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THE IMPACT OF PREDATORS AND PARASITOIDS ON NATURAL AND EXPERIMENTALLY CREATED POPULATIONS OF FOREST TENT CATERPILLAR, MALACOSOMA DISSTRIA HÜBNER (LEPIDOPTERA: LASIOCAMPIDAE)

BY

DYLAN PARRY ©

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

FALL 1994

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John R Spence

Dr. John R. Spence

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July 27th, 1994

DEDICATION

To my mother, Ruth.

ABSTRACT

I studied the impact of parasitoids in endemic, outbreak and post-outbreak field populations of the forest tent caterpillar (FTC), *Malacosoma disstria* Hübner, at 20 sites in Alberta. As well, I created experimental populations in an area where FTC were at low density to determine whether parasitoids and predators are capable of regulating FTC between outbreaks. Experimental plots were located in upland and lowland aspen forests to examine if forest type influences the response of natural enemies to changes in FTC density.

Eighteen primary parasitoids attacked FTC in Alberta. The tachinid *Leschenaultia exul* (Townsend) was the most common larval parasitoid, parasitizing more than 60% of the final instar larvae in some populations. Another tachinid, *Patelloa pachypyga* (A & W) was also abundant but parasitism levels declined in older outbreaks. Other larval parasitoids were of minor significance during outbreaks although several were more important in low density FTC populations.

Although the sarcophagid *Arachnidomyia aldrichi* (Parker) was the most common pupal parasitoid reared from outbreak populations, it was less abundant in Alberta than has been recorded in eastern North America. *Arachnidomyia aldrichi* parasitism was significantly higher in undergrowth vegetation than in the aspen canopy. As well, *A. aldrichi* parasitism varied along 100 m transects extending from stand edges toward the forest interior. Parasitism was high at the edge and at 100 m into the stand, perhaps reflecting between stand and within stand movement by female flies.

In the experimentally created populations, the braconid *Aleiodes malacosomatos* (Mason) exhibited spatial density-dependence in the upland aspen forest. *Patelloa pachypyga* was the most abundant parasitoid and also responded in a spatially density-dependent manner but defoliation level in the plots was a better predictor of parasitism than was FTC density. *Leschenaultia exul* was common but did not respond to variations in larval density.

The northern oriole, *Icterus galbula* (L.), was the dominant source of late instar and pupal mortality in the experimental plots. There was no significant difference in avian predation on pupae deployed at two distances from the plots suggesting that birds have a major impact at a variety of FTC densities and potentially can maintain FTC populations at low levels in some forests.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

FIGURE PAGE

1. INTRODUCTION

1.1 BACKGROUND

1.1.1 Distribution, hosts and life history.

The forest tent caterpillar (FTC), *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), is one of the most important defoliators of hardwood trees in North America. Native to this continent, it has a wide geographical range extending from 60°N latitude southward to include most of the United States (Prentice 1963; Stehr & Cook 1968).

FTC are highly polyphagous and defoliation of oaks (*Quercus* spp.), sugar maple (*Acer saccharum* Marsh), basswood (*Tilia americana* L.), water tupelo (*Nyssa aquatica* L.), black gum (*Nyssa sylvatica* L.) and cottonwood (*Populus deltoides* Bartr. ex Marsh) occurs in different regions of North America (Stehr & Cook 1968). In Alberta and across much of the northern range of FTC, oviposition and early instar feeding are primarily restricted to trembling aspen, *Populus tremuloides* Michx., although fourth and fifth instar larvae will feed on a wide variety of other trees and shrubs.

FTC overwinter as pharate larvae within eggs. Between 60-400 eggs are laid in a cylindrical band around terminal twigs in the mid and upper crowns of host trees. Egg bands are covered with a frothy brown substance known as spumaline which has hygroscopic properties and may provide protection from cold temperatures and egg parasitoids (Hodson 1939a; Hodson 1941; Prentice 1953). In Alberta, eggs hatch in late April and early May (Ives 1973). Hatching is usually synchronous with aspen bud break but first instars are resistant to starvation and can emerge several days before buds are soft enough to mine (Smith & Raske 1968). True tents are not constructed by FTC although silken mats are built for resting and molting. During the first three instars, caterpillars remain in the tree on which they hatched. Fourth and especially fifth instars wander extensively, a behavior that is not always related to food availability or conspecific density (Parry & Spence unpublished data). In central and northern Alberta, the five larval instars are completed by the third week of June.

Most cocoons are spun between folded leaves although at high population densities a variety of other locations are used including bark crevices, logs and anthropogenic structures. The outer portion of the cocoon is loosely spun and surrounds a tightly knit inner layer. Just before molting to pupae, the larvae smear the inner layer with a yellowish substance excreted from their Malpighian tubules, the function of which is unknown (Stehr & Cook 1968). In Alberta, pupation generally lasts 10-21 days.

Adults emerge late in June or early July. They have vestigial mouth parts, do not feed and only live for a few days. Both sexes fly well but little is known about their dispersal. Mass flights of up to 480 km have been reported in association with favorable weather fronts (Brown 1965). Although females emit pheromones (Struble 1970), males apparently rely on visual cues to find mates at close range (Bieman & Witter 1983). After mating, all eggs are laid in a single batch. Embryonic development is completed three weeks after oviposition at which time an obligatory overwintering diapause takes place (Ives 1973).

1.1.2 Population dynamics.

FTC populations are characterized by irruptive dynamics. In the Lake States and the Canadian provinces of Ontario, Manitoba, Saskatchewan and Alberta, outbreaks occur at 6-16 year intervals with a average periodicity of ten years (Hodson 1941; Hildahl & Reeks 1960; Sippell 1962). High density populations usually are present for 3-6 years at any one locality although outbreaks as long as nine years are not uncommon (Sippell 1962).

Outbreaks of FTC in Canada have been documented as far back as 1868 (Baird 1917). In the prairie provinces where the historical record is not as complete, outbreaks have been recorded since 1890 (Baird 1917). The first reported outbreak in Alberta was near St. Albert in 1902 (Wolley-Dod 1906). High populations occurred in Alberta from 1908-1912 and again in 1917 (Baird 1917; Tothill 1923). High populations were present from 1924-1928 (deGryse 1924; Hodson 1941) and a large outbreak was recorded in northwestern and east-central Alberta from 1939-1943 (Brown 1941, 1942, 1943). Little defoliation was reported again until 1951 when populations expanded and remained high until collapsing in 1954 (McGuffin & Reid 1952; Brown & Cumming 1954).

With the advent of modern survey methods, forest tent caterpillar defoliation has been recorded in Alberta every year since 1957. Annual defoliation records indicate that large regional outbreaks occurred from 1959-1964 and 1977-1983 (Ives 1971; Hiratsuka et al. 1980, 1981; Moody & Cerezke 1983, 1984). The most recent population upswing began in 1986 and peaked in 1988 when 2 766 000 ha of aspen were defoliated in Alberta (Emond & Cerezke 1989). Populations began to decline in 1989 (Fig. 1.1) and a low of 19 000 ha were defoliated in 1993 (Brandt 1994).

Several factors are thought to be important in the collapse of outbreak populations. Inclement early spring weather has caused the collapse of several outbreaks (Sweetman 1940; Prentice 1954; Blais et al. 1955; Gatreau 1964). Most often, these declines were associated with an early hatch followed by frosts or cold, wet weather. However, Raske (1975) found that first instar larvae in the laboratory survived lower temperatures for longer durations than are usually found in Alberta in spring and suggested that weather alone can not account for large scale population collapses.

Reduction of outbreak populations has been attributed to starvation of final instar larvae in some studies (Sippell 1957; Hodson 1977; Witter 1979). Usually starvation is associated with very high egg band densities and good early instar survivorship. Because starvation appears to be localized (Hodson 1977), it is unlikely to determine population trends over large areas. However, partial starvation of final instar larvae causes marked reductions in fecundity and may contribute to outbreak decline.

