.4)
	4	22.1 (±2.5)	7.7 (±2.5)	6.2 (±2.5)
	5	28.8 (±3.9)	23.5 (±3.9)	18.2 (±3.9)

Table 3-7. Repeated measures analysis of variance evaluating percent mortality (100q[x]) for different larval instars of *P. thomsoni* from mortality experiments, 1994. Variation is partitioned between locations (Edmonton and George Lake) and among treatments (branches bagged with fine mesh, those bagged with coarse mesh, and open branches). Orthogonal treatment contrasts are also presented. Values for "eggs" are from a separate analysis of data from George Lake only.

Effect	Source	df	MS	F	p
eggs	Tree	4,8	430.0	1.42	0.310
	Treatment	2,8	1615.5	5.35	0.033
	Fine Mesh vs. rest	1,8	3180.6	10.54	0.012
	Coarse Mesh vs. Open	1,8	50.4	0.17	0.694
1st instar	Location	1,8	2523.6	3.83	0.086
	Tree(Location)	8,16	659.3	3.96	0.009
	Treatment	2,16	3577.3	21.50	0.0001
	Treatment x Location	2,16	916.8	5.51	0.015
	Fine Mesh vs. rest	1,16	6723.0	40.40	0.0001
	Coarse Mesh vs. Open	1,16	431.7	2.59	0.127
2nd instar	Location	1,8	46.3	0.28	0.612
	Tree(Location)	8,16	166.0	2.13	0.095
	Treatment	2,16	344.3	4.41	0.030
	Treatment x Location	2,16	226.3	2.90	0.084
	Fine Mesh vs. rest	1,16	509.3	6.52	0.021
	Coarse Mesh vs. Open	1,16	179.4	2.30	0.149
3rd instar	Location	1,8	92.5	1.08	0.329
	Tree(Location)	8,16	85.5	1.51	0.229
	Treatment	2,16	183.2	3.24	0.066
	Treatment x Location	2,16	145.2	2.57	0.108
	Fine Mesh vs. rest	1,16	342.6	6.06	0.026
	Coarse Mesh vs. Open	1,16	23.8	0.42	0.526
4th instar	Location	1,8	448.4	1.89	0.207
	Tree(Location)	8,16	237.6	3.78	0.011
	Treatment	2,16	771.0	12.27	0.001
	Treatment x Location	2,16	259.9	4.14	0.036
	Fine Mesh vs. rest	1,16	1531.5	24.38	0.0001
	Coarse Mesh vs. Open	1,16	10.4	0.17	0.689

Table 3-7. Continued.

Effect	Source	df	MS	F	p
5th instar	Location	1,8	2054.1	4.36	0.070
	Tree(Location)	8,16	470.8	3.12	0.025
	Treatment	2,16	285.4	1.89	0.183
	Treatment x Location	2,16	353.3	2.34	0.128
	Fine Mesh vs. rest	1,16	426.4	2.83	0.112
	Coarse Mesh vs. Open	1,16	144.3	0.96	0.343
Among instars	Location	1,8	18.7	0.20	0.670
	Tree(Location)	8,16	95.5	1.24	0.338
	Treatment	2,16	457.2	5.95	0.012
	Treatment x Location	2,16	46.5	0.60	0.558
	Instar	4,64	3054.4	27.91	0.0001
	Instar x Location	4,32	1286.54	3.38	0.021
	Instar x Tree(Loc)	32,64	380.9	3.48	0.0001
	Instar x Treatment	8,64	1176.0	10.74	0.0001
	Instar x Loc x Treat	8,64	463.8	4.24	0.0004

Table 3-8. Analyses of variance evaluating the proportion of immature *P. thomsoni* surviving to final instar larvae in mortality experiments, 1994. Variation was partitioned between locations (Edmonton and George Lake, 5 trees per location) and among treatments (branches bagged with fine mesh, those bagged with coarse mesh, and open branches). A, survivorship at George Lake only, with egg mortality included; B, survivorship at both locations, with egg mortality excluded.

A.

Source	df	MS	F	p
Tree	4,8	0.002	0.44	0.777
Treatment	2,8	0.048	12.26	0.004
Fine Mesh vs. rest	1,8	0.097	24.46	0.001
Coarse Mesh vs. Open	1,8	0.0002	0.05	0.823

B.

Source	df	MS	F	p
Location	1,8	0.371	16.08	0.004
Tree(Location)	8,16	0.023	1.47	0.243
Treatment	2,16	0.108	6.91	0.007
Treatment x Location	2,16	0.003	0.20	0.822
Fine Mesh vs. rest	1,16	0.198	12.59	0.003
Coarse Mesh vs. Open	1,16	0.019	1.23	0.284

Table 3-9. Life table for larvae of *P. thomsoni* from the mortality experiment in Edmonton, 1994. Mortality causes 1-4 d(x) for larvae: 1d(x)=dead (unknown causes), 2d(x)=competition (resources exhausted), 3d(x)=ripped from mine, 4d(x)=early leaf fall. No estimates of egg mortality were obtained.

Treatment	Instar (x)	q(x)	l(x)	d(x)	1d(x)	2d(x)	3d(x)	4d(x)
Open	egg	-	-	-				
	1	0.313	1.000	0.313	0.253	0.000	0.059	0.000
	2	0.151	0.687	0.104	0.075	0.000	0.021	0.007
	3	0.156	0.584	0.091	0.086	0.001	0.004	0.000
	4	0.043	0.493	0.021	0.000	0.017	0.005	0.000
	5	0.313	0.471	0.148	0.018	0.117	0.008	0.004
	6		0.324					
Coarse Mesh	egg	-	-	-				
	1	0.204	1.000	0.204	0.193	0.000	0.011	0.000
	2	0.050	0.796	0.040	0.034	0.003	0.003	0.000
	3	0.107	0.757	0.081	0.052	0.004	0.025	0.000
	4	0.094	0.676	0.064	0.024	0.010	0.027	0.003
	5	0.425	0.612	0.260	0.041	0.153	0.026	0.041
	6		0.352					
Fine Mesh	egg	-	-	-				
	1	0.106	1.000	0.106	0.104	0.000	0.000	0.002
	2	0.009	0.894	0.008	0.008	0.000	0.000	0.000
	3	0.004	0.886	0.003	0.003	0.000	0.000	0.000
	4	0.137	0.883	0.121	0.000	0.121	0.000	0.000
	5	0.317	0.762	0.242	0.005	0.232	0.000	0.005
	6		0.520					

Table 3-10. Life table for eggs and larvae of *P. thomsoni* from the mortality experiment at George Lake, 1994. Mortality causes or symptoms 1-4 d(x) for eggs: 1d(x)=brown, 2d(x)=crushed, 3d(x)=parasitized by *Trichogramma* sp., 4d(x)=early leaf fall. Mortality causes 1-4 d(x) for larvae: 1d(x)=dead (unknown cause), 2d(x)=competition (resources exhausted), 3d(x)=ripped from mine, 4d(x)=early leaf fall.

Treatment	Instar (x)	q(x)	l(x)	d(x)	1d(x)	2d(x)	3d(x)	4d(x)
Open	egg	0.559	1.000	0.559	0.139	0.363	0.058	0.000
	1	0.573	0.441	0.253	0.223	0.000	0.029	0.000
	2	0.163	0.163	0.031	0.028	0.000	0.003	0.000
	3	0.149	0.158	0.023	0.020	0.000	0.003	0.000
	4	0.341	0.134	0.046	0.008	0.024	0.014	0.000
	5	0.639	0.088	0.056	0.021	0.030	0.006	0.000
	6		0.032					
Coarse Mesh	egg	0.604	1.000	0.604	0.112	0.479	0.013	0.001
	1	0.497	0.396	0.197	0.189	0.000	0.004	0.003
	2	0.256	0.199	0.051	0.034	0.013	0.001	0.002
	3	0.21[illegible]	0.148	0.031	0.013	0.015	0.002	0.000
	4		0.117	0.036	0.018	0.012	0.006	0.000
	5		0.081	0.040	0.017	0.013	0.007	0.003
	6		[illegible]					
Fine Mesh	egg			0.273	0.036	0.208	0.000	0.029
	1			0.053	0.033	0.001	0.000	0.019
	2			0.024	0.018	0.005	0.000	0.001
	3			0.036	0.007	0.029	0.000	0.000
	4			0.213	0.004	0.209	0.000	0.000
	5		0.400	0.193	0.003	0.188	0.000	0.002
	6		0.207					

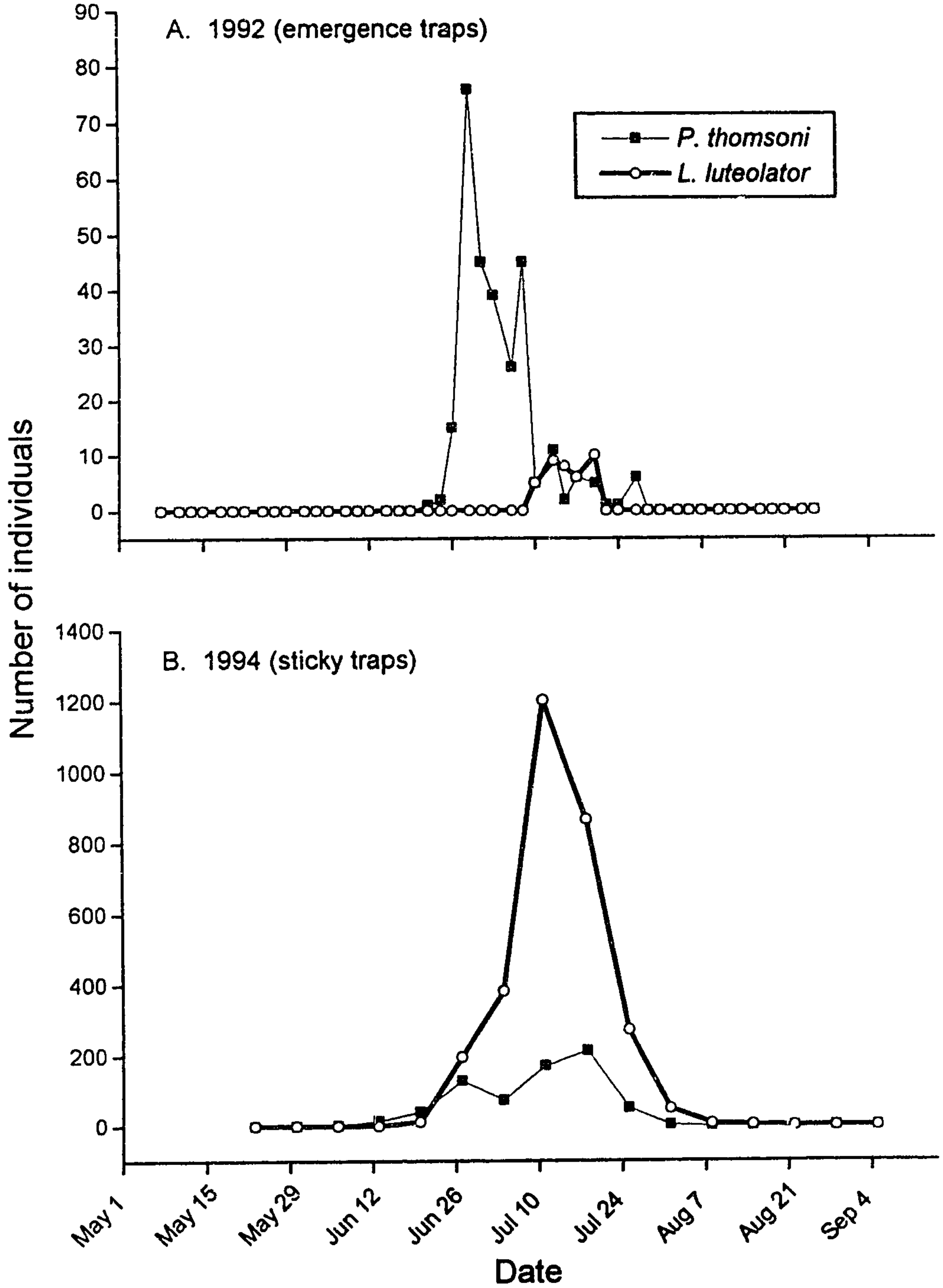

Figure 3-1. Activities of adult *P. thomsoni* and *L. luteolator* in 1992 (2 emergence traps at each of 6 trees) and 1994 (1 yellow sticky trap on each of 5 trees) in Edmonton.

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4. Competitive and host quality effects on populations of exotic birch leafminers

4.1 Synopsis

Intraspecific competition for leaf resources affected weights of larval *Fenusa pusilla* (Lepeletier), but affected survivorship of larval *Profenusa thomsoni* (Konow). The extreme rarity of *P. thomsoni* during outbreaks of the native birch skeletonizer, *Bucculatrix canadensisella* Chambers (Lepidoptera: Lyonetiidae), suggests direct interspecific competition, but this could not be confirmed in field experiments executed when populations of *B. canadensisella* were lower. Indirect interspecific competition, mediated by the host plant, was detected between *F. pusilla* and *P. thomsoni*. Both *F. pusilla* damage and artificial damage to leaves early in the season decreased larval survivorship of the later-occurring *P. thomsoni*.

Aspects of host quality affected larval survival and oviposition choices of *P. thomsoni* in unexpected ways. Females discriminated only weakly among leaves of different sizes on a branch, and tended to lay eggs on leaves already bearing eggs, even though this increased the probability of larval competition and decreased larval survivorship. More variation in *P. thomsoni* larval survivorship occurred among individual trees than between an urban and a rural location.

4.2 Introduction

One of the most controversial topics in community ecology concerns the contribution of competition in structuring ecological communities (Begon et al. 1990). Strong et al. (1984) found that assemblages of phytophagous insects generally are not structured by competition, although this perspective has been challenged recently as more evidence of competition has accumulated (Denno et al. 1995). Many leafmining insects compete, perhaps because they are restricted to feed within a single leaf for at least part of their life cycle and thus cannot avoid competition behaviourally (Faeth 1991).

Competition has been inferred when the weight or survivorship of leafmining larvae is decreased in the presence of other phytophages (e.g., Tuomi et al. 1981). In this way, intraspecific competition has been detected in several leafminer species (Tuomi et al. 1981; Quiring and McNeil 1984a, b, d; Bultman and Faeth 1985, 1986; Potter 1985; Kato 1994), but interspecific competition is more rare. When detected, it is usually asymmetric in favor of a free-feeding folivorous competitor (Faeth 1986, 1990; Hartley and Lawton 1987; West 1985; Denno et al. 1995), and is often indirect, in that previous damage by phytophages modifies the host plant, resulting in decreased leafminer fitness. Such inducible changes include: increased plant chemical defences (Bergelson et al. 1986; Faeth 1986); increased propensity for leaf abscission (Faeth et al. 1981b; Faeth 1986); and attraction of natural enemies (Faeth and Bultman 1986; Faeth 1986).

These mechanisms of competition emphasize that host quality can greatly affect leafminers. Because of the extreme intimacy of this host-insect interaction (Mattson et al. 1988; Faeth 1991) and non-vagility of leafmining larvae, oviposition site selection by females is predicted to strongly influence the fitness of their progeny. Thus, the ability of female leafminers to distinguish host quality should be favored by natural selection (Faeth 1991).

There are a variety of potential host effects on leafminers in addition to those induced by competitors. For example, chemical differences among leaves within a tree or among trees (Haukioja et al. 1978; Niemelä and Tuomi 1993; Suomela and Ayres 1994) can affect the distribution of insect attacks (Denno and McClure 1983, Barbosa and Wagner 1989; Suomela and Nilson 1994). However, defensive phytochemicals do not consistently affect leafminer distributions or abundances (Feeny 1970; Faeth et al. 1981a; Bultman and Faeth 1988; Faeth 1990). Leafminers may be better adapted to hosts because of the intimacy of their associations, or they may feed selectively on tissues not containing defensive phytochemicals (Faeth 1991). More important host effects usually arise from host phenology and structure. Leafminers may experience differential success in leaves of different ages, due to seasonal changes in nutritional content (DeClerck and Shorthouse 1985), leaf age at abscission (Faeth 1987), or presence / absence of potential competitors (Quiring and McNeil 1984a). Leaf area can also affect leafminer fitness; larger leaves are often preferred (Tuomi et al. 1981; Quiring and McNeil 1984a), especially by species requiring a large proportion of the leaf to complete development (Faeth 1991). All of these effects are compounded by environmental and genetic influences, which can affect host quality both within and between plants (Marino et al. 1993).

Intraspecific competition may occur in species colonizing new areas if they are freed from other population-limiting factors with which they have evolved (e.g., specific natural enemies). Preliminary data suggest that two species of birch-leafmining sawflies, *Fenusa pusilla* (Lepeletier) and *Profenusa thomsoni* (Konow), which have been introduced to North America from Europe, compete with conspecifics for leaf resources (Chapter 2). Larvae of these species are restricted to feeding within the birch leaf on which they originated as eggs, and it is common to observe leaves completely mined by *F. pusilla* or *P. thomsoni* that still contain immature larvae unable to complete their development.

Direct interspecific competition may be expected between newly-invading species and native species if their niches overlap. Larvae of *P. thomsoni* and of the native birch skeletonizer *Bucculatrix canadensisella* Chambers (Lepidoptera: Lyonetiidae) co-occur in space and time (Chapter 2), and thus are potential direct competitors for leaf resources.

Two species which do not interact in their native ranges may begin interacting when they colonize new areas, especially if components of their native community were left behind (i.e. competitors or natural enemies) or if relative abundances of the two species differ between the native and new ranges (as for *F. pusilla* and *P. thomsoni*; Chapter 2). *Fenusa pusilla* is present in early summer, and only mines young leaves at branch tips, whereas *P. thomsoni* occurs later and mines mature leaves throughout the tree (Martin 1960; DeClerck and Shorthouse 1985; Chapter 2). This results in temporal and spatial separation of these species, precluding direct competition between them (Chapter 2). However, they may compete indirectly if early-season mining damage by *F. pusilla* reduces the quality of nearby leaves for the later-occurring *P. thomsoni*.

During 1993 and 1994, I investigated several potential competitive interactions within and between the birch-leafmining sawflies in Alberta: intraspecific competition for leaf resources within *F. pusilla* and *P. thomsoni*; interspecific competition between larval *P. thomsoni* and larval *B. canadensisella*; and indirect interspecific competition, mediated by the host plant, between larval *F. pusilla* and larval *P. thomsoni*. I also examined variation in host plant quality for *P. thomsoni* on several spatial scales.

4.3 Materials and Methods

All field experiments examining competition and host quality used fine mesh bags to enclose birch foliage. Unless otherwise stated, fine mesh bags were made from "no-see-um" style mesh (irregular weave; no opening larger than 0.1 mm^2). Those enclosing entire branches were roughly 60.0 cm long and 30.0 cm wide, and enclosed 50-70 leaves. Those enclosing individual leaves were roughly 8.0 cm long by 8.0 cm wide, and were sealed around the leaf petiole using Velcro®. All leaves in all experiments were measured for length and width, from which leaf area was derived using an empirical regression (area = 0.637 [length x width] - 70.784; see Chapter 2). The amount of area consumed on each leaf was estimated visually using 11 percentage classes (0%, 10%, 20%, ..., 100%).

4.3.1 Intraspecific competition. Leaves with varying densities of similar-instar larvae of *F. pusilla* or *P. thomsoni* (1 to 10 larvae/leaf) were clipped from branches of young nursery trees (*F. pusilla*, 1993 [experiment 1] and 1994), mature trees nearby the nursery stock (*F. pusilla*, 1993 [experiment 2] and *P. thomsoni*, 1993), or mature native birch from a rural birch stand southwest of Edmonton (*P. thomsoni*, 1994). Leaves were severed from branches, their petioles were wrapped in wet cotton to maintain turgor, and leaves were placed individually in vented 25.0 mL plastic vials in the laboratory at room temperature. I assessed survivorship of larvae to the final non-feeding instar, and weighed all final instar larvae. In addition, final instar larvae were reared individually to adults in 25.0 mL plastic vials containing soil (see also Chapter 3), and adults were weighed to assess fitness consequences of larval competition that might be evident in the adult stage. In 1994 experiments, the percent leaf area damage on the five or six leaves nearest to each study leaf was also recorded to test the hypothesis that short-term, localized induced responses of the host plant affect intraspecific competition.

The 1993 data for both *F. pusilla* and *P. thomsoni* were analyzed using simple linear regression, with the leaf area used per larva serving as a composite measure of larval density and resource consumption. Outliers were rejected from the analysis if they exceeded suggested cut-offs for Cook's D or leverage (*h*) statistics, because such points exert disproportionate influence on the regression if included (SAS Institute 1988). In 1994, leaves were selected from several larval density classes to permit comparison using a randomized complete block ANOVA model (SAS Institute 1988). Larval density classes for 1994 laboratory experiments involving *F. pusilla* were 1-4, 5-6, 7-8, and 9-10 larvae per leaf. Non-normality in the data was corrected using an appropriate transformation (Zar 1984), Blom's normal rank scores (SAS Institute 1988), or, as a last resort, ranks. Multiple regression analyses were also performed on the 1994 *F. pusilla* data, including both the leaf area used per larva and damage to nearby leaves as regressors. The best equation was chosen using the backward elimination selection procedure, with a rejection criterion of p>0.10 (SAS Institute 1988). Unfortunately, mortality of larval *P. thomsoni* was too high in 1994 laboratory experiments to permit analysis. This excess mortality seemed to have resulted from sharp declines in leaf quality following removal of leaves from branches.

To reduce leaf deterioration, field experiments evaluating intraspecific competition were conducted on trees on the University of Alberta campus, Edmonton (*F. pusilla*), and on trees in a birch stand southwest of Edmonton (*P. thomsoni*) in 1994. Individual leaves containing either *F. pusilla* or *P. thomsoni* were isolated on trees using small mesh bags, and survivorship and dry weights of final instar larvae were recorded. Emerged final instar larvae were not reared to adults, because they desiccated too quickly in the field to permit live recovery. For each leaf, damage to the nearest five or six leaves on the branch was also recorded at the end of the experiment. The data were analyzed using a randomized complete block ANOVA with density classes of 1-4, 5-6, 7, 8, 9, and 10 larvae per leaf for *F. pusilla* and 2, 4, 6, 8, and 10 larvae per leaf for *P. thomsoni*. In addition, further analyses were performed using multiple regression models identical to those used in analyses of the 1994 laboratory experiment involving *F. pusilla*.

4.3.2 Interspecific competition between *P. thomsoni* and *B. canadensisella*. A survey of 55 sites in central and northern Alberta was conducted during 1992-1994 to assess the distribution and abundance of *B. canadensisella* and its potential to compete with birch leafminers (see Figure 2-1 for a map of the survey region and Chapter 2 for additional details of the survey). Damage attributable to *B. canadensisella* was recorded, and the effects of this damage on the distribution of birch leafminers were noted.

Effects of *B. canadensisella* on *P. thomsoni*, at the scale of whole branches, were examined near Fox Creek, Alberta, where *B. canadensisella* had been abundant for several years (Cerezke and Brandt 1993; Brandt 1994). Three branches were selected at bud-burst on each of six trees. Two branches per tree were enclosed in fine mesh bags, but the third was left exposed to permit oviposition by *B. canadensisella*, after which it too was enclosed in a fine mesh bag. Subsequently, females of *P. thomsoni* (collected near Edmonton) were introduced into the bags covering each branch and allowed to oviposit. One female was introduced for every 10 leaves on each branch. After completion of oviposition, one initially-enclosed branch was left enclosed within its fine mesh bag, to permit development of larval *P. thomsoni* in the absence of *B. canadensisella* and natural enemies. The other two branches (one initially-enclosed, one initially-exposed) were placed within bags having a fine mesh underside (to permit recovery of final instar *P. thomsoni* larvae) and a coarse mesh topside (holes roughly 2.0 cm in diameter, to permit immigration and emigration of *B. canadensisella* larvae). Thus, the second initially-enclosed branch was subjected to the effects of immigrant *B. canadensisella* only, whereas the initially-exposed branch was affected by both immigrant and local *B. canadensisella* larvae. The fitness of *P. thomsoni* progeny (measured as dry weight of final instar larvae, and survivorship to the final larval instar) was assessed for each branch. Larval mortality directly attributable to *B. canadensisella* feeding was also recorded.

A second experiment examined effects of *B. canadensisella* feeding on *P. thomsoni* at the scale of individual leaves on three trees in a birch stand southwest of Edmonton in 1994. Different densities of *B. canadensisella* larvae (0, 2, and 4 larvae per leaf) were introduced into fine mesh bags enclosing individual leaves having different densities of similar-instar *P. thomsoni* larvae (2, 4, or 6 larvae per leaf), constituting a 3x3 randomized complete block design using trees as blocks. Survivorship of *P.*

thomsoni larvae was evaluated on each leaf, but not enough larvae were recovered to assess treatment effects on larval dry weight. Data were analyzed using a randomized complete block ANOVA model, and also using multiple regression with two regressors: the leaf area used per *P. thomsoni* larva, and the leaf area skeletonized per *P. thomsoni* larva. The best equation was chosen using backward elimination with a rejection criterion of p>0.10 (SAS Institute 1988).

4.3.3 Indirect interspecific competition between *F. pusilla* and *P. thomsoni*. To examine the effects of *F. pusilla* mining on later leaf quality for *P. thomsoni*, five branches were selected on each of four trees in urban settings in Edmonton in 1994. Four branches on each tree were enclosed with fine mesh bags before bud-burst, and one was left exposed to allow oviposition by *F. pusilla*. Following oviposition, exposed branches were also enclosed in fine mesh bags, and the *F. pusilla* larvae were allowed to develop. Of the four originally enclosed branches, one was left untreated as a control, and the other three were subjected to artificial leaf damage treatments wherein 10, 50, or 90% of their leaves had one lateral half of their area finely punctured by pressing the bristle ends of a wire brush repeatedly into the leaf. This caused gradual drying and browning of the damaged area. All bags were removed from branches in late June to permit oviposition by *P. thomsoni*. After oviposition, fine mesh bags were replaced over all branches to protect *P. thomsoni* larvae from natural enemies and to allow their recovery for weighing. The number of eggs laid, survivorship of eggs and larvae, dry weights of final instar larvae, and the leaf area used per final instar larva were compared among treatments using a randomized complete block ANOVA model (with trees as blocks). Preplanned orthogonal contrasts (SAS Institute 1988) were used to compare the number eggs laid and larval survivorship among treatment levels: no damage versus any type of damage; *F. pusilla* damage versus artificial damage; 10% artificial damage versus higher levels of artificial damage; and 50% artificial damage versus 90% artificial damage. Unbalanced ANOVA models resulted from analyses of dry weights and the leaf area used per larva, which precluded orthogonal treatment comparisons of these variables.

Additional analyses were performed to test the hypotheses that larval survival and the leaf area used per larva differed between artificially damaged and undamaged leaves. Only the three branches bearing artificial damage were included in these analyses, and these branches were pooled for each tree in the ANOVA model such that only variation among trees and within the damaged vs. undamaged comparison was partitioned and tested.

4.3.4 Effects of host quality on *P. thomsoni*. Oviposition site selection was examined in *P. thomsoni* to explore the fitness consequences of intraspecific competition for adult leafminers, and to assess variation in host quality among leaves on a branch. Twelve branches on one native birch at the Northern Forestry Centre in Edmonton were enclosed inside fine mesh bags at bud burst in 1993. Female *P. thomsoni* were captured using emergence traps set southwest of Edmonton; these females had not oviposited prior to use in experiments. Five females were released sequentially onto nine of the branches, but the remaining three branches received only four females because *P. thomsoni* adults became rare later in the season. Each female was allowed to oviposit until death before the release of the next female, so that only one female was ovipositing on each branch at any given time (first females started 5 July, last female died 5 August; mean oviposition period length per female ± SE: 3.3 ± 0.2 days). The fate of all offspring was recorded weekly until all had died or successfully emerged from their leaves.