FTC are attacked by a variety of pathogens of which the fungi *Entomophthora crustosa* MacLeod & Tyrrell and *Beauveria bassiana* (Balsamo) Vuillemin, the microsporidian *Nosema* sp. and nuclear polyhedrosis virus (NPV) are the most important (Bird 1971; Stairs 1972; Wilson 1979). Failure to develop pathogens as biological control agents for FTC led some workers to suggest that they may have a relatively minor role in population regulation (Ives 1984). Recently, attention has refocused on the role pathogens play and it has been suggested that they are the driving force in the periodic outbreak and decline of tent caterpillar populations (Myers 1988, 1993).

More attention has focused on parasitoids than on other sources of FTC mortality. Eggs, larvae and pupae of FTC are attacked by more than 90 species of parasitoid (Witter & Kulman 1972). Although long recognized as important, relatively few quantitative studies have been done on the impact of parasitoids. Because egg parasitism is a minor source of mortality and appears to change little with density (Ives 1971; Witter & Kulman 1979), it is not likely to be important in population regulation. On the other hand, larval parasitism can have a significant impact on populations and often increases in the latter years of outbreaks. The tachinids *Leschenaultia exul* (Townsend) and *Patelloa pachypyga* (Aldrich & Webber) commonly parasitize up to 25% of the final instar larvae in aspen feeding FTC populations (Sippell 1957; Witter & Kulman 1979). Although other parasitoids such as *Aleiodes* (= *Rogas*) *malacosomatos* (Mason) (Hymenoptera: Braconidae) and *Lespesia frenchii* (Williston) (Diptera: Tachinidae) have less impact in outbreak populations, they may have a greater role at lower host densities (Sippell 1957).

The majority of research on parasitism has concentrated on pupal parasitoids, particularly *Arachnidomyia* (= *Sarcophaga*) *aldrichi* (Parker) (Diptera: Sarcophagidae). In many outbreaks in Ontario and Minnesota, pupal parasitism by *A. aldrichi* has been reported to approach 90% (Caesar 1915; Hodson 1939b, 1941, 1977; Sippell 1957; Witter & Kulman 1979). Sippell (1957) suggested that the competitive dominance of *A. aldrichi* may dictate the population dynamics of other parasitoids, particularly tachinids attacking late instar larvae. Outbreaks have collapsed due to *A. aldrichi* parasitism augmented by prior population reduction from starvation and poor weather (Hodson 1977, Witter 1979).

Based on correlations between amount of forest edge and duration of outbreaks, Roland (1993) suggested that parasitism may be reduced in stands with a high edge component although evidence for this hypothesis is scant. In one study, Batzer (1955) did find that *A. aldrichi* parasitism rates were low near a lake edge and increased toward the forest interior but it is unknown if this pattern of parasitism is a general phenomenon or if it applies to other species of parasitoid.

Few studies have been done on the impact of predation at any FTC population density. Birds are frequently mentioned as predators of FTC in the literature but most observations are anecdotal (e.g., Forbush 1896, McAtee 1926). Predation by ants on early instars have eliminated FTC in localized areas (Green & Sullivan 1950). The pentatomid, *Podisus brevispinus* Phillips, can also inflict considerable mortality particularly on first instars (D. Parry unpublished data). Other invertebrate predators such as *Calosoma frigidum* Kirby (Coleoptera: Carabidae) often increase to high levels during FTC outbreaks (Hodson (1941).

Studies on mortality factors affecting FTC have concentrated on the outbreak portion of the cycle because of very low population densities between outbreaks (Hodson 1941). Information on mortality agents and other factors potentially responsible for keeping endemic populations in check is lacking (Witter et al. 1975; Witter 1979). Although Sippell (1957) speculated that generalist parasitoids could be important between outbreaks, little research has been done on their impact. In the only published study on mortality in low density populations, Harmsen and Rose (1983) found that parasitism of early instar larvae was higher in upland aspen forest than in low lying areas. Although their results were preliminary, they do suggest that habitat heterogeneity could be important in the low density dynamics of FTC. The paucity of information on mortality factors in low density populations is a major obstacle to understanding the population dynamics of FTC.

1.2 OBJECTIVES OF THE THESIS

Little is known about the influence of natural enemies on FTC dynamics in the prairie provinces. Ives (1971) published a species list and recorded total parasitism rates during an outbreak in Alberta but did not partition the mortality among the individual species. Information on the role of natural enemies in endemic FTC populations is entirely lacking. The first objective of this thesis is to describe the dynamics and abundance of parasitoids in field populations of FTC in Alberta. A second objective is to investigate the role of natural enemies in the dynamics of low density populations using an experimental approach.

In Chapter 2, I ask which species of parasitoids attack FTC in both outbreak and low density populations and how the dynamics of different parasitoids change depending on the FTC population phase. To understand how some aspects of parasitoid biology can affect parasitism rates, I recorded the host stage attacked and from which developmental stage different parasitic Diptera emerge. As well, vertical spatial variation in pupal parasitism was examined in the undergrowth and canopy at four sites. Using transects extending from the forest edge to the interior, I also describe the change in parasitism rates of tachinid and sarcophagid flies with increasing distances from the edge. Comparison of the results with two well known studies from Ontario (Sippell 1957) and Minnesota (Witter & Kulman 1979) allowed me to draw conclusions about the generality of parasitoid impacts on FTC populations.

Difficulties in working with the extremely low densities of FTC encountered between outbreaks necessitated an experimental approach. Chapter 3 describes the impact of natural enemies in twelve plots stocked with three different densities of larvae in an area where natural FTC populations were very low. Plots were located in two different aspen forest types to determine if forest type influences the response of natural enemies to variations in density. I attempted to detect spatial density-dependent responses by parasitoids. As well, FTC pupae were deployed at two distances from the plots to examine the response of predators and parasitoids.

Finally in Chapter 4, I provide a summary and short general discussion of the results obtained in this study. I end with some suggestions about future research on FTC population dynamics.

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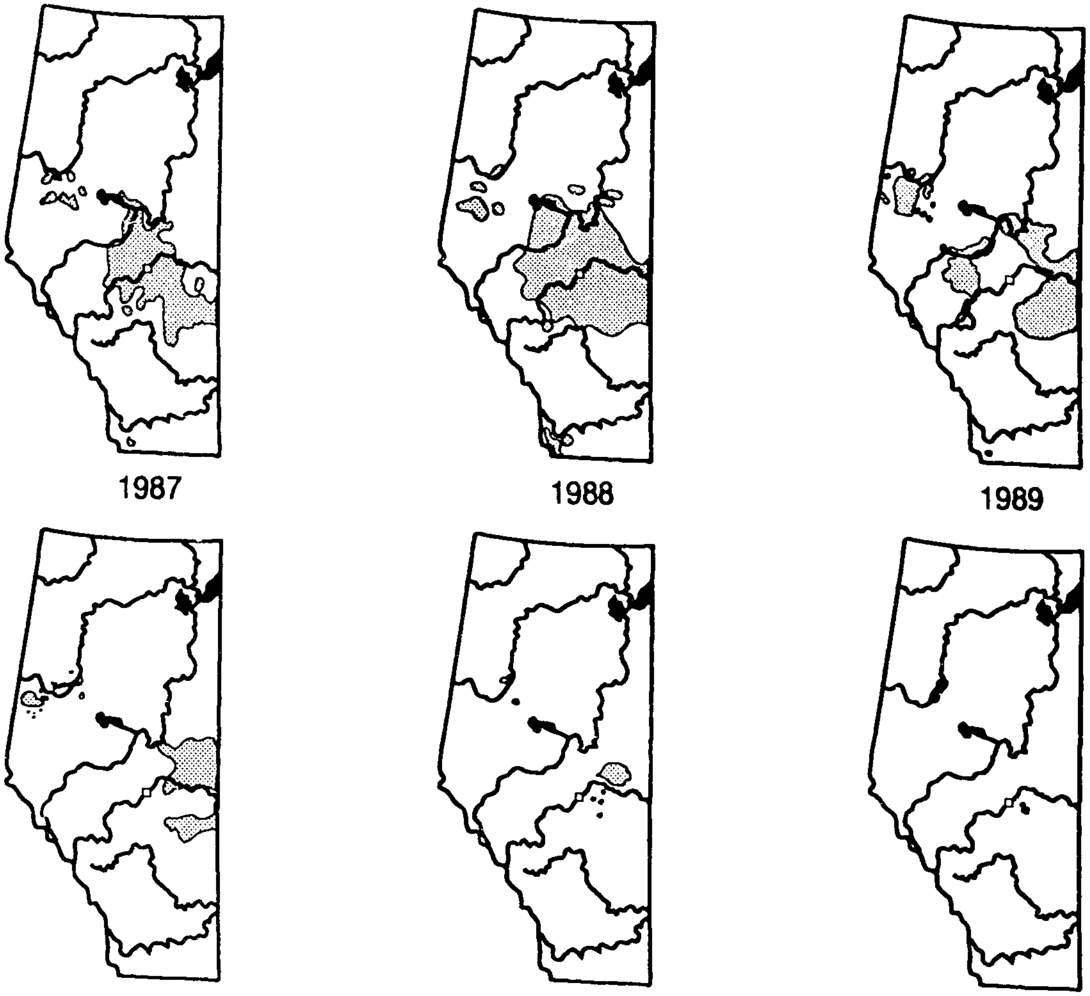