The parentage of all eggs was determined by examining all leaves after each female had oviposited, and recording the exact placement of all eggs. Eggs occupying the same leaf were mapped using a leaf grid system. Each leaf was divided into right and left halves, and each half was subdivided into sectors delimited by major veins (5 to 9 sectors per half). It was possible to retain the parentage of all larvae as well, even on crowded leaves when mines merged, since larvae resulting from different females differed in age.

I examined oviposition by *P. thomsoni* relative to the oviposition choices of previous females by comparing the percent of eggs laid by females (other than the first one) on leaves bearing eggs from a previous female, using a randomized complete block ANOVA model with branches as blocks (SAS Institute 1988). In addition, I determined the percent of previously-unused leaves that were used as oviposition sites by each female (other than the first one), and then analyzed these percentages using a randomized complete block ANOVA model. This was done to determine whether the proportion of egg-free leaves selected for oviposition changed as the number of egg-free leaves decreased with each succeeding female. I examined the fitness consequences of oviposition decisions by analyzing the percent of eggs hatching and the percent of larvae surviving to the final instar for each of the five sequentially-introduced females.

To examine leaf size preferences of ovipositing *P. thomsoni*, leaves on each of the 12 branches were divided into 18 sequential area categories (<100, 100-199, ..., 1700-1799 mm^2) to create 12 empirical frequency distributions of leaf areas. The expected number of egg-bearing leaves per size class, assuming no size preference, was generated by multiplying the total number of egg-bearing leaves on a branch by the proportion of the total leaves occurring in each size class. The observed numbers of egg-bearing leaves in each size class on each branch were then compared with the expected numbers using a chi-square test (Zar 1984). To test whether females placed more eggs on larger leaves, all leaves having eggs were divided into the same 18 area categories described above, and the number of eggs per leaf was calculated in each area category for each of the 12 replicate branches. Data were analyzed using simple linear regression.

The overall distribution of eggs among leaves was examined by using chi-square analysis to compare the observed frequency of leaves having a given number of eggs to the expected frequency assuming a random (Poisson) distribution of eggs among leaves. All "eggs per leaf" categories with expected values below one were pooled in the analysis (Zar 1984).

The within-leaf selection of oviposition sites by *P. thomsoni* and its consequences were examined by comparing the number of eggs laid and larval survivorship in leaf sectors as defined by the major veins branching off the midrib (same as those used above to determine egg parentage). Sectors were numbered consecutively starting nearest the petiole.

Differences in host quality among trees, with respect to *P. thomsoni*, were investigated in an experiment to partition mortality in 1994 (Chapter 3). Oviposition choices were assessed on four branches on each of five trees at both Edmonton and George Lake (40 branches total). Groups of females were introduced onto each branch simultaneously (one female per 10 leaves), and I assessed their selection of leaves of different areas (divided into 24 area categories: <100, 100-199, ..., 2300-2399 mm^2), and whether the frequency of leaves having a given number of eggs conformed to Poisson expectation (identical analyses to those explained above). The effect of host quality on larval performance was examined on only two of the four branches on each of five trees at both locations (20 branches total). Both branches on each tree remained enclosed in fine mesh throughout the summer, which excluded natural enemies. Larval survivorship and weights of final instar larvae were measured, and were compared between locations and among trees using a repeated measures ANOVA model with larval instar as the repeated measure (SAS Institute 1988).

4.4 Results

4.4.1 Intraspecific competition. Competition for leaf resources affected weights of final instar larvae of *F. pusilla* in 1993 and 1994, but affected larval survivorship only in 1993 (Figures 4-1 and 4-2). In both field and laboratory experiments in 1994, weights of final instar *F. pusilla* varied considerably among trees (Table 4-1A), and decreased as larval density increased (Figures 4-2A and B; Table 4-1). Much variation in larval weight was explained by the leaf area used per larva in laboratory and field experiments in 1994, and in the first laboratory experiment in 1993, but not in the second laboratory experiment in 1993 (Figures 4-1A and B, and 4-2A and B; Table 4-1B). *Fenusa pusilla* survivorship increased as the leaf area used per larva increased in two laboratory experiments in 1993 (Figures 4-1C and D), but the leaf area used per larva generally explained less of the variation in survivorship than in weights in 1993 and 1994 (compare R^2 values, Table 4-1B). These relationships between leaf area used per larva and survivorship in *F. pusilla* in 1993 (Figures 4-1C and D) were probably due to an inordinate decrease in leaf quality under laboratory conditions, since the relationship was not evident in 1994 (Figures 4-2C and D) when steps were taken to lessen leaf deterioration. A small and statistically insignificant amount of variation in *F. pusilla* survivorship was explained by the damage to nearby leaves in the field experiment in 1994 (Table 4-1B).

These experiments suggest that weight is an important 'currency' of competition for *F. pusilla*. Thus, any fitness effects of larval competition should be evident in weight-fecundity or weight-survivorship relationships of adult *F. pusilla*. There was a positive linear relationship between wet weight of final instar larvae and that of adults for specimens reared in the laboratory (R^2=0.973, p<0.0001, N=15). Males were significantly smaller than females as adults (mean ± SE: males, 0.98 ± 0.09 mg; females, 1.37 ± 0.14 mg; two-tailed t-Test, p=0.033, df=22), but were only marginally smaller as larvae (males, 2.31 ± 0.16 mg; females, 2.84 ± 0.25 mg; two-tailed t-Test, p=0.103, df=22).

Some *F. pusilla* collected and reared from laboratory experiments in 1994 emerged as second generation adults later in 1994. These were larger as final instar larvae (2.68 ± 0.23 mg) than were those that have remained in the soil (2.15 ± 0.23 mg), but this difference is not statistically significant (two-tailed t-Test, p=0.119, df=26). At present, the fate of those remaining in the soil is unknown; either they are dead, or are alive and overwintering.

In contrast to results for *F. pusilla*, *P. thomsoni* showed statistically significant variation in larval survivorship among larval density treatments (Figure 4-3; Table 4-2). This suggests that survivorship is the more important 'currency' of competition for *P. thomsoni*. Since larval survivorship increased with the leaf area used per larva but body weight did not (Figure 4-3), adults of *P. thomsoni* are not expected to show weight-related fitness effects attributable to larval competition as seen in adults of *F. pusilla*.

4.4.2 Interspecific competition between *P. thomsoni* and *B. canadensisella*. Most sites surveyed across Alberta in 1992-1994 had little *B. canadensisella* damage, but the region around Fox Creek (approximately 300 km northwest of Edmonton; see map, Figure 2-1, Chapter 2) had severe *B. canadensisella* damage in both 1992 and 1993. In these years, birch leafminers were not detected in this region. However, in 1994, the *B. canadensisella* population at Fox Creek crashed, and small, natural populations of both *F. pusilla* and *P. thomsoni* were found at that time. This suggests that competitive exclusion of birch leafminers may occur during outbreaks of *B. canadensisella*.

Little variation occurred in dry weight of *P. thomsoni* on branches experiencing different exposure to *B. canadensisella* at Fox Creek, but survivorship varied significantly among treatments (Table 4-3A). Orthogonal contrasts revealed that most of the variation arose from the low *P. thomsoni* survivorship in the 'immigrant *B. canadensisella* only' treatment (mean larval survivorship ± SE: No *B. canadensisella*, 30.0 ± 8.6%; immigrant *B. canadensisella* only, 11.9 ± 8.6%; local + immigrant *B. canadensisella*, 39.6 ± 8.6%). However, this result is suspect, because of the low population levels of *B. canadensisella* at Fox Creek in 1994 discussed above. Few leaves had significant skeletonization damage, and very few deaths of *P. thomsoni* larvae were attributable to skeletonization effects. Regression analyses revealed that more variation in survivorship of *P. thomsoni* was explained by the density of *P. thomsoni* than by the mean percent of leaf skeletonization, although neither regressor was significant enough to be retained in the model (Table 4-3B).

The effect of *B. canadensisella* on *P. thomsoni* at the scale of individual leaves appeared negligible (Table 4-4A), but again this may have been due to inadequacies in the application of treatments. The scarcity of *B. canadensisella* larvae in 1994 precluded standardization of the instars of skeletonizers used in the experiment. Thus, some *B. canadensisella* larvae were older than others, and therefore fed less, resulting in unpredictable damage effects among *B. canadensisella* treatment levels. Regression analyses revealed that most of the variation in *P. thomsoni* survivorship was explained by *P. thomsoni* density (expressed as the leaf area used per *P. thomsoni* larva; Table 4-4B).

4.4.3 Indirect interspecific competition between *F. pusilla* and *P. thomsoni*. There were no significant differences in the number of *P. thomsoni* eggs laid per leaf, the mean dry weight of final instar larvae, or the amount of leaf area used per final instar larva on branches having different amounts of leaf damage (Table 4-5; for means, see Table 4-6A). Orthogonal contrasts revealed that the number of eggs laid per leaf was marginally lower on undamaged than damaged branches, and on branches having *F. pusilla* damage than on those having artificial damage (Tables 4-5 and 4-6A). There were significant differences in survivorship of larval *P.*

thomsoni to the final instar (Table 4-5), which was lower on branches having *F. pusilla* damage than on those having artificial damage, and was also lower on branches having 90% of their leaves artificially damaged than on those having 50% artificially damaged (see orthogonal contrasts in Table 4-5 and means in Table 4-6A).

At the scale of individual leaves, females of *P. thomsoni* laid fewer eggs on damaged leaves than expected in the three artificial damage treatments (chi-square analysis; see Table 4-6A). However, larval survivorship was similar on damaged and undamaged leaves (ANOVA: MS[leaf damage]=342.3, F=2.66, p=0.201, df=1,3; means in Table 4-6B), as was the leaf area used per larva (MS[leaf damage]=14339, F=2.28, p=0.228, df=1,3; means in Table 4-6B). One reason for the high survivorship may have been low overall larval densities. Most leaves (70.02 ± 3.33%, n=20 branches) had only one egg laid on them, and even more (84.02 ± 4.07%, n=19 branches) produced only one final instar larva of *P. thomsoni*.

4.4.4 Effects of host quality on *P. thomsoni*. The oviposition site selection experiment conducted in 1993 revealed that earlier-introduced *P. thomsoni* females behaved differently than later-introduced ones. Females introduced earlier tended to lay more eggs (Figure 4-4A), although the differences were not statistically significant (Table 4-7A). All females after the first were found to lay some eggs on leaves already having eggs from one or more previous females. However, the percent of eggs laid on previously-used leaves increased for each subsequent female, dramatically so for the fourth and fifth females introduced (Figure 4-5A; Table 4-7D). The scarcity of unused leaves is unlikely to explain this pattern because almost half of the available leaves remained unexploited after the last female had been allowed to oviposit (Figure 4-5B). Thus, females introduced later chose significantly fewer egg-free leaves as oviposition sites (Figure 4-5C; Table 4-7E). This suggests that later females began selecting leaves already bearing eggs from previous females, just the opposite of expectation, given that fitness of *P. thomsoni* larvae is reduced under crowded conditions. Significantly fewer larvae survived to the final larval instar for later-occurring females (Figure 4-4C; Table 4-7C), even though similar percentages of eggs hatched for all females (Figure 4-4B; Table 4-7B).

Females of *P. thomsoni* did not discriminate among leaves of different sizes for oviposition in either 1993 or 1994 (Table 4-8A). Of those leaves chosen for oviposition, larger ones received more eggs than smaller ones (Figure 4-6), but there was much unexplained variation in this relationship (compare R^2 values, Table 4-8B). In addition, the overall pattern of oviposition was highly clumped among leaves (Table 4-8A).

The within-leaf distributions of *P. thomsoni* eggs were similar for all five sequentially-introduced females; most eggs were laid in the larger basal leaf sectors (Figure 4-7). Eggs appear to be distributed randomly among leaf sectors, since all distributions in Figure 4-7 roughly resemble the shape of half a birch leaf. In addition, larval survivorship did not vary according to the leaf sector a larva originated in as an egg (Figure 4-8; Table 4-9).

Variation in the percent of larvae dying was greater among trees than between locations for most instars of *P. thomsoni*, and for all instars combined (Table 4-10A). A similar trend is reflected in survivorship of larvae to the final instar (Table 4-10B). One reason for this variation may have been differential larval densities among trees. There was more variation among trees than among locations in both the number of eggs laid per leaf and the percent of leaf area mined, although the differences were not statistically significant (Table 4-11).

4.5 Discussion

4.5.1 Intraspecific competition and host effects. Competition has been suspected before in *F. pusilla* (Cheng and LeRoux 1965), and larval density was shown to have no effect on larval survival by Chichester (1994), similar to the results obtained here. Competition has also been previously suspected in *P. thomsoni* (Martin 1960), but this study is the first to confirm its effects experimentally. Both *F. pusilla* and *P. thomsoni* appear to compete primarily through exploitation, since no cannibalism or behavioural interference was observed, even though most larvae were in physical contact with others at some point during development. Larval cannibalism has not been reported in any birch-leafmining sawfly species (Friend 1933; Martin 1960; Cheng and LeRoux 1965; Tuomi et al. 1981), although it has been observed in lepidopteran and dipteran leafminers (Condrashoff 1964; Quiring and McNeil 1984a; Auerbach and Simberloff 1989; Faeth 1990), and may be more common in leafminers than in free-feeding folivores (Faeth 1991). Significant leafminer mortality can occur when larger larvae interfere with the feeding of smaller larvae (Murai 1974), however larval size was controlled in my experiments. Undermining of eggs by feeding larvae can be a significant agent of egg mortality in *F. pusilla* and *P. thomsoni* (Martin 1960; Cheng and LeRoux 1965), especially if the oviposition period is long and there is less synchrony among instars. This source of mortality was not investigated in this study.