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Fig. 1.1 Moderate to severe defoliation by the forest tent caterpillar in Alberta, 1987-1993. Adapted from Canadian Forest Service maps augmented with personal observations.
▨ = moderate to severe defoliation

2. POPULATION DYNAMICS OF LARVAL AND PUPAL PARASITOIDS OF THE FOREST TENT CATERPILLAR IN ALBERTA

2.1 INTRODUCTION

The forest tent caterpillar (FTC), *Malacosoma disstria* Hübner, is an important native defoliator of deciduous trees in North America. High density populations of this forest pest, periodically defoliate vast areas of trembling aspen, *Populus tremuloides* Michx., in the Lake States and the Canadian provinces of Ontario, Manitoba, Saskatchewan and Alberta. Outbreaks occur at 6-16 year intervals with an average periodicity of ten years (Hodson 1941; Hildahl & Reeks 1960; Sippell 1962). Following three to six consecutive years of defoliation at any one locality, outbreak populations generally collapse and may remain at low densities for many years (Sippell 1962). Inclement spring weather, starvation, disease and parasitoids are thought to contribute to the termination of outbreak populations (Sweetman 1940; Prentice 1954; Blais et al. 1955; Sippell 1957a; Gatreau 1964; Stairs 1966; Witter & Kulman 1979).

Elevated levels of parasitism are often associated with collapsing populations. Studies in Minnesota and Ontario found that more than thirty species of parasitoid attack FTC during outbreaks (Sippell 1957a; Witter & Kulman 1979). Egg parasitism is relatively low and remains constant across a wide range of FTC densities (Hodson 1939a; Ives 1971; Witter & Kulman 1979). Larval and pupal parasitoids may be more important than egg parasitoids in the dynamics of FTC populations because they cause increasing levels of mortality in older outbreaks. The parasitoids *Aleiodes* (= *Rogas*) *malacosomatos* (Mason) (Hymenoptera: Braconidae), *Leschenaultia exul* (Townsend) (Diptera: Tachinidae) and *Patelloa pachypyga* (Aldrich & Webber) (Diptera: Tachinidae) are consistently reared from larvae in aspen feeding FTC populations and can cause significant mortality (Sippell 1957a; Witter & Kulman 1979; Eggen 1987). Parasitism of pupae by *Arachnidomyia* (= *Sarcophaga*) *aldrichi* (Parker) (Diptera: Sarcophagidae) can approach levels of 90% in older outbreaks (Hodson 1941, 1977; Sippell 1957a; Witter & Kulman 1979). High parasitism of pupae by *A. aldrichi*, augmented by poor weather, has been credited with terminating some FTC outbreaks (Hodson 1977).

Although thought to be important in western Canadian populations of FTC, most observations on the impact of parasitoids have been anecdotal (e.g., Brown & Cumming 1953; Cumming 1954; Elliot 1961). During a lengthy study in Alberta, Ives (1971) found that the parasitoid complex associated with FTC was similar to that recorded in Ontario and Minnesota. No attempt was made to partition mortality caused by specific parasitoids, but his data did suggest that parasitism of larvae and pupae increased with the age of an outbreak.

The distribution of FTC pupae within a forest can influence the parasitism rate. Batzer (1955) found that pupal parasitism by *A. aldrichi* increased as collections were made at successive distances from the stand edge toward the forest interior. Others have found that host plant species and canopy level can also affect rates of parasitism (Turnock 1961; Witter & Kulman 1979). To date, these factors have not been investigated in Alberta.

The objective of this study was to determine the abundance of parasitoids attacking larvae and pupae of FTC in Alberta and describe their dynamics at different population phases of their host. Differences in attack phenology and emergence as well as location of FTC pupae within forest stands were investigated as potential sources of variation in parasitism rates. The results of this study were compared with research from other regions across the northern range of FTC.

2.2 MATERIALS AND METHODS

2.2.1 Sampling and rearing.

Forest tent caterpillar larvae and pupae were collected from 20 sites in Alberta from 1989-1994 (Fig 2.1). Collections at each site were always made at the same location. Some populations collapsed during the course of the study and as a result, FTC were not collected from all sites in every year. Generally, at least three sampling sites were located within an outbreak area. Outbreaks were considered to be terminated when defoliation was no longer visible from the ground even though some sites still had detectable levels of larvae. I refer to these sites as post-outbreak. At two sites near Edmonton, populations have been at low but measurable levels from 1988-1993 and were considered endemic. Sampling locations were chosen at least 10 m into continuous aspen forest to avoid edge effects (see Batzer 1955). At each site, collections were taken from four or more trees. In outbreak populations from 1989-1991, 100 larvae or pupae were collected at each site and from 1992-1994 at least 200 individuals were collected. In post-outbreak and endemic populations where densities were low, as many larvae or pupae were collected as could be found in a two hour search. If samples from low density populations consisted of less than fifty individuals, they were not used in determining the population dynamics of parasitoids.

This study was restricted to parasitoids attacking the larvae and pupae of FTC. The categorization of parasitoids as larval or pupal was based on the host stage actually attacked. Following Sippell (1957a) and Witter & Kulman (1979), separate collections were made to estimate larval and pupal parasitism. Collections for late larval parasitoids were timed to coincide with the appearance of the first cocoons in the field. Pupal collections were made as the FTC moths were beginning to emerge. Supplementary collections of second, third and fourth instars were made from 1992-1994 to determine the impact of parasitoids on early instars.

Larvae and pupae were reared individually in 150 ml wax paper cups (Lily Cup, Scarborough, Ontario.) at 20°C. Larvae were provided fresh aspen foliage every other day until pupation. Cups were checked every two days for dead larvae, emerged parasitoids or moths and the fate of each FTC was recorded. Adult parasitoids were preserved upon emergence and subsequently identified using the keys of Ross (1953), Sippell (1961) and D. J. M. Williams et al. (unpublished manuscript). Reference collections housed at the Strickland Museum, Department of Entomology, University of Alberta, Edmonton, Alberta and the Northern Forest Centre (NoFC), Canadian Forest Service, Natural Resources Canada, Edmonton, Alberta were used extensively to aid in the identification of parasitoids. Ichneumonid, chalcidoid and braconid nomenclature followed Townes

(1969), Yoshimoto (1984) and Marsh et al. (1987) respectively. Taxonomic nomenclature for Diptera followed McAlpine et al. (1981).

Hymenopteran parasitoids needed no special treatment before adults emerged. However, many dipteran parasitoids required an overwintering diapause. After exiting the host, maggots were placed in 7 dram plastic vials (Premo Plastics Engineering Ltd., Victoria, BC) with a moistened 3:1 mixture of potting soil and sterilized sand. Tachinids, particularly *P. pachypyga,* required soil that was moist but never wet. They desiccated very quickly if not placed in soil shortly after emerging from the host. A few years of experimentation were required to find optimum conditions for overwintering Diptera. Dipteran parasitoids were maintained at 15°C for six weeks in a controlled temperature chamber to permit development of the pharate adult within the puparia. Following gradual chilling over a two week period, parasitoids were placed at 1C° for six months to break diapause. The vials were then placed at 20°C and the adult flies allowed to emerge.

2.2.2 Parasitoid dynamics.

Apparent rates of parasitism were calculated by dividing the proportion of parasitized individuals by the total number of individual FTC in each sample. Superparasitized hosts were tallied as one individual species whereas each species emerging from a multiple parasitized host was credited as a fraction of the number of species present. In the case of obligate hyperparasitoids, the mortality was attributed to the primary parasitoid if it could be identified.

The spreading pattern of outbreaks tends to coalesce different populations making outbreak age difficult to estimate. For this reason, outbreak age was determined by counting the number of years following the first observed defoliation at a given location. Defoliation maps provided by the NoFC were used to augment my own observations on outbreak histories. Because time constraints prohibit longitudinal studies, the dynamics of all parasitoids were estimated using a chronosequential approach. Where possible, parasitism rates for each parasitoid species were recorded from endemic, outbreak and post-outbreak FTC populations. Unweighted means ± SE were calculated from all populations examined each year and analyzed through simple graphs to determine population trends.

2.2.3 Distribution of dipteran attack and emergence.

In 1993, the distribution of attacks in each host stage was estimated for *L. exul* , *P. pachypyga* and *A. aldrichi*. For the two tachinids, this was accomplished by making collections of larvae at each molt and shortly before pupation. Data for *L. exul* was obtained from two FTC populations at Edmonton and Elk Island National Park. Larvae for estimating *P. pachypyga* oviposition phenology came from the South Cooking Lake area and Elk Island National Park. Total parasitism rates for each species were calculated from the final larval sample. For each species, the parasitism rate at each FTC stage was then expressed as a proportion of the total parasitism adjusted for the proportion parasitized in the previous stage. The distribution of attacks by *A. aldrichi* were estimated from four sites, two at Cooking Lake and two near Peace River. *Arachnidomyia aldrichi* maggots kill their host immediately upon entry (Hodson 1939b), allowing easy estimation of each stage attacked. Total *A. aldrichi* parasitism was estimated at the end of the pupal period and the proportion of parasitism that occurred in each stage was calculated as above.

The host stage abandoned by tachinids after completion of larval development can significantly influence their population dynamics because it determines their vulnerability to competition by aggressive pupal parasitoids such as *A. aldrichi* (Sippell 1957a). The FTC developmental stage that was abandoned was recorded for four tachinid species from larval and pupal collections made at eight sites in the Peace River and Cooking Lake outbreaks.

2.2.4 Spatial variation.

The effect of height above ground on pupal parasitism was determined from cocoons collected in two aspen stands near South Cooking Lake and two stands near Peace River. At each site, pupae were obtained from two levels, from woody undergrowth vegetation below 1.5 m and from the forest canopy at least 10 m from the ground. Pupae were reared as above and parasitism rates recorded. The χ^2 statistic with Yates continuity correction was used to detect differences in parasitism between heights in each stand based on a null hypothesis of no difference in parasitism between undergrowth and canopy samples.

To determine if parasitism varies with increasing distance from the forest edge, two parallel 100 m transects were laid out from the edge toward the interior of a continuous mature aspen forest near South Cooking Lake. This forest had been heavily defoliated for two consecutive years. Individual co-dominant trees were chosen at distances of 0 m, 10 m, 20 m, 30 m and 100 m from the forest edge and marked with flagging. All pupae from undergrowth below 1.5 m within a 1 m radius around the base of the tree were collected. The tree was then felled and all pupae from the canopy above 10 m were collected. Unfortunately, no cocoons were present in the canopy at 30 m and 100 m on the second transect. Parasitism levels were then compared along the transects and between the two heights.

2.3 RESULTS

2.3.1 Forest tent caterpillar parasitoids.

From a total of 17 102 FTC collected during the study, eighteen species of parasitoid were reared (Table 2.1). Ten parasitoids attacked FTC larvae and another eight species were reared from pupae. The most abundant larval parasitoid was *Leschenaultia exul* (Townsend) followed by *Patelloa pachypyga* (A & W), *Lespesia frenchii* (Williston), *Aleiodes malacosomatos* (Mason) and *Carcelia malacosomae* (Sellers). *Arachnidomyia aldrichi* (Parker), *Agria housei* (Shewell) and *Aprostocetus esurus* (Riley) were the most common pupal parasitoids. Other species listed were sporadically abundant or were reared on only a few occasions. Three species, *L. exul, A. malacosomatos* and *C. malacosomae,* were reared from endemic FTC populations in Alberta.

2.3.2 Larval parasitism.

Collections of larvae at the second and third molts suggested that only *A. malacosomatos* attacked early instar FTC in Alberta. Few caterpillars were parasitized prior to the second molt. Highest parasitism was in FTC larvae collected at the third molt suggesting that most attacks occurred during the third instar. At low host density and during the first year of a population upswing, rates of parasitism by *A. malacosomatos* were 12.4% and 10%, respectively (Fig. 2.2). In outbreaks older than one year, this species was relatively rare and levels of parasitism below 1% were recorded for the second through fourth year. Following the collapse of outbreaks, *A. malacosomatos* parasitism increased to 3.5%. All *A. malacosomatos* cocoons (n = 43) collected from a sixth year FTC outbreak population near Peace River, Alberta, were attacked by hyperparasitoids indicating that hyperparasitism can have a significant impact on this parasitoid.

The most important late larval parasitoid in endemic and many outbreak populations was *L. exul*. This tachinid parasitized 12.7% of larvae in endemic populations and 9.2% in the first year of an outbreak. After a decline in the second year, mean percentage parasitism increased to 17% in the third year and remained near this level for the duration of outbreaks (Fig. 2.3a). Parasitism by *L. exul* was more variable than any other species in this study. Very high levels of parasitism were observed in northern Alberta FTC populations along the Peace River. In this area, *L. exul* parasitism rose to 66.0 ± 3.3% (mean ± SE) by the fourth year in contrast to the 5-20% observed in central Alberta FTC populations.

The second most abundant larval parasitoid was *Patelloa pachypyga* (A & W). Parasitism by *P. pachypyga* increased dramatically from 1.6% following the first year of visible defoliation to a high of 22.9% in the second year. After this peak, declining rates of parasitism were observed in each consecutive year (Fig. 2.3b). Despite its apparent importance during FTC outbreaks, *P. pachypyga* was not reared from endemic FTC populations.

At low FTC densities, an important component of the parasitoid complex was *C. malacosomae*. Nearly 5% of larvae collected from endemic populations were parasitized by this tachinid. After FTC populations reached defoliating densities, this species was not reared until the fourth year and even then at levels less than 1%. Late in outbreaks and following their collapse, *C. malacosomae* parasitism rates appear to increase (Fig. 2.4a). However, the post-outbreak sample was obtained from a single site and it is unknown if this is a general trend.