Intraspecific competition generally reduced larval, and hence adult, weight in *F. pusilla* (Figures 4-1 and 4-2), but reduced larval survival in *P. thomsoni* (Figure 4-3). One reason for this difference in the effect of competition may be that *F. pusilla* larvae are less likely to exit leaves prior to completion of development than are *P. thomsoni* larvae. Once leaves were totally mined, immature *F. pusilla* generally remained in the leaf, and some third and fourth instar larvae completed their development without feeding fully. This behaviour should result in high survivorship regardless of density, and lower weights of all survivors at high densities. In contrast, *P. thomsoni* larvae usually quickly dropped out of completely-mined leaves, regardless of instar. Indeed, any deterioration in leaf quality prompted immature *P. thomsoni* larvae to exit their leaf. Third or fourth instar larvae that emerge from leaves probably usually die on the soil surface, but some fifth instar larvae manage to molt to the non-feeding sixth instar on the ground, and burrow in successfully (personal observation). Thus, final instar larvae of *P. thomsoni* would be expected to have variable weights, but fewer of them would survive at higher densities per leaf.

These species-specific differences in the propensity to emerge from leaves before reaching the final larval instar may be related to differences in habitat quality and digestive efficiency. Mature birch leaves occupied by *P. thomsoni* are a poorer resource than the young long-shoot leaves used by *F. pusilla*, because mature leaves contain less nitrogen and more tannins, and are tougher (Haukioja et al. 1978; Haukioja and Niemelä 1979; Tuomi et al. 1981; DeClerck and Shorthouse 1985; Boomsma et al. 1987; Chichester 1994). The lower nutritional value of mature leaves may explain why *P.*

thomsoni requires more leaf area per larva to complete development (Chapter 2). In addition, *F. pusilla* has been found to digest leaf tissue more efficiently than *Messa nana* Klug (DeClerck and Shorthouse 1985), a birch-leafmining sawfly which feeds in mature short-shoot leaves, similar to those used by *P. thomsoni*. If a similar difference in feeding efficiency exists between larvae of *F. pusilla* and *P. thomsoni*, then competition is likely to occur at lower larval densities in *P. thomsoni* than in *F. pusilla*, and birch leafminers feeding on mature foliage may be more susceptible to changes in leaf quality than those feeding in young, long-shoot leaves.

The different impacts of intraspecific competition on *F. pusilla* and *P. thomsoni* suggest that the evolutionary consequences of competition differ between these species. In *P. thomsoni*, competition resulted in lower survival of larvae to the final instar (Figure 4-3), which should result in strong selection for females that avoid crowded leaves as oviposition sites. However, in *F. pusilla*, competition may directly affect adult lifetime reproductive success through its effects on adult weights (Figures 4-1 and 4-2). In many insects, heavier females live longer and/or lay more or larger eggs (Derr et al. 1981; Solbreck et al. 1989; Marshall 1990; McLain 1991; Honek 1993), but this is not always the case (Slansky 1980; Boggs 1986; Leather 1988; Larsson 1989; Johnson 1990; Klingenberg and Spence 1995). For the dipteran leafminer *Agromyza frontella* (Rondani) in alfalfa, larger females laid more eggs and lived longer than smaller females (Quiring and McNeil 1984c). Similar size-fitness relationships could be investigated in females of *F. pusilla*, but elucidation of size-fitness relationships for males will be more difficult. *Fenusa pusilla* adults mate promiscuously, and facultative parthenogenesis occurs in females (Friend 1933), making it very difficult to assess males' genetic contribution to offspring. Since males are carried around by females during mating (Friend 1933; Cheng and LeRoux 1965), smaller males may be preferred by females, and therefore may have improved mating success. In addition, smaller males are sometimes better dispersers, which can increase the number of females mated and improve fitness (Ghiselin 1974).

Because larval *P. thomsoni* survivorship decreased with increased larval density (Figure 4-3), it is expected that there is strong selective pressure on females to develop behaviours that permit the detection of other females' eggs, and thereby allow females to avoid crowded leaves as oviposition sites. However, *P. thomsoni* did not avoid leaves bearing eggs from previous females, even though unexploited leaves were available (Figure 4-5). In addition, females tended to clump their eggs among leaves, and they discriminated only weakly among leaves of different sizes (Figure 4-6; Table 4-8). Thus, *P. thomsoni* females did not appear to behave "optimally" when selecting leaves on a branch for oviposition, unlike other leafminers (Godfray 1986; Auerbach and Simberloff 1989; Faeth 1991). However, it may be that *P. thomsoni* oviposits optimally on a spatial scale not investigated, since optimal behaviours operating on one spatial scale may be undetectable on others (Thompson 1988; Koricheva and Haukioja 1994). Females of *F. pusilla* have been found to avoid birch trees on which larvae do poorly (Fiori and Dolan 1984; Braker 1986; Fiori and Craig 1987). Thus, *P. thomsoni* may be ovipositing optimally among trees or groups of trees, rather than within trees.

Alternatively, females of *P. thomsoni* may have aggregated their eggs because they responded to inherent variation in leaf quality along a branch that was greater than that produced by crowding effects. This may explain why oviposition strategies used by other leafminers to avoid intraspecific competition do not seem to apply to *P. thomsoni*. Eggs of the lepidopteran leafminer *Lithocolletis quercus* Ams. on oak are aggregated among leaves, but oviposition patterns within leaves mitigate the negative effects of among-leaf clumping (Auerbach and Simberloff 1989). This is unlikely to explain egg clumping in *P. thomsoni*, since the within-leaf distribution of eggs appears random (i.e. the percent of eggs laid per leaf sector seems proportional to the leaf area contained in that sector; see Figure 4-7). *Agromyza frontella* uses oviposition-deterring pheromones to minimize larval competition (Quiring and McNeil 1984b). *Profenusa thomsoni*, on the other hand, actually seem to select previously-used leaves for oviposition (Figure 4-5). *Stigmella* spp. leafminers on birch (Boomsma et al. 1987), and several taxa of leafminers on oak (Bultman and Faeth 1985), have clumped intraspecific distributions among leaves, compete intraspecifically, and may select leaves based on inherent quality rather than the presence of conspecifics. *Profenusa thomsoni* females seemed to aggregate their eggs among leaves similarly to *Stigmella* spp. (Boomsma et al. 1987), which suggests that later-introduced females of *P. thomsoni* oviposited on previously-used leaves because all remaining unexploited leaves were less satisfactory larval habitats. Suomela and Ayres (1994) found significant variation in water content, specific weight, and toughness among short-shoot leaves from the same shoots and branches on *Betula pubescens* Ehrhart ssp. *tortuosa* (Ledebour) Nyman, although variation among shoots and branches was less than that among trees and ramets. These patterns of host quality affected success of free-feeding larvae on birch (Hanhimäki et al. 1994; Suomela and Nilson 1994). Similar variation in host quality may affect oviposition decisions of *P. thomsoni*, and may override the threat of intraspecific competition posed by the presence of conspecific eggs.

It is possible that the observed oviposition patterns were an artifact of the mesh bags pressing against some leaves, making them difficult to oviposit on. In addition, some leaves may have been more exposed to wind than others on the same branch, and therefore received fewer eggs, since *P. thomsoni* oviposition appears most frequent when winds are light (Martin 1960; personal observation). However, I believe that the experiment reveals a true effect because similar aggregated among-leaf distributions of eggs have been observed on non-experimental birches during 1992-1994 and in other studies (Martin 1960; Drouin and Wong 1984).

4.5.2 Interspecific competition and host effects. Challenges are currently being raised to previous syntheses (e.g., Strong et al. 1984) which suggested that competition has a minor or non-existent role in structuring phytophagous insect communities. Denno et al. (1995) found that 76% of 193 pair-wise interactions surveyed demonstrated interspecific competition. Interspecific competition most commonly involved phytophagous insects that were exotic, closely related, and occupied concealed habitats. It was often asymmetric, and was mediated more often by the host plant than by natural enemies, physical factors or intraspecific competition. No interspecific competition was found to occur between leafminer species (five interactions surveyed), however all eight interactions involving a free-living phytophage and a leafminer were competitive (Denno et al. 1995). Thus, competition was expected between *P. thomsoni* and the abundant, free-living phytophage, *B. canadensisella*. Unfortunately, experimental data were insufficient to assess this interaction, because *B. canadensisella* population levels were low in 1994. The experiments did show that population levels of one or both species must be high for competition to occur. The degree of phenological synchrony between these species may also affect competition, since delayed emergence of free-feeding stages of *B. canadensisella* would allow many *P. thomsoni* larvae to escape any competitive effects. Competition between these species is suspected based on the observations that *P. thomsoni* was present at the Fox Creek site in 1994, when *B. canadensisella* populations were low, but was absent in 1992 and 1993, when population levels of *B. canadensisella* were very high. Further experiments are required to determine the strength and effects of competition between *P. thomsoni* and *B. canadensisella*. These experiments should include higher densities and similar-instar larvae of *B. canadensisella*, and should assess competitive effects on both *P. thomsoni* and *B. canadensisella* to reveal the degree to which competition is asymmetrical.

Damage inflicted by *F. pusilla* and high levels of artificial damage were sufficient to reduce survivorship of larval *P. thomsoni* (Tables 4-5 and 4-6). In addition, *P. thomsoni* survivorship was equivalent on damaged and undamaged leaves, and was lowest in the *F. pusilla* treatment (Table 4-6), which had negligible leaf area reduction due to *F. pusilla* mining. This suggests that *P. thomsoni* was affected by an induced response of the plant, and was not simply limited by the reduced leaf area available on branches bearing early-season damage. This is consistent with the findings of Denno et al. (1995) that host plants often mediate interspecific competition, and with those of Boomsma et al. (1987) that such competition is possible among low-density populations of leafminers on birch. Feeding damage in previous years, or earlier in the same year, has been found to decrease quality of mountain birch (*B. pubescens* ssp. *tortuosa*) foliage for late-feeding [illegible]fly species (Neuvonen et al. 1988; Hanhimäki 1989; Niemelä and T[illegible]. Some late-season herbivores on birch elude the effects of induc[illegible]s by simply increasing consumption of the inferior leaf tissue (F[illegible]acGarvin 1986). *Profenusa thomsoni* did not appear to respond i[illegible]way, since the leaf area used per surviving larva did not differ among treatments (Tables 4-5 and 4-6A).

In some leafminer systems (Faeth 1985), but not all (Bergelson and Lawton 1988; Hawkins 1988), leaf damage can decrease leafminer survivorship by attracting natural enemies. Natural enemies were excluded in my experiments, but it is possible that generalist arthropodan predators and the parasitoid *Lathrolestes luteolator* (Gravenhorst) (Chapter 3) respond to leaf damage to locate leafminer prey. Such responses by effective natural enemies have the potential to amplify the effects of all competitive interactions investigated in this study.

It was surprising that females of *P. thomsoni* laid similar numbers of eggs on branches subjected to different levels of natural and artificial damage (Tables 4-5 and 4-6A). However, they did prefer undamaged leaves for oviposition (Table 4-6A), suggesting that they perceive host quality differences among individual leaves but not among branches. This may explain the observed among-leaf aggregation of *P. thomsoni* eggs in both 1993 and 1994 (Table 4-8A). However, this oviposition pattern gives rise to a paradox, since it is the opposite of the pattern observed in larval survivorship. Survival was similar on damaged and undamaged leaves, but was reduced on branches bearing leaves damaged artificially or by *F. pusilla* mining (Table 4-6). Additional complexities in patterns of larval success arise at larger spatial scales; larval survivorship varied more among trees than among locations (Table 4-10). Together, these results reveal a hierarchical array of effects on larval fitness to which ovipositing *P. thomsoni* could be responding. The inconsistencies between patterns of oviposition site selection and larval survivorship in *P. thomsoni* may be resolvable by determining how female preference is genetically related to larval performance (Thompson 1988). It may be that Nearctic birches are still evolutionary "new" habitats for *P. thomsoni*, and that oviposition behaviours evolved to maximize larval survival on Palearctic birches are not optimal on Nearctic birches.

This study shows that birch leafminers participate in intraspecific and interspecific competitive interactions, and respond to variation in leaf quality at several spatial scales. These interactions have probably contributed to the unique Nearctic population dynamics of these sawflies, and may also have a prominent role in the "new" Nearctic community of birch-feeding insects, of which birch leafminers are a major component.

Table 4-1. Variation in weights and survival of final instar larvae of *F. pusilla* on leaves with different larval densities from intraspecific competition experiments in 1993 and 1994. A, analyses of variance for experiments in 1994; B, regression analyses for experiments in 1993 and 1994 (leafminer density expressed as "area used / larva"). All analyses used untransformed data, except Blom's normal rank scores (SAS Institute 1988) were used for "Field 1994, dry weight." Partial R^2 values are shown for each regressor in the multiple regressions.

A.

Experiment, variable	Source	df	MS	F	p
Field 1994, dry weight	Tree	3,14	11.42	9.32	0.001
	Larval Density	5,14	4.39	3.59	0.027
	Tree x Larval Density	14	1.23		
Field 1994, survivorship	Tree	3,14	370.52	0.90	0.467
	Larval Density	5,14	278.86	0.68	0.649
	Tree x Larval Density	14	412.74		
Lab 1994, wet weight	Tree	3,9	10.25	15.76	0.001
	Larval Density	3,9	3.03	4.67	0.031
	Tree x Larval Density	9	0.65		
Lab 1994, survivorship	Tree	3,9	98.43	0.24	0.865
	Larval Density	3,9	34.51	0.08	0.967
	Tree x Larval Density	9	407.95		

Table 4-1. Continued

B.

Experiment, variable	Equation	Source	df	R^2	F	p
Field 1994, dry weight	$y = 0.004 (x1) + 0.281$	x1 = Area used / larva	1,21	0.669	42.44	0.0001
		x2 = Nearby leaf damage	1,21	0.015	0.96	0.339
Field 1994, survivorship	$y = 0.776 (x2) + 66.791$	x1 = Area used / larva	1,21	0.027	1.65	0.430
		x2 = Nearby leaf damage	1,21	0.157	3.92	0.061
Lab 1994, wet weight	$y = 0.017 (x1) + 0.961$	x1 = Area used / larva	1,14	0.547	16.89	0.001
		x2 = Nearby leaf damage	1,14	0.000	0.00	0.978
Lab 1994, survivorship	none	x1 = Area used / larva	1,14	0.003	0.04	0.854
		x2 = Nearby leaf damage	1,14	0.000	0.00	0.983
Lab 1993, wet weight 1	$y = 0.014 (x) + 1.235$	x = Area used / larva	1,31	0.659	59.83	0.0001
Lab 1993, survivorship 1	$y = 0.107 (x) + 70.000$	x = Area used / larva	1,34	0.201	8.53	0.006
Lab 1993, wet weight 2	none	x = Area used / larva	1,19	0.025	0.48	0.496
Lab 1993, survivorship 2	$y = 0.507 (x) + 25.441$	x = Area used / larva	1,19	0.305	8.35	0.009

Table 4-2. Variation in weights and survival of final instar larvae of *P. thomsoni* on leaves with different larval densities from intraspecific competition experiments in 1993 and 1994. A, analyses of variance for experiments in 1994; B, regression analyses for experiments in 1993 and 1994 (leafminer density expressed as "area used / larva"). Survivorship values from 1994 were arcsine-transformed for analysis. Partial R^2 values are shown for each regressor in multiple regressions.