The tachinid *L. frenchii* was associated with declining FTC populations. During outbreaks, *L. frenchii* was not reared until the third year. After the third year, ascending rates of parasitism reached peaked at 33% of fifth instar larva in the first year after the collapse of an outbreak (Fig. 2.4b). Again, the post-outbreak sample came from a single site. Unlike *C. malacosomae*, *L. frenchii* was not detected in endemic FTC populations.

Four other tachinid parasitoids were sporadically reared from FTC but occurred too rarely to assess their dynamics. Five specimens of *Exorista mella* (Walker) were reared from larvae collected in a second year outbreak near Twin Butte in the southern Alberta foothills and single specimens were reared from two other locations. Several specimens of *Chaetogena edwardsii* (Williston) were reared from FTC at two locations. At both sites, contemporaneous populations of northern tent caterpillar, *Malacosoma californicum pluviale* (Dyar) had high levels of *C. edwardsii* parasitism suggesting that FTC may only be attacked when associated with a preferred host. Five specimens of *Euexorista futilis* (Osten Sacken) were tentatively identified from puparial characters after adults failed to develop. Two specimens of *Lespesia archippovora* (Riley) were also recovered.

2.3.3 Pupal parasitism.

The sarcophagid fly *Arachnidomyia aldrichi* was the most common parasitoid of FTC in Alberta. In outbreaks older than two years, 20-35% of the pupae contained this species. At two sites, parasitism by *A. aldrichi* exceeded 70%. Generally, parasitism increased as outbreaks progressed (Fig. 2.5a). However, parasitism by this species varied considerably within populations and between populations of the same age. For example, *A. aldrichi* parasitism exhibited precipitous declines in two outbreak populations despite similar pupal densities in both years. At one site near South Cooking Lake, Alberta, 70% of the pupae collected in 1992 yielded this species and at the same site in 1993 only 23% of the pupae were parasitized. Similarly, near Peace River, percentage parasitism decreased from 33.5% in 1992 to 2.5% in 1993. The cause of these large fluctuations is unknown. At endemic FTC densities, the impact of *A. aldrichi* could not be assessed because of the extreme difficulty in locating cocoons. However, the low levels of *A. aldrichi* in new outbreaks suggest that it is unlikely to have a large impact in low density populations.

Another sarcophagid fly was reared frequently from FTC pupae. *Agria housei* (Shewell) increased in abundance as outbreaks progressed. From low levels in the first year of an outbreak *A. housei* reached an average high of 4.5% in the fifth year (Fig. 2.5b). Like *A. aldrichi*, this species is unlikely to play a major role between outbreaks as it was not present in first year outbreak populations.

The ichneumonids *Pimpla pedalis* (Cresson), *Theronia atalantae fulvescens* (Cresson) and *Itoplectis conquisitor* (Say) were reared from many pupal collections but parasitism rarely exceeded 1% for any of these species. Clear patterns were not evident in their dynamics although all appeared less frequently in older outbreaks (Fig. 2.6a). Two other species of ichneumonid parasitized FTC pupae. *Gambrus canadensis canadensis* (Provancher) was reared from four specimens and *Iseropus stercorater orgyiae* (Ashmead) was reared twice.

The most common hymenopteran pupal parasitoid was *Aprostocetus esurus* (Eulophidae). This wasp is polyembryonous and approximately 150 individuals emerged from each parasitized FTC pupa. *A. esurus* parasitism rates ascended from 0.7% in the first year of an outbreak to a high of 3.7% in the final year (Fig. 2.6b). This was the only hymenopteran parasitoid that showed a steadily increasing impact as outbreaks progressed.

2.3.5 Phenology of attack and emergence.

Oviposition for both *L. exul* and *P. pachypyga* began when larvae were in the fourth instar. Almost 25% of the total *L. exul* parasitism occurred during the fourth instar compared to less than 5% for *P. pachypyga* (Fig. 2.7). Unfortunately, *C. malacosomae* and *L. frenchii* were reared so infrequently from the Elk Island and South Cooking Lake populations that their phenology could not be reliably assessed. However, *C. malacosomae* were reared from both fourth and fifth instars and *L. frenchii* from fifth instars in other populations. Tachinids were not reared from FTC larvae obtained prior to the third molt during this study.

Arachnidomyia aldrichi successfully attacked pre-pupae and pupae with close to 70% of the total parasitism occurring in pupae (Fig. 2.7). No *A. aldrichi* were reared from any FTC collected as larvae. The female fly probably requires cocoon silk as an cue for larviposition because hosts were only attacked if they had initiated construction of a cocoon.

All tachinids parasitizing FTC in this study abandon the host as third instar maggots and form puparia in the soil. The host stage that is abandoned depended on the tachinid species (Fig. 2.8). Both *L. exul* and *C. malacosomae* emerged from fifth instar larvae, pre-pupae and pupae. *Lespesia frenchii* emerged only from pre-pupae and pupae. More than 95% of *P. pachypyga* exited from FTC pupae. The only *P. pachypyga* to emerge from a larva did so when *L. exul* was present in the same host which may have forced a premature abandonment.

2.3.6 Spatial variation in parasitism.

The effect of vegetation height on parasitism by tachinids was quite variable. At one central Alberta site near Cooking Lake, there was no significant difference in parasitism between pupae from the upper canopy and those collected from the undergrowth while at the second site, parasitism of pupae in the upper canopy was significantly higher than in the undergrowth (Table 2.2a). At the northern Alberta sites near Peace River, there was no difference in parasitism between the canopy and undergrowth at the first site and at the second site, tachinid parasitism in the undergrowth pupae was significantly higher than in the canopy (Table 2.2a). These results may reflect a difference in tachinid fauna in the two regions. The Cooking Lake sites are dominated by *P. pachypyga* whereas *L. exul* was far more abundant in the Peace River sites.

The spatial distribution of sarcophagid parasitism was more consistent than for tachinids. At both Cooking Lake sites, parasitism in the undergrowth pupae was significantly higher than in the canopy and (Table 2.2b). A similar pattern was seen at the two northern Alberta sites where parasitism in the undergrowth was significantly higher than in the canopy at first site and although not significant, parasitism was higher in the undergrowth at the second site (Table 2.2b). These results primarily represent the action of *A.*

aldrichi because it accounted for more than 90% of the total sarcophagid parasitism.

Variation in defoliation levels along the transects and the absence of canopy pupae at 30 m and 100 m on the second transect complicated the comparison of parasitism at various distances from the forest edge. Nevertheless, some trends were apparent in the data. Tachinid parasitism tended to increase with distance from the edge to the interior although in the canopy, it apparently leveled off after 20 m (Fig. 2.9a). Although variable near the edge, after 20 m parasitism in the upper canopy was higher than in the undergrowth.

Sarcophagid parasitism was consistently higher in the undergrowth than in the canopy along the transects although rates were variable over the first 20 m at both heights (Fig. 2.9b). In the undergrowth, high levels of parasitism were recorded at 0 m. The highest rates of parasitism were recorded at 100 m, the furthest distance from the edge.

2.4 DISCUSSION

2.4.1 The biology and dynamics of FTC parasitoids.

The parasitoid fauna associated with FTC in Alberta was similar to that recorded from other aspen feeding FTC populations. In both Ontario and Minnesota, the five most abundant parasitoids recorded in outbreaks were *Arachnidomyia aldrichi* (Parker), *Leschenaultia exul* (Townsend), *Patelloa pachypyga* (A & W), *Lespesia frenchii* (Williston) and *Aleiodes (= Rogas) malacosomatos* (Mason) (Sippell 1957a; Witter & Kulman 1979). A similar ranking for these species in Alberta FTC populations suggests that throughout its northern range, the parasitoid complex associated with FTC is relatively constant.