A.

Experiment, variable	Source	df	MS	F	p
Field 1994, dry weight	Tree	3,7	0.19	0.81	0.528
	Larval Density	4,7	0.38	1.60	0.276
	Tree x Larval Density	7	0.24		
Field 1994, survivorship	Tree	3,10	0.09	1.62	0.247
	Larval Density	4,10	0.47	8.72	0.003
	Tree x Larval Density	10	0.05		

B.

Experiment, variable	Equation	Source	df	R^2	F	p
Field 1994, dry weight	none	x1 = Area used / larva	1,13	0.085	1.20	0.293
		x2 = Nearby leaf damage	1,13	0.085	1.22	0.291
Field 1994, survivorship	y = 0.251 (x1) - 14.914	x1 = Area used / larva	1,16	0.631	27.35	0.0001
		x2 = Nearby leaf damage	1,16	0.026	1.14	0.302
Lab 1993, wet weight	none	Area used / larva	1,29	0.031	0.92	0.343
Lab 1993, survivorship	y = 0.189 (x1) + 0.204	Area used / larva	1,38	0.377	23.02	0.0001

Table 4-3. Variation in weights and survival of final instar larvae of *P. thomsoni* from interspecific competition experiments with *B. canadensisella* at Fox Creek, 1994. A, analyses of variance on Blom's normal rank scores (SAS Institute 1988) for dry weight, and on ranks for survivorship, showing orthogonal contrasts; B, regression analyses. Partial R² values are shown for each regressor in the multiple regression.

A.

Variable	Source	df	MS	F	p
mean dry weight	Tree	5,7	4.12	5.10	0.027
	Treatment	2,7	0.26	0.32	0.738
	Tree x Treatment	7	0.81		
survivorship	Tree	5,10	15.13	1.00	0.467
	Treatment	2,10	128.17	8.43	0.007
	Tree x Treatment	10	15.20		
	No *B. canadensisella* vs. rest	1,10	56.25	3.70	0.083
	Local + immigrant *B. canadensisella* vs. immigrant only	1,10	200.08	13.16	0.005

B.

Variable	Equation	Source	df	R²	F	p
mean dry weight	none	x = % leaf skeletonized	1,13	0.032	0.435	0.521
survivorship	none	x1 = % leaf skeletonized	1,15	0.035	0.619	0.444
		x2 = *P. thomsoni* per leaf	1,15	0.113	2.041	0.173

Table 4-4. Variation in survival of final instar larvae of *P. thomsoni* from interspecific competition experiments with *B. canadensisella* using individual leaves from trees southwest of Edmonton, 1994. A, analysis of variance; B, multiple regression. Partial R^2 values are shown for each regressor.

A.

Source	df	MS	F	p
Block	2	0.94	5.31	0.019
P. thomsoni density	2	0.41	2.29	0.138
B. canadensisella density	2	0.40	2.29	0.138
P. thomsoni density x *B. canadensisella* density	4	0.26	1.49	0.259
Error	14	0.18		

B.

Equation	Source	df	R^2	F	p
$y = 0.301 (x1) - 25.642$	x1 = Area used per *P. thomsoni*	1,23	0.624	38.23	0.0001
	x2 = Area skeletonized per *P. thomsoni*	1,23	0.019	1.15	0.295

Table 4-5. Analyses of variance evaluating differences in eggs laid per leaf, larval dry weights, leaf area used per larva, and survivorship to the final larval instar for *P. thomsoni* from experiments investigating indirect interspecific competition between *F. pusilla* and *P. thomsoni* in Edmonton, 1994. Orthogonal contrasts are presented for treatment levels of "eggs laid per leaf" and "larval survivorship". The number of eggs laid per leaf and larval dry weights were transformed using Blom's normal rank scores (SAS Institute 1988).

Variable	Source	df	MS	F	p
eggs laid per leaf	Tree	3,12	1.99	3.92	0.037
	Treatment	4,12	1.40	2.76	0.078
	Tree x Treatment	12	0.51		
	No damage vs. rest	1,12	2.27	4.47	0.056
	F. pusilla damage vs. artificial damage	1,12	2.63	5.19	0.042
	10% damage vs. high damage	1,12	0.58	1.15	0.305
	50% vs. 90% damage	1,12	0.12	0.23	0.638
mean dry weight	Tree	3,11	3.05	2.27	0.138
	Treatment	4,11	2.58	1.91	0.178
	Tree x Treatment	11	1.35		
mean area used per surviving larva	Tree	3,9	43335	2.54	0.122
	Treatment	4,9	8153	0.48	0.751
	Tree x Treatment	9	17039		
mean survivorship	Tree	3,12	708.9	3.91	0.037
	Treatment	4,12	633.1	3.49	0.041
	Tree x Treatment	12	181.2		
	No damage vs. rest	1,12	155.4	0.86	0.373
	F. pusilla damage vs. artificial damage	1,12	1095.4	6.05	0.030
	10% damage vs. high damage	1,12	285.0	1.57	0.234
	50% vs. 90% damage	1,12	996.8	5.50	0.037

Table 4-6. Variables measured in the experiment examining indirect interspecific competition between *F. pusilla* and *P. thomsoni* in Edmonton, 1994. A, means (±SE) for each damage treatment are presented for all variables except the number of eggs laid on artificially damaged leaves, for which chi-square statisitics are presented (corrected for continuity [Zar 1984]; four trees pooled for each treatment; α=0.05, df=1, critical value=3.84). B, means (±SE) for variables measured on artificially damaged leaves and on undamaged leaves, disregarding the treatment structure (calculated by excluding the "No damage" and "*F. pusilla*" damage treatments, and pooling the three artificial damage treatments on each tree).

A.

Variable	Damage Treatment				
	No damage	*F. pusilla*	10% artificial	50% artificial	90% artificial
eggs laid per leaf	0.149 (±0.058)	0.148 (±0.058)	0.389 (±0.058)	0.094 (±0.058)	0.250 (±0.058)
larval dry weight (mg)	1.91 (±0.09)	2.32 (±0.08)	2.07 (±0.05)	2.31 (±0.09)	2.16 (±0.14)
percent larval survivorship	37.9 (±6.7)	15.6 (±6.7)	42.4 (±6.7)	21.1 (±6.7)	16.4 (±6.7)
leaf area used per surviving larva (mm^2)	365.0 (±18.3)	367.6 (±35.6)	376.7 (±15.7)	350.5 (±28.5)	381.5 (±59.3)
chi-square for eggs laid on artificially-damaged leaves	-	-	23.01	12.87	11.22

B.

Variable	Artificially damaged leaves	Undamaged leaves
percent larval survivorship	30.4 (±3.8)	22.2 (±3.3)
leaf area used per surviving larva (mm^2)	340.0 (±22.2)	380.7 (±15.4)

Table 4-7. Analyses of variance evaluating oviposition decisions by *P. thomsoni* females released sequentially onto birch branches at the Northern Forestry Centre, 1993. A, number of eggs laid per female per branch; B, percent of eggs hatching successfully; C, Blom's normal rank scores (SAS Institute 1988) for percent of larvae surviving to the final instar; D, percent of eggs laid on leaves already having eggs from any previous female; E, percent of egg-free leaves that were oviposited on by a newly-introduced female.

A.

Source	df	MS	F	p
Branch	11	152.4	0.81	0.629
Female	4	395.6	2.10	0.098
Error	41	188.0		

B.

Source	df	MS	F	p
Branch	11	2239.4	3.88	0.001
Female	4	372.5	0.66	0.622
Error	41	562.7		

C.

Source	df	MS	F	p
Branch	11	1.42	2.70	0.012
Female	4	3.18	6.04	0.001
Error	41	0.53		

D.

Source	df	MS	F	p
Branch	11	655.3	1.29	0.279
Female	3	5433.5	10.67	0.0001
Error	30	509.1		

E.

Source	df	MS	F	p
Branch	11	81.9	0.28	0.966
Female	3	887.9	3.80	0.020
Error	30	233.9		

Table 4-8. Analyses of the distribution of eggs among leaves by ovipositing *P. thomsoni*. A, chi-square statistics on the number of leaves in different size categories bearing eggs of *P. thomsoni*, and the degree of egg clumping among leaves in 1993 (one tree, 12 branches as blocks) and 1994 (five trees per location as blocks, with four branches pooled per tree). B, linear regression analyses of the log number of eggs laid per egg-bearing leaf (y) against leaf size (x). Leaves were divided into 18 (1993) and 24 (1994) 100mm^2 categories for size analyses. Maximum numbers of eggs per leaf were 12 in 1993, 58 in 1994.

A.

Location	Block	Leaf size preferences			Egg clumping among leaves		
		Chi-square	df	p	Chi-square	df	p
NoFC, 1993	1	6.01	13	0.966	99.7	8	<0.0001
	2	7.27	12	0.888	46.7	7	<0.0001
	3	7.23	14	0.951	17.8	6	0.0068
	4	7.59	13	0.910	33.2	6	<0.0001
	5	3.60	12	0.995	20	6	0.0028
	6	6.03	10	0.871	19.6	6	0.0033
	7	10.3	9	0.411	13.8	6	0.0320
	8	4.83	11	0.964	26.4	6	0.0002
	9	2.38	12	0.999	31.3	6	<0.0001
	10	11.20	12	0.593	22.2	5	0.0005
	11	10.00	17	0.931	52.1	5	<0.0001
	12	9.54	12	0.731	33.7	6	<0.0001
Edmonton, 1994	1	29.41	19	0.060	3302.5	10	<0.0001
	2	12.92	16	0.678	861.4	8	<0.0001
	3	30.61	22	0.105	323.8	7	<0.0001
	4	11.78	20	0.923	2134.3	10	<0.0001
	5	13.54	13	0.407	440.2	6	<0.0001
George Lake, 1994	1	10.98	16	0.811	1116.6	9	<0.0001
	2	13.52	16	0.634	2456.5	10	<0.0001
	3	19.78	20	0.472	1320.6	9	<0.0001
	4	9.89	16	0.872	2774.6	11	<0.0001
	5	8.70	18	0.966	1211.7	10	<0.0001

B.

Location	Equation	df	R^2	F	p
NoFC, 1993	$y = 0.0001 (x) + 0.367$	1,122	0.133	18.52	0.0001
Edmonton, 1994	$y = 0.0002 (x) + 0.452$	1,266	0.151	47.43	0.0001
George Lake, 1994	$y = 0.0002 (x) + 0.542$	1,234	0.086	21.94	0.0001

Table 4-9. Analysis of variance evaluating the within-leaf variation in survivorship of larval offspring of sequentially-introduced *P. thomsoni* females at the Northern Forestry Centre, 1993.

Source	df	MS	F	p	Error Term
Branch	11	6450.2	7.76	0.0001	Error
Leaf Sector	5	1920.6	1.27	0.289	Branch x Leaf Sector
Branch x Leaf Sector	54	1509.4	1.82	0.004	Error
Female	4	1866.4	1.00	0.420	Branch x Female
Branch x Female	41	1871.2	2.25	0.0004	Error
Leaf Sector x Female	20	1016.5	1.22	0.249	Error
Error	113	830.7			

Table 4-10. Analyses of variance evaluating survivorship of larval *P. thomsoni* reared within fine mesh bags (predators excluded) on five trees at each of two locations (Edmonton and George Lake) in 1994. A, repeated measures ANOVA on 100q(x) values for different larval instars of *P. thomsoni*; B, ANOVA on percent of *P. thomsoni* surviving to the final larval instar.

A.

Effect	Source	df	MS	F	p
1st instar	Location	1,8	9.70	0.18	0.681
	Tree (Location)	8,10	53.22	1.94	0.162
2nd instar	Location	1,8	1.92	0.18	0.679
	Tree (Location)	8,10	10.36	2.66	0.075
3rd instar	Location	1,8	71.29	2.43	0.158
	Tree (Location)	8,10	29.33	60.54	0.0001
4th instar	Location	1,8	1258.17	3.58	0.095
	Tree (Location)	8,10	351.55	3.50	0.034
5th instar	Location	1,8	479.42	1.08	0.330
	Tree (Location)	8,10	445.92	3.91	0.024
Among instars	Location	1,8	82.32	0.39	0.548
	Tree (Location)	8,10	1672.45	11.35	0.0004
	Instar	4,40	3178.65	55.75	0.0001
	Instar x Location	4,32	434.54	2.55	0.058
	Instar x Tree (Loc)	32,40	170.33	2.99	0.001

B.

Source	df	MS	F	p
Location	1,8	0.172	2.96	0.124
Tree (Location)	8,10	0.058	10.36	0.001
Error	10	0.006		

Table 4-11. Analyses of variance evaluating the success of *P. thomsoni* reared within fine mesh bags (predators excluded) on five trees at each of two locations (Edmonton and George Lake) in 1994. A, number of eggs laid per leaf by females introduced onto branches; B, mean percent of leaf area mined by *P. thomsoni* larvae.

A.

Source	df	MS	F	p
Location	1,8	2.09	0.57	0.473
Tree (Location)	8,10	3.68	2.98	0.055
Error	10	1.23		

B.