Aleiodes malacosomatos probably has the widest distribution of any FTC parasitoid. It is found across North America wherever *Malacosoma* spp. occur (Langston 1957; Stehr & Cook 1968). Considering its ubiquity, little is known about its biology. The wasp attacks early instar tent caterpillars and the solitary, endoparasitic larvae usually kills the host as a fourth instar. It pupates inside the inflated host skin and the adult emerges about ten days later through a hole chewed in the rear of the mummified caterpillar (Mason 1979).

Sippell (1957a) indicated that *A. malacosomatos* populations began to increase in the late years of outbreaks. However, the low parasitism levels observed by Witter & Kulman (1979) throughout their study in Minnesota are similar to the dynamics I recorded in Alberta. The abundance of this species in low density and early outbreak FTC populations suggests that it could be important in regulating FTC populations between outbreaks. High levels of hyperparasitism in some Alberta populations may contribute to the reduced effectiveness of *A. malacosomatos* in older outbreaks as Sippell (1957a) suggested for this species in Ontario. Voltinism is unknown for this species. However, because adult *A. malacosomatos* emerge in early June (personal observation) they may be bivoltine and a reduction in hosts for second generation *A. malacosomatos* in previously defoliated areas could contribute to low levels of parasitism in older outbreaks.

Leschenaultia exul is widely distributed in North America (Bess 1936; Brooks 1946). A detailed description of the biology of this tachinid is given by Bess (1936). *Leschenaultia exul* lays microtype eggs and is univoltine. Host records indicate that it parasitizes only *M. disstria* and *M. americanum* (L.) (Arnaud 1978) although I have also reared it from *M. californicum pluviale* (Dyar) in western Alberta.

This study showed that after the second year, *L. exul* increased to much higher levels than were reported in Ontario (Sippell 1957) and Minnesota (Witter & Kulman 1979) (Fig. 2.10a). However, my data are pooled from several populations and high parasitism in northern Alberta inflated the mean parasitism rate. With the northern Alberta data removed, the dynamics of *L. exul* appeared similar to Sippell's (1957a) results from Ontario.

Earlier host abandonment may contribute to the success of *L. exul*. Several authors have reported that the pupal parasitoid *A. aldrichi* can inflict considerable mortality on tachinid parasitoids developing in FTC pupae (Hodson 1941; Sippell 1957a; Witter & Kulman 1979). My observations on host abandonment suggest that almost 18% of the *L. exul* population escapes competition with pupal parasitoids by emerging from larvae. Another substantial portion of the population abandon pre-pupae and also avoid the peak larviposition period of *A. aldrichi*. Pathogens such as nuclear polyhedrosis virus (NPV) can cause significant mortality to fifth instar FTC in older outbreak populations. Because *L. exul* maggots are developmentally advanced, they can survive in hosts dying from NPV infection (Sippell 1957b). It is likely that phenologically delayed species such as *P. pachypyga* would be killed when the caterpillar succumbs to the pathogen because they are still dependent on the host for oxygen.

In contrast to *L. exul*, relatively little is known about the biology of *P. pachypyga*. It is also a univoltine tachinid laying microtype eggs and has a restricted host range (Thompson 1953; Arnaud 1978). Comparisons with the dynamics reported by Sippell (1957a) and Witter & Kulman (1979) in eastern North America indicate that *P. pachypyga* populations behave similarly in Alberta (Fig. 2.10b). The characteristic decline in parasitism in the later years has been attributed to competition with increasing levels of *A. aldrichi* parasitism in older outbreaks. Interestingly, *P. pachypyga* declined after the second year in Alberta despite considerably lower *A. aldrichi* parasitism rates than recorded elsewhere. This suggests that either *A. aldrichi* are preferentially attacking pupae containing the developing *P. pachypyga* or other factors must be responsible for the downward trend in the rate of *P. pachypyga* parasitism.

The results of this study indicate that *P. pachypyga* may be an outbreak specialist. *Patelloa pachypyga* was not reared from larvae collected in endemic populations, was rare when outbreaks began and returned to low levels as outbreaks collapsed. The late attack phenology observed suggests a reason for their scarcity in low density populations. Fifth instar FTC larvae are solitary and highly dispersed in endemic populations and foliage ovipositing tachinids are unlikely to have many of their eggs ingested at these densities. Other tachinids laying microtype eggs such as *L. exul* circumvent this problem by initiating oviposition when larvae are fourth instars and are still feeding gregariously. My data showed that few larvae are parasitized by *P. pachypyga* prior to the fifth instar.

Carcelia malacosomae is a univoltine, oligophagous species that attaches pedicillate eggs to the setae of fourth and fifth instar larvae (Sippell 1957a; Arnaud 1978). *Carcelia* was rare in Ontario and was not found in

Minnesota although it is quite common in the prairie provinces (Brown & Cumming 1953; Cumming 1954; Sippell 1957a; Witter & Kulman 1979). In Alberta, its abundance in endemic and post-outbreak populations and scarcity in outbreak populations suggest that *C. malacosomae* is specializing on low density populations. This is supported by an extensive survey of FTC at different population densities in New England where *C. malacosomae* was the most common parasitoid reared (as *Zenillia protuberans* A & W) (Schaffner & Griswold 1934). Studies have shown that *C. malacosomae* frequently superparasitizes hosts (Sippell 1957a; Eggen 1987; personal observation). As many as four individuals commonly emerge from a single larva which could be an adaptation for maximizing reproductive output in sparse host populations.

Both Sippell (1957a) and Witter & Kulman (1979) speculated that *L. frenchii* could be important between outbreaks because it increases as outbreaks collapse. However, none were reared from endemic populations during this study. Because it appears to attack only fifth instars (personal observation; McLeod & Ayre 1956) the considerable search time involved in finding highly dispersed final instars may limit its success. Only parasitoids that can attack prior to the fourth molt were reared from endemic FTC populations. Although highly polyphagous, the bivoltine *L. frenchii* may be limited by the abundance of hosts for the second generation.

Ives (1971) recorded the tachinid *Euexorista futilis* as common in Alberta although few were collected during this study. No adults were deposited in the reference collection at NoFC and it is possible that his specimens may have been misidentified using puparial characters. The puparia of *E. futilis* are superficially similar to those of *P. pachypyga* (Ross 1953; Sippell 1961).

Undoubtedly, the most important parasitoid of outbreak FTC populations in North America is the sarcophagid *A. aldrichi*. First observations on its parasitic behavior were made by Caesar (1915) who noted that 90% of the pupae collected in an Ontario FTC outbreak contained *A. aldrichi*. Hodson (1939b) demonstrated that *A. aldrichi* could successfully attack both healthy and previously parasitized FTC pupae. Females larviposit onto the silk cocoon surrounding the pre-pupa or pupa. The maggot penetrates and immediately kills the pupa completing its development surrounded by the dissolving tissues of its host. This feeding style has lead to the suggestion that *A. aldrichi* represents an intermediate between true parasitism and saprophagy (Schmidt 1993).

The parasitism rates for *A. aldrichi* during this study (Fig. 2.11) were considerably lower than recorded in other studies (Sippell 1957a; Hodson 1977; Witter & Kulman 1979). Ives (1971) recorded successive mean parasitism rates of 6%, 19.5%, 11.6%, 29.8%, 42.2% and 45.2% from cocoons collected at five localities during an extensive FTC outbreak in Alberta from 1958-1965. Although he did not partition pupal parasitism among individual parasitoid species, the overall similarity of this data to my results suggest that *A. aldrichi* is not as prevalent in Alberta as it is in eastern North America.

Very high rates of parasitism by *A. aldrichi* in conjunction with other mortality agents have been credited with the termination of some outbreak populations (Hodson 1977). Lower rates of parasitism observed in this study could potentially contribute to increased outbreak duration in Alberta. The real pupal mortality caused by this fly is often considerably less than the high percentage parasitism rates indicate. Both Hodson (1939b, 1941) and Sippell (1957a) recognized that many of the pupae attacked were already parasitized by other species.