Source	df	MS	F	p
Location	1,8	349.36	1.08	0.329
Tree (Location)	8,10	322.69	2.01	0.149
Error	10	160.62		

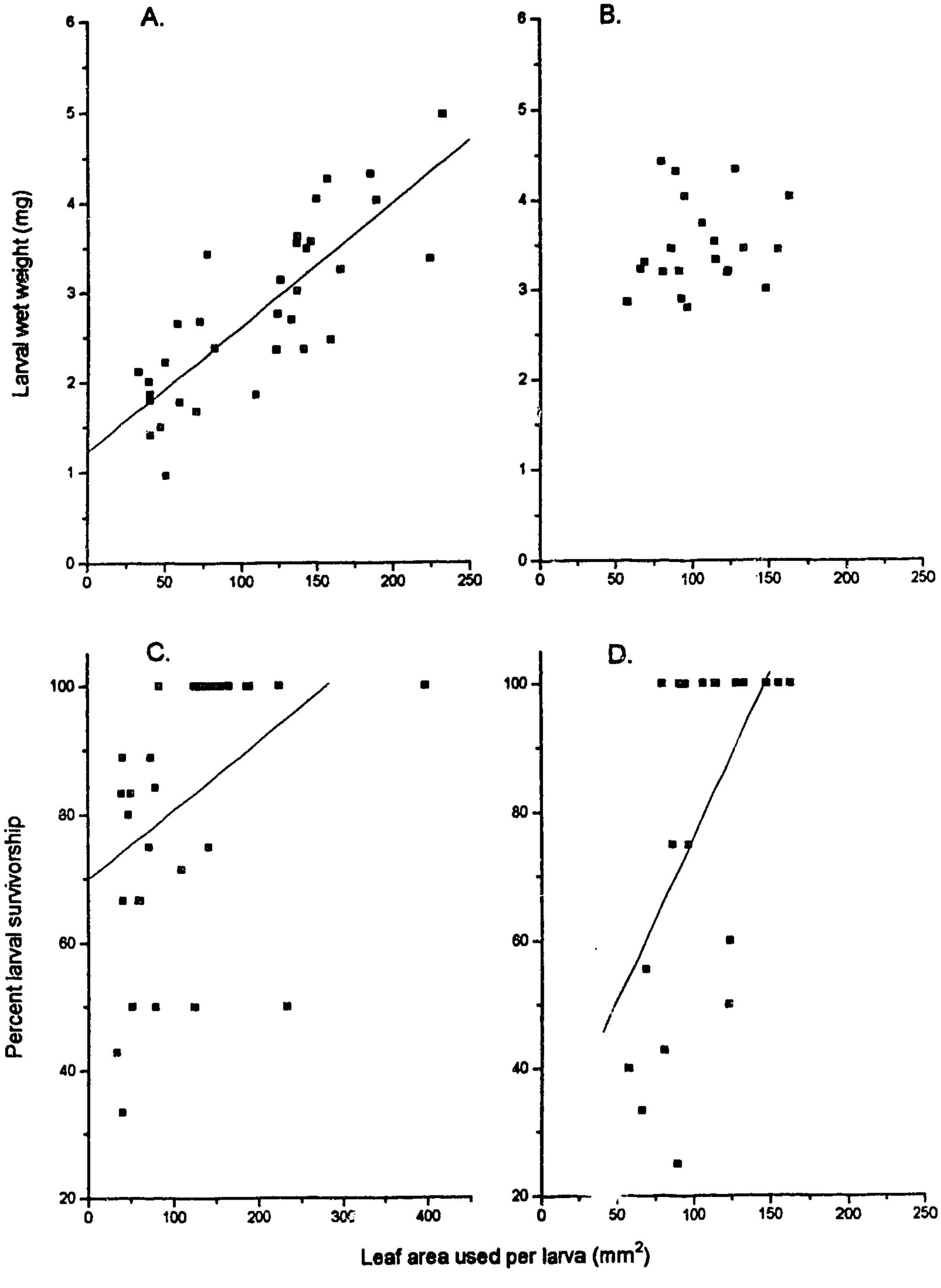

Figure 4-1. Relationships of weights and survival of larval *F. pusilla* with leaf area used per larva from two laboratory experiments, 1993. A, wet weight, experiment 1; B, wet weight, experiment 2; C, percent survivorship, experiment 1; D, percent survivorship, experiment 2. See Table 4-1B for regression statistics.

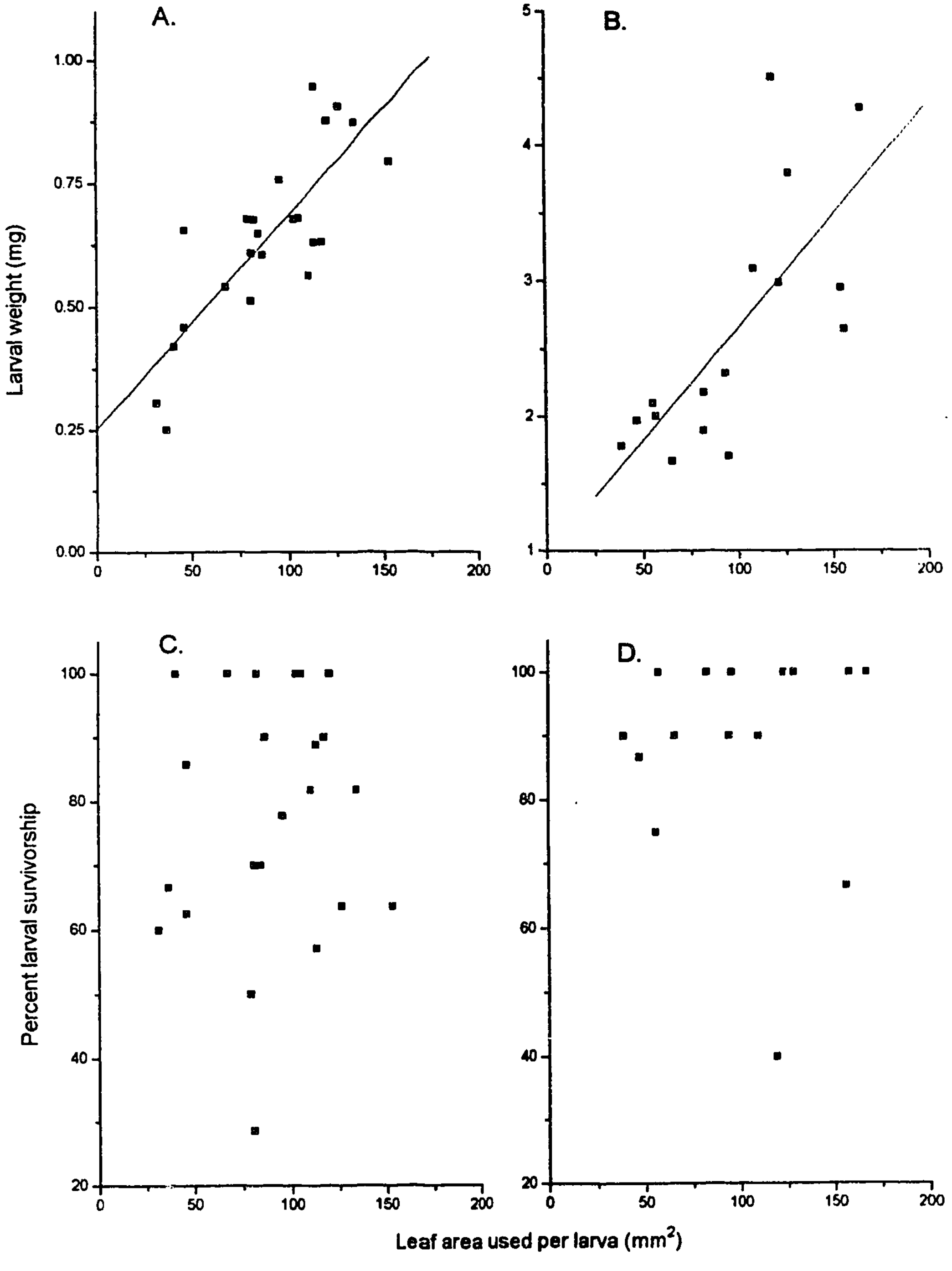

Figure 4-2. Relationships of weights and survival of larval *F. pusilla* with leaf area used per larva from a field and a laboratory experiment, 1994. A, dry weight, field; B, wet weight, laboratory; C, percent survivorship, field; D, percent survivorship, laboratory. See Table 4-1B for regression statistics.

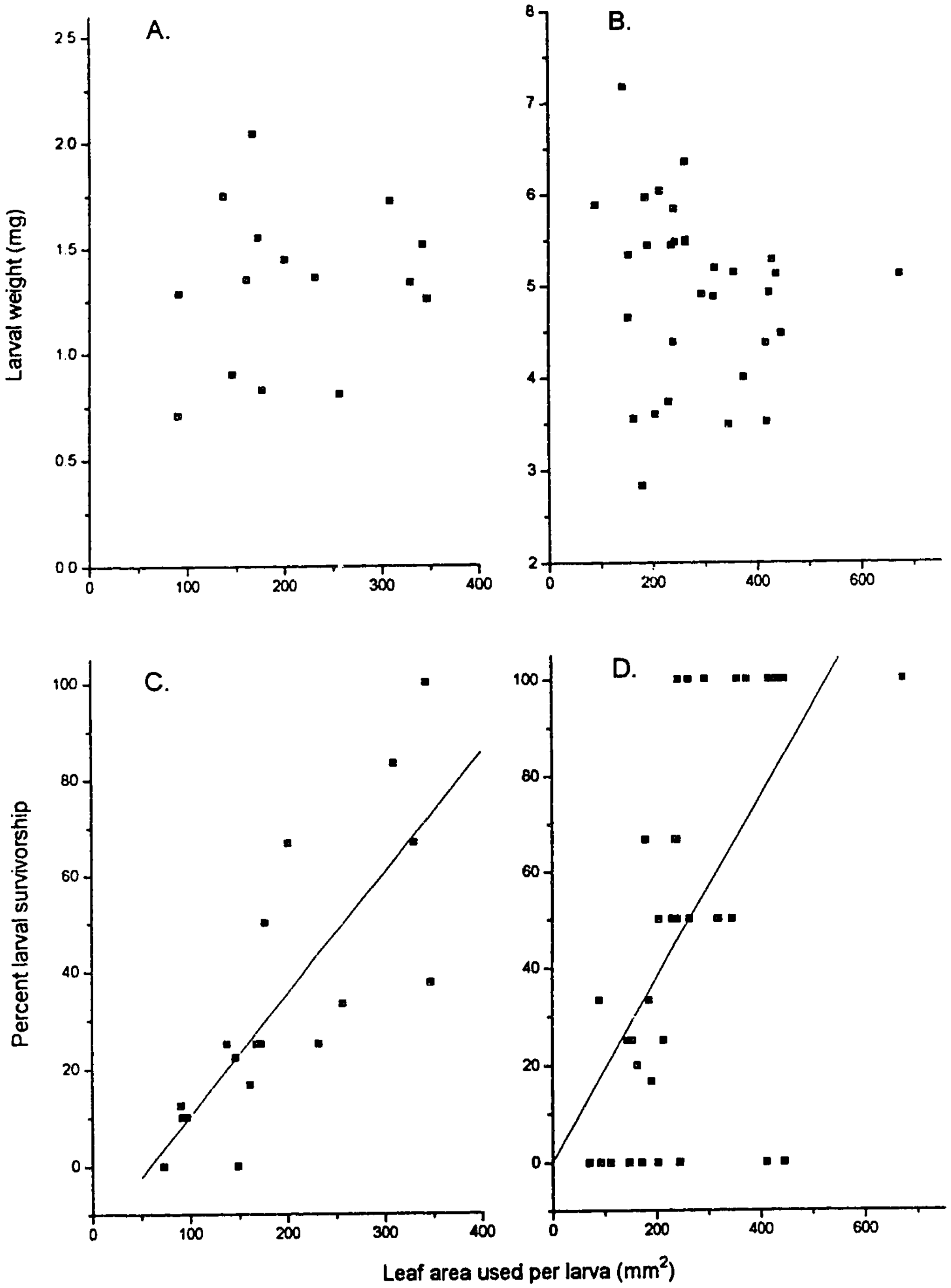

Figure 4-3. Relationships of weights and survival of larval *P. thomsoni* with leaf area used per larva from experiments in 1993 and 1994. A, dry weight, field, 1994; B, wet weight, laboratory, 1993; C, percent survivorship, field, 1994; D, percent survivorship, laboratory, 1993. See Table 4-2B for regression statistics.

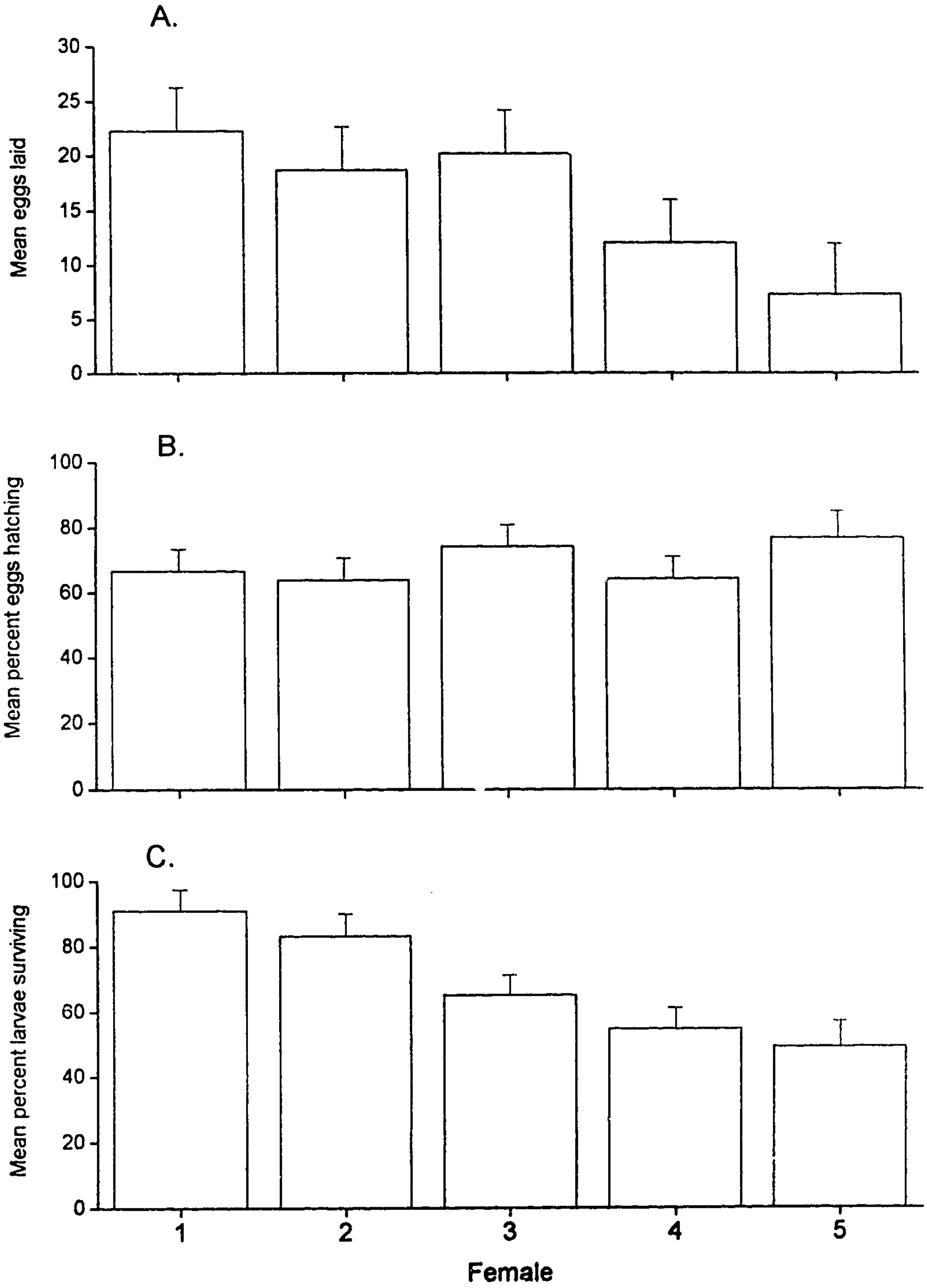

Figure 4-4. Mean differences in the numbers and success of offspring of five sets of *P. thomsoni* females sequentially-introduced onto birch branches in 1993. A, mean number of eggs laid per female; B, mean percent of eggs hatching; C, mean percent of larvae surviving to the final instar (n=12 for females 1-4; n=9 for female 5). Error bars = SE.

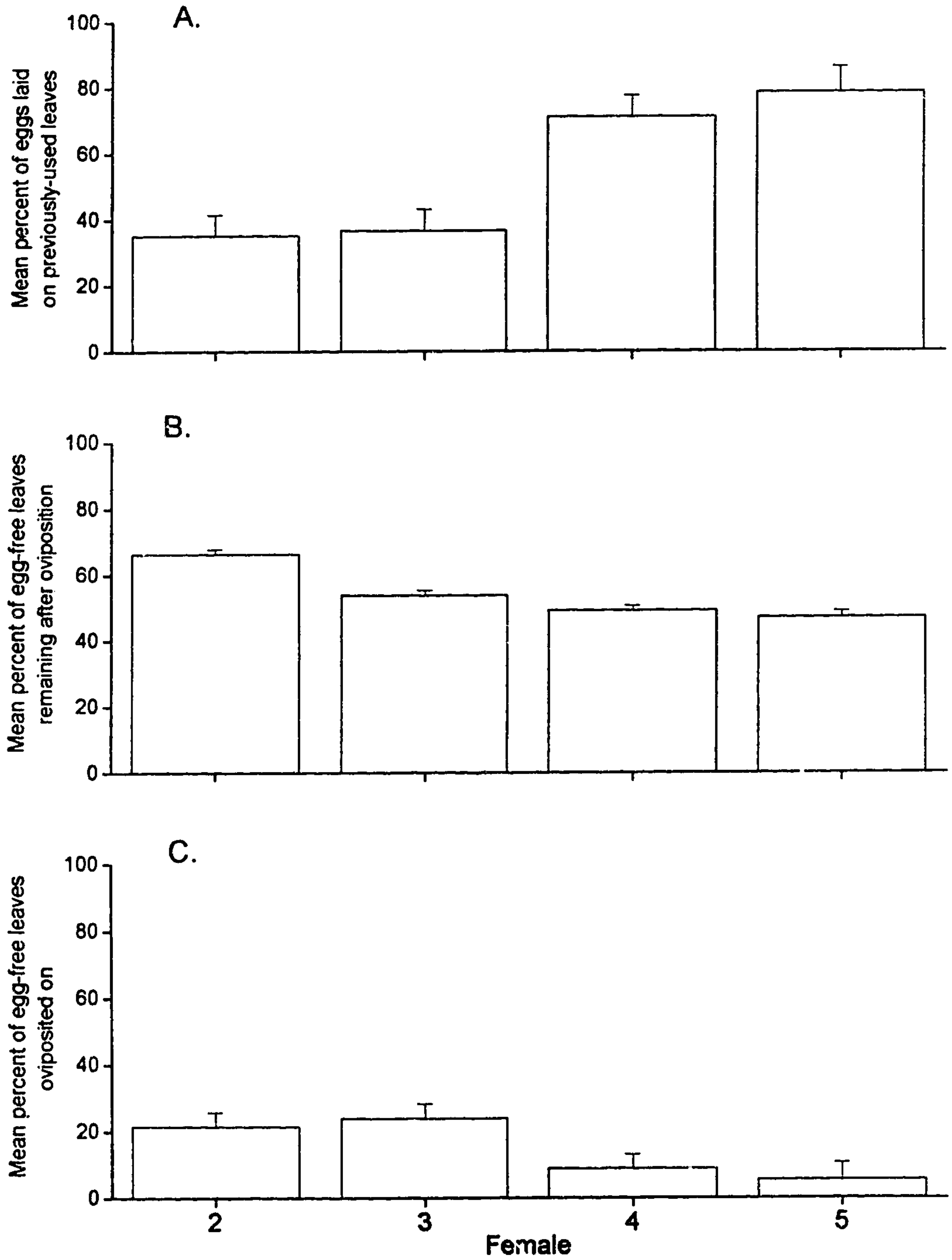

Figure 4-5. Variation in oviposition relative to eggs of other females for five sets of *P. thomsoni* females sequentially-introduced onto birch branches in 1993. A, mean eggs laid per female on leaves already bearing eggs from a previous female; B, mean percent of egg-free leaves left after the specified female has oviposited; C, mean percent egg-free leaves oviposited on (n=12 for females 1-4; n=9 for female 5). Error bars = SE.

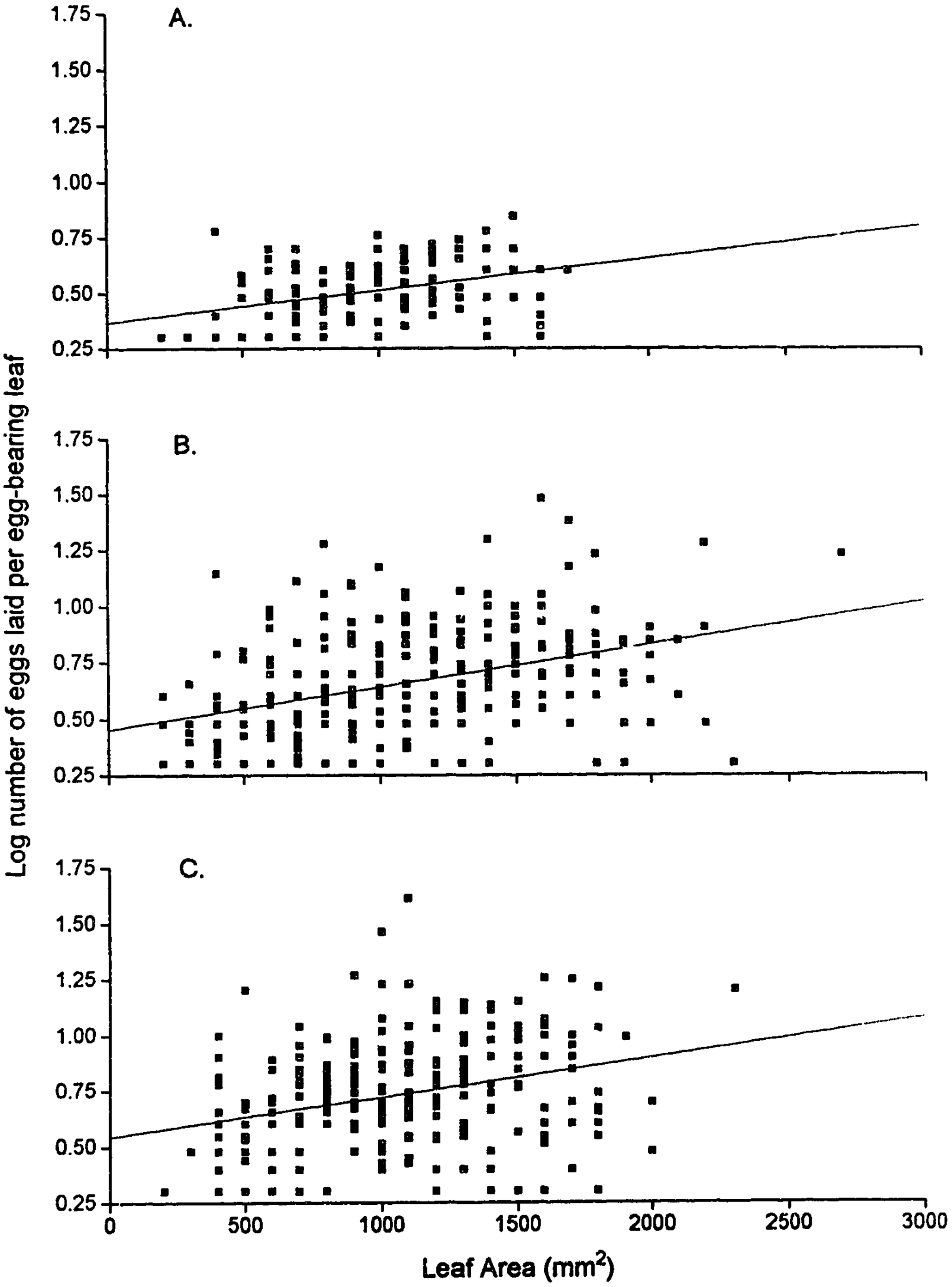

Figure 4-6. Numbers of eggs laid per leaf on leaves of different sizes. A, 12 branches on one tree at the Northern Forestry Centre, 1993; B, 4 branches on 5 trees in Edmonton, 1994; C, 4 branches on 5 trees at George Lake, 1994. See Table 4-8B for regression statistics.

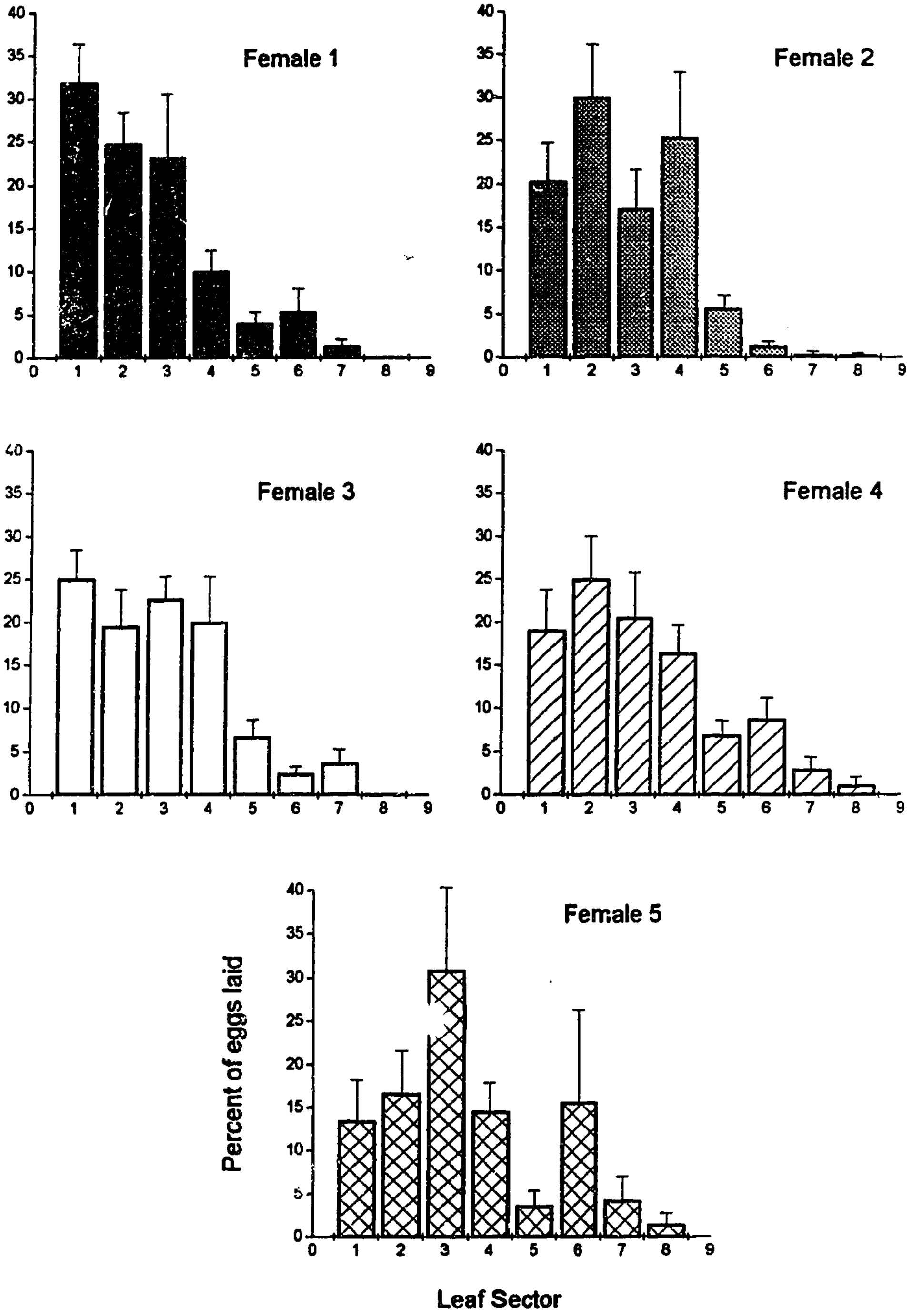

Figure 4-7. Mean percent of eggs laid by sequentially-introduced females of *P. thomsoni* in different sectors of birch leaves. Sectors delimited by major leaf veins; sector 1 is most proximal.