The biology of the sarcophagid *Agria housei* is similar to that of *A. aldrichi* (Coppell et al. 1959). Females larviposit first instar maggots on silk surrounding FTC pre-pupae and pupae. Levels of parasitism recorded in this study indicate that *A. housei* is more common in western Canada than elsewhere. Sippell (1957a) recorded parasitism rates of 0.8%, 0.3%, 0.3% and 0.1% in Ontario and Witter & Kulman (1979) considered it rare in Minnesota. In Alberta, the impact of *A. housei* increased in each successive year of outbreak. Lower parasitism by its major competitor, *A. aldrichi* , may contribute to the higher parasitism observed in this area. *Agria housei* is also a common parasitoid of large aspen tortrix, *Choristoneura conflictana* (Walker), in western Canada (Prentice 1955). Large aspen tortrix is common in Alberta and its range overlaps with areas where FTC outbreaks occur. This could contribute to the higher parasitism recorded in Alberta by providing an abundant alternative host.

About 15 species of ichneumonid wasp have been reared from aspen feeding FTC populations (Witter & Kulman 1972). The majority of the species are rare and occur only sporadically. In this study, *Theronia atalantae fulvescens, Pimpla pedalis* and *Itoplectis conquisitor* were reared in small numbers from most populations. Apart from the first year of outbreak neither Sippell (1957a) or Witter & Kulman (1979) found ichneumonids to be abundant. The dynamics of the ichneumonids in Alberta had no clear pattern although all appeared to become rarer as outbreaks aged. As all three species are multivoltine generalists (Bradley 1974), hosts for the second or third generation wasps may be at low levels after several years of FTC defoliation.

The small, polyembryonous wasp attacking FTC pupae referred to by deGryse (1924) and Hodson (1941) was probably *Aprostocetus esurus*. Both Sippell (1957a) and Witter & Kulman (1979) encountered *A. esurus* in their studies in Ontario and Minnesota but at much lower levels than in Alberta. Little is known about the biology of this wasp. It appears to be univoltine and is the only FTC parasitoid that overwinters within the host pupae. Records indicate that *A. esurus* attacks a diverse array of hosts including several non-forest insects (Peck 1963). As with other pupal parasitoids, reduced levels of *A. aldrichi* parasitism in Alberta may lead to the increased importance of *A. esurus* .

2.4.2 Spatial variation in parasitism.

Because fifth instar larvae are highly mobile and continuously redistribute themselves within a stand, the observed spatial pattern of tachinid parasitism was surprising. Lower densities of larvae near the stand edge at the time of tachinid oviposition may lead to the reduced parasitism rates observed. Egg band density and subsequent defoliation tend to be higher in the stand center than at the edge because the co-dominant trees in the interior of stands appear to be preferred by females for oviposition over the smaller edge trees (personal observation). Experiments suggest that *P. pachypyga*, the dominant tachinid at this site, can respond in a spatially density-dependent manner to patches of FTC (Chapter 3) and the higher tachinid parasitism in the forest interior may reflect this. Reduced pupal mortality from tachinids in the undergrowth after 20 m is likely the result of higher *A. aldrichi* parasitism destroying a portion of the tachinid population.

Sarcophagid parasitism was clearly more important in the undergrowth than in the canopy. Such spatially organized parasitism by *A. aldrichi* is a concern when estimating mortality for a population. In severely defoliated areas, collections from the undergrowth will accurately estimate pupal parasitism because few cocoons are located in the canopy. At lighter levels of defoliation, the cocoons are found in both undergrowth and canopy in varying proportions. Samples from different heights are required to quantify pupal mortality in populations at these densities. Although Batzer (1955) suggested that *A. aldrichi* parasitism did not vary with height, Witter & Kulman (1979) found significant differences in pupal parasitism in collections from herbaceous, shrub and canopy levels.

Although Roland (1993) speculated that forest fragmentation may reduce parasitism rates at the forest edge, results from the transects in this study indicate that with respect to *A. aldrichi*, the effects of forest edge are more complicated and are unlikely to be linear. Because *A. aldrichi* are strong fliers (Hodson 1939b), they can easily move between stands. Pupae on the forest edge are the first hosts encountered in inter-stand movement and high parasitism at 0 m in the undergrowth could reflect this activity. Elevated parasitism at 100 m may be indicative of larvipositional preferences of female flies within a stand.

2.4.4 Directions for future research.

The consistency of the parasitoid dynamics described by Sippell (1957a), Witter & Kulman (1979) and this study, suggests that common processes are operating in many FTC populations. Although information on the relative dynamics of parasitoids provides a framework for any subsequent studies, I suggest that a more quantitative approach is required to measure their real impact. Before this can be done, standardized methods for accurately estimating the densities of FTC larvae and pupae need to be developed. Methodology for estimating larval densities in other defoliator systems such as frass collection and head capsule recovery

(Liebhold & Elkinton 1988; Higashiura 1990), potentially could be adapted for use with FTC in higher density populations.

Experiments are required to determine the importance of inter-specific parasitoid interactions particularly for common species such as *L. exul, P. pachypyga* and *A. aldrichi*. Resolution of these problems will allow the use of promising new demographic methods such as marginal attack rates for estimating the impact of contemporaneous mortality factors (Elkinton et al. 1992). Such techniques will be important in ascertaining the impact of individual parasitoid species on the population dynamics of FTC.

This in turn, will allow us to couple sound knowledge about parasitoid population dynamics with detailed data about the population dynamics of the host. Perhaps then, the enigmatic and illusive relationship of FTC populations and their parasitoid assemblage can be fully understood.

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Table 2.1. Primary parasitoids reared from the forest tent caterpillar, *Malacosoma disstria* Hübner, in Alberta 1989-1993.

Larval Parasitoids	**Family**	**# FTC Parasitized**
Aleiodes malacosomatos (Mason)	Braconidae	39
Phobocampe clisiocampe (Weed)	Ichneumonidae	2
Leschenaultia exul (Townsend)	Tachinidae	1010
Patelloa pachypyga (Aldrich & Webber)	"	576
Carcelia malacosomae (Sellers)	"	48
Lespesia frenchii (Williston)	"	52
Lespesia archippovora (Riley)	"	2
Chaetogena edwardsii (Williston)	"	7
Euexorista futilis (Osten Sacken)	"	5
Exorista mella (Walker)	"	7
Pupal Parasitoids		
Arachnidomyia aldrichi (Parker)	Sarcophagidae	1614
Agria housei (Shewell)	"	183
Itoplectis conquisitor (Say)	Ichneumonidae	19
Theronia atalantae fulvescens (Cresson)	"	15
Pimpla pedalis (Cresson)	"	26
Gambrus canadensis (Provancher)	"	4
Iseropus stercorator orgyiae (Ashmead)	"	2
Aprostocetus esurus (Riley)	Eulophidae	162

Table 2.2 Parasitism of pupae in the undergrowth and canopy by tachinids and sarcophagids at four sites in Alberta

(a) Tachinids	% Parasitism (n)			
Cooking Lake	undergrowth	canopy	χ^2	p
Site A	14.5 (137)	11.3 (319)	6.638	0.01
Site B	25.3 (126)	39.4 (246)	0.693	0.405
Peace River				
Site A	30.6 (111)	32.3 (235)	0.615	0.253
Site B	30.8 (117)	18.9 (244)	5.736	0.017
(b) Sarcophagids				
Cooking Lake				
Site A	47.6 (137)	12.2 (319)	55.095	0.0001
Site B	8.0 (126)	1.5 (246)	9.988	0.0016
Peace River				
Site A	28.8 (111)	12.7 (319)	11.688	0.0006
Site B	15.3 (117)	9.0 (244)	2.641	0.1042