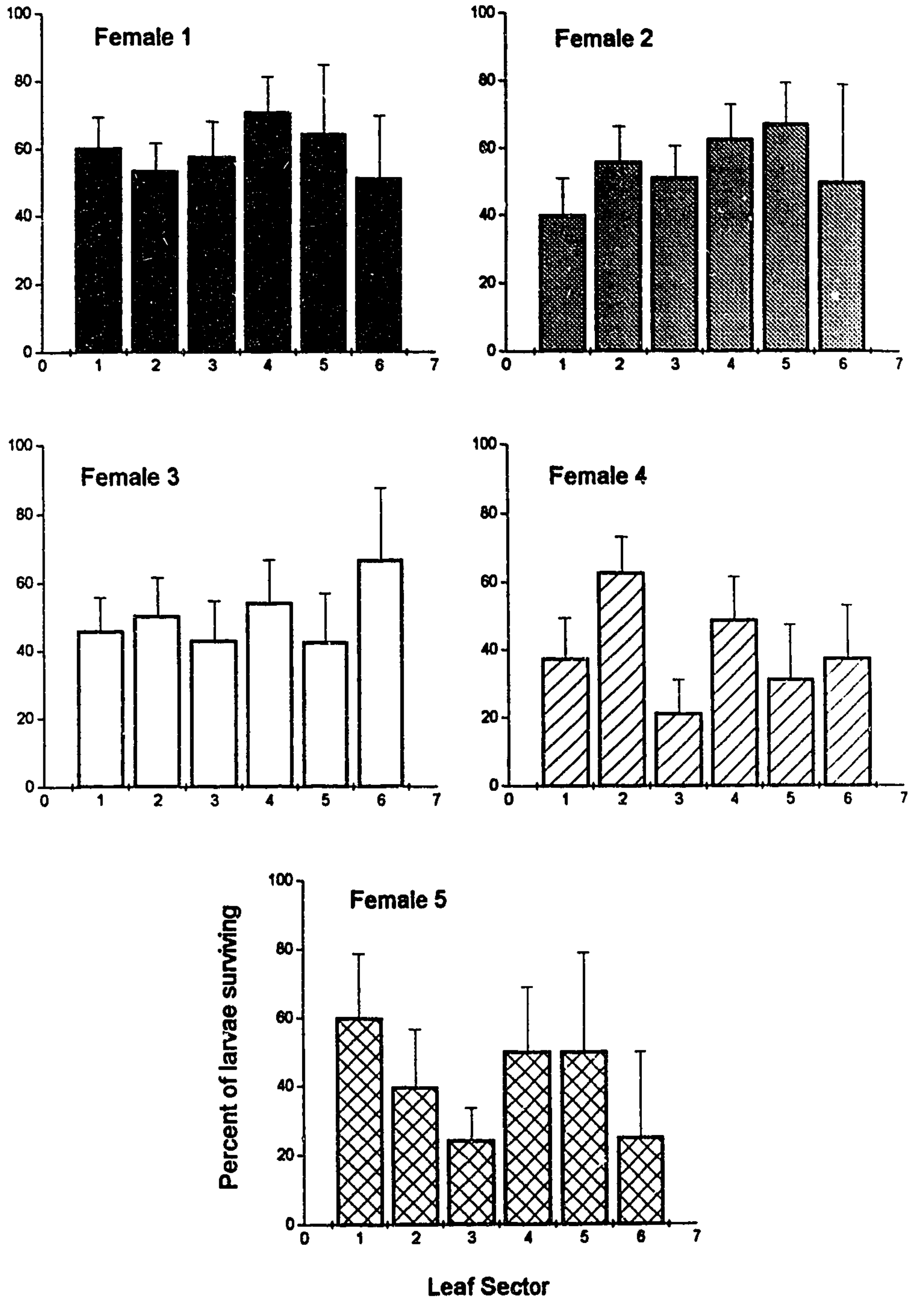

Figure 4-8. Mean percent survival of larvae originating as eggs in different sectors of birch leaves, laid by sequentially-introduced female *P. thomsoni*. Sectors delimited by major leaf veins; sector 1 is most proximal.

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5. Conclusion

5.1 Integration of introduced insects into native communities

Detailed studies of the biologies of introduced pest insects can establish the ecological characteristics and consequences of the pest's integration into the community of native organisms. These data can be used to address management objectives as well as general ecological hypotheses about the structure and evolution of communities. A fundamental biological approach avoids the problems of a "top-down" approach to pest management (see Chapter 1), and can contribute to the strong tradition of co-development that exists between applied and ecological perspectives on insect ecology. This thesis contributes to a birch leafminer management program for urban areas of Alberta, and also examines the population consequences for introduced birch leafminers of interactions within the Nearctic community on birch.

Birch leafminers are recognized as prey by many native natural enemies (Chapter 3). The consequences of this can be examined for management potential and population-regulating qualities. At present, many homeowners and municipalites attempt to control birch leafminers using systemic insecticides (e.g. Cygon 2e®). These control methods have been effective against both *Fenusa pusilla* (Lepeletier) and *Profenusa thomsoni* (Konow) (Shread 1966; Cheng and LeRoux 1968; Drouin and Wong 1984), but they can have serious phytotoxic effects (Drouin and Wong 1984), are likely to decrease in effectiveness as the target insects develop resistance (Mallet 1989), and have unknown long-term effects on the rest of the birch-inhabiting arthropod community. The diverse guilds of parasitoids and predators that have switched onto birch leafminer hosts are composed mostly of generalists (Chapter 3), as theory would predict (Cornell and Hawkins 1993). Arthropod predators may have significant regulatory effects on birch leafminer populations under certain conditions, but bird predators appear to have little impact on leaf-inhabiting stages (Chapter 3). In addition, the specialist parasitoid *Lathrolestes luteolator* (Gravenhorst) has switched onto *P. thomsoni*, and appears to be having an increasing regulatory effect on their population (Chapter 3). *Lathrolestes* species are often effective parasitoids of leafmining sawflies (Pschorn-Walcher and Altenhofer 1989), thus *L. luteolator* should be investigated as a potential natural control agent of *P. thomsoni.* Given the known negative impacts of chemical pesticides on natural enemies (LaSalle 1993), there is strong impetus to minimize the use of systemic insecticides against birch leafminers until precise estimates of the regulatory effects of individual mortality agents are made.

Insect ecologists have often been unsuccessful at analyzing population dynamics using life tables alone (Price 1987). The combined experimental and life table approach used in this study (Chapter 3) should avoid many of the problems traditional life table analyses suffer in detecting density dependence and regulatory effects (Price 1987). Users of traditional analyses are often forced to infer causation from correlative relationships between mortality agents and regulatory patterns in populations (Morris 1969; Price 1987), and cannot detect regulatory effects operating within generations (Hassell 1985, 1987). Detailed analyses and experimental removals of individual mortality agents can be used to reliably quantify these regulatory mechanisms (e.g., Preszler and Price 1988; Stein et al. 1994). With increased ability to partition birch leafminer mortality among specific causes, further use of a combined experimental and life table approach should reveal important population-regulatory processes affecting these insects.

Birch leafminer integration into the Nearctic birch community has probably been affected by their relationship with new host plant genotypes. Differential leafminer performance at several spatial scales (Chapter 4) suggests that birch trees vary in quality at similar scales. Understanding the mechanisms of this variation may provide useful management tools. The similarity of trees between Edmonton and George Lake for *P. thomsoni* larvae (Chapter 4) suggests that host quality is not responsible for the observed population size differences between these locations (Chapter 2). There were some differences in mortality of leaf-dwelling stages of *F. pusilla* between locations, but only minimal differences for *P. thomsoni* (Chapter 3). In addition, there were differences in the canopy-dwelling predator guild between the two locations (Chapter 3), and it was suspected that there may be differences in the mortality of ground-inhabiting birch leafminer stages, although this was not investigated. Thus, location-specific patterns of abundance may reflect location-specific impacts of mortality agents. Further combined experimental and life table analyses of these differences may suggest specific ways in which urban birch habitat design could simulate forest habitats, and thereby augment key mortality agents.

Variation in larval survivorship was consistently greater among trees than between locations (Chapters 3 and 4), suggesting that the tree is an ecologically-important scale of habitat quality that could be exploited in management strategies. Among-tree variation may be due to tree-specific effects of natural enemies (Chapter 3), or to direct host tree effects on leafminers (Chapter 4). Similar among-tree variation in birch leafminer success has been attributed to ant predation and the proximity of host birches to ant nests (Pezzolesi and Hager 1994), or to variation in the resistance of birch species to leafminer oviposition and feeding (Fiori and Dolan 1984; Braker 1986; Fiori and Craig 1987). These differences could potentially be exploited in management strategies through augmentation of specific natural enemies and plantings of resistant birches. Population-regulatory effects of host quality on birch leafminers could be determined using a combined experimental and life table approach similar to that used by Preszler and Price (1988).

The observed spatial hierarchy of host-specific variation (Chapter 4) may translate into a hierarchy of fitness effects which influence the evolution of birch leafminer life history traits. Since leafminers are restricted to a single habitat patch for most or all of their larval life, natural selection should favor females that exploit the best habitat patches (Faeth 1991). Small leaves or those containing conspecifics are poor habitats for both *F. pusilla* and *P. thomsoni*, since both species can suffer from intraspecific competition (Chapter 4). In addition, leaf quality for *P. thomsoni* is affected by the type and amount of early-season leaf damage (Chapter 4). Despite these differences in larval performance among leaves, ovipositing *P. thomsoni* did not appear to choose the best quality leaves for oviposition (Chapter 4). Detection of optimal habitat choices can depend on the spatial scale examined (Valladares and Lawton 1991; Koricheva and Haukioja 1994), and females of *P. thomsoni* may discriminate among leaves or trees of different quality, but not among branches (Chapter 4). Establishing the evolutionary significance of these oviposition choices depends on discovering the degree of genetic connection between female preference and larval performance (Thompson 1988).

Birch leafminers appear to have integrated easily into the community of native herbivorous insects on birch, probably due to the paucity of potential competitors for leaf resources (Chapter 2). This paucity is surprising, given that birch is a much-used host plant in Britain by insects in general (Southwood 1961), and by leafminers in particular (Godfray 1984). Theory predicts that similar numbers of potential niches should be available on similar resources, such as congeneric plants (Price 1983). Thus, leafmining niches on Alberta birches may have been relatively "unoccupied" when birch-leafmining sawflies were first introduced. Vacant niches appear common in insect herbivore communities, and are evident through low occupancy of resources (Price 1983) or unpredictable differences in parts not fed upon among closely-related plant species (Strong et al. 1984). However, the relatively "unoccupied" leaf-feeding niche on birch may be periodically filled during outbreaks of the birch skeletonizer, *Bucculatrix canadensisella* Chambers (Chapters 2 and 4); this may have precluded the evolution of a consistently abundant and diverse leaf-feeding guild on Nearctic birches. Thus, the combination of a vacant niche and escape from specific European parasitoids (Eichorn and Pschorn-Walcher 1973; Chapter 3) may help explain why high population levels of birch leafminers have been sustainable in Alberta (Drouin and Wong 1984).

Both *F. pusilla* and *P. thomsoni* appear to occupy quite different spatio-temporal niches in North America, probably as a result of niche partitioning evolved in Europe (Chapter 2). These strict niche constraints appear unnecessary in the Nearctic, given that there are few potential folivorous competitors (Chapter 2). Thus, Nearctic populations of birch leafminers may lose these life history traits over time. Data documenting such a change would be valuable in assessing the effects of competition on the evolution of temporal niche partitioning.

The absence of *P. thomsoni* at Fox Creek during outbreaks of *B. canadensisella* (Chapter 4) may be an example of competitive exclusion. The competitive exclusion principle suggests that guilds of species sharing a resource will either evolve to use different parts of the resource (niche differentiation), or will experience local extinctions of inferior competitors (competitive exclusion) (Begon et al. 1990). Introduced species should be good candidates to demonstrate competitive exclusion because they have evolved under different conditions than the native fauna, and therefore cannot have undergone niche differentiation with its members. Some introduced species have displaced native ones on a common resource (Ehler and Hall 1982; Bennett 1993), but the reverse may occur if introduced species are inferior competitors. Competition between *P. thomsoni* and *B. canadensisella* is probably asymmetric in favor of *B. canadensisella* (Chapter 4), and therefore local extinctions of birch leafminers are expected during severe outbreaks of *B. canadensisella* in native birch stands. These extinctions may limit forest populations of introduced birch leafminers by "resetting" them to very low levels after every outbreak; this, in combination with efficient predation of localized high density patches of leafminers (Chapter 3), may help prevent forest populations of birch leafminers from building up to levels observed in urban areas.

It is evident that birch leafminers have established many connections within the community surrounding birch in Alberta, and have become integrated within it. They have occupied a largely vacant niche as birch folivores, and have developed interactions with other herbivores on birch, such as *B. canadensisella*. In addition, they are a consistently abundant resources for native predator and parasitoid guilds, which have switched effectively onto the new hosts and may impact their populations. Further studies of these interactions could advance both the management and general ecological objectives of this study. Clarification of the regulatory effects of individual mortality agents will increase management options and explore the usefulness of experimental life table analyses in identifying population-regulatory processes. Determination of the evolutionary consequences of competition for both *F. pusilla* and *P. thomsoni* would provide further insight into size-fitness relationships (*F. pusilla*) and the optimality of oviposition site selection (*P. thomsoni*). Further study of differential birch leafminer success within and between host trees, as well as of the effects of *B. canadensisella* on birch leafminers, may reveal additional population regulatory mechanisms that will improve models of birch leafminer population dynamics.

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