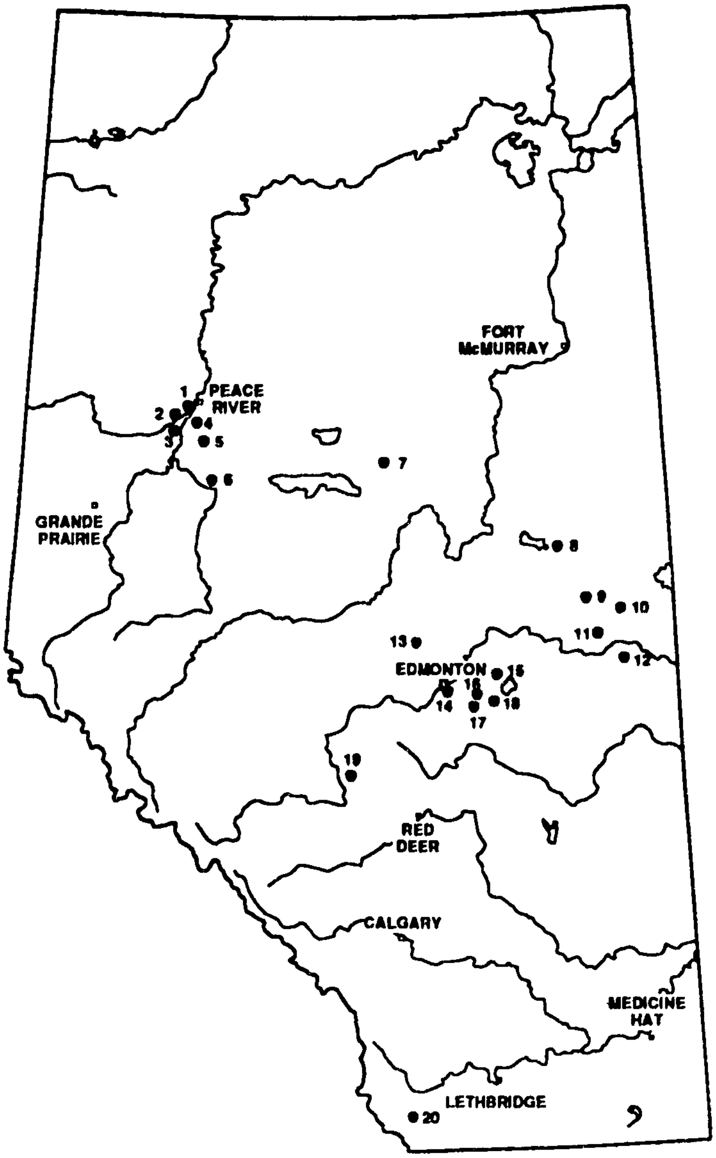


Fig. 2.1. Collection sites for forest tent caterpillar in Alberta 1989-1994.

(1) Peace River Town
(2) MacKenzie Cairn
(3) Judah
(4) Shaftsbury Crossing
(5) Guy
(6) Little Smokey
(7) Calling Lake
(8) Lac la Biche
(9) Mallaig
(10) Kehiwin Lake
(11) Lafonde
(12) Derwent
(13) George Lake
(14) Edmonton - Two sites
(15) Elk Island Nat. Park
(16) South Cooking Lake 1
(17) South Cooking Lake 2
(18) Hastings Lake
(19) Alder Flats
(20) Twin Butte

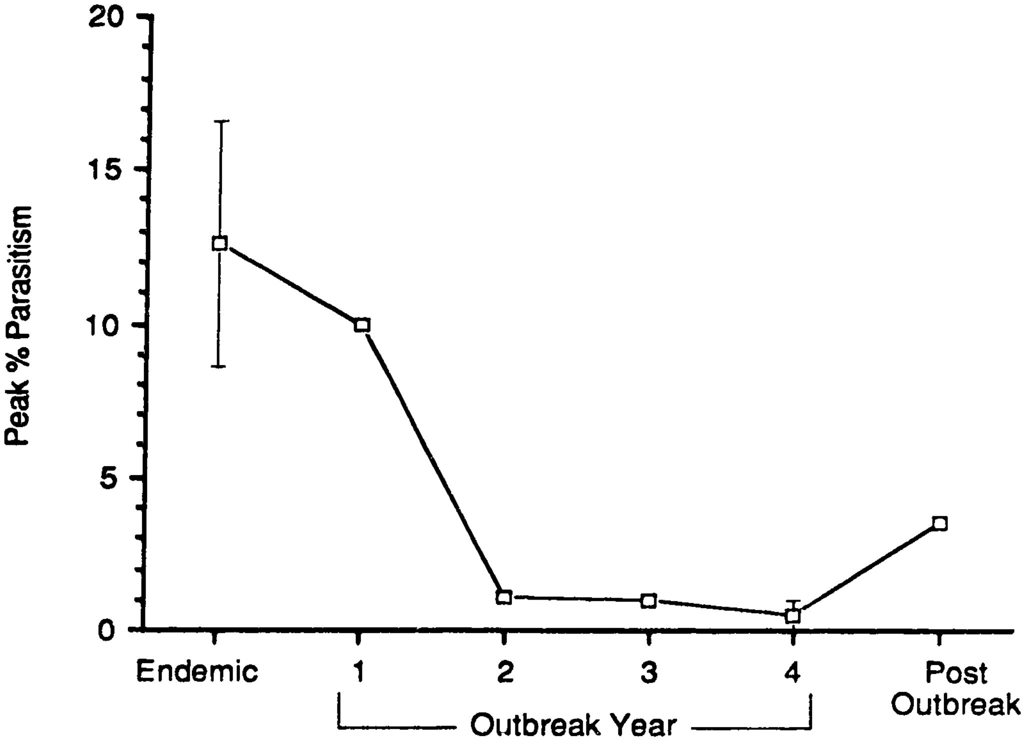
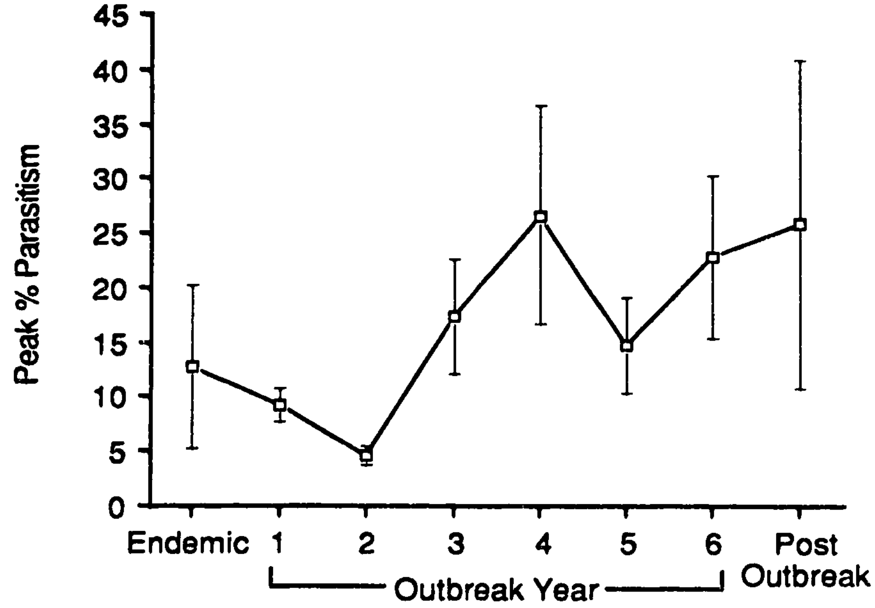


Fig. 2.2. Percentage parasitism (+/- SE) by *Aleiodes malacosomatos* in relation to different population phases of the forest tent caterpillar.
Sites collected: Endemic (14, n = 330), Year 1 (14, n = 100), Year 2 (15, n = 100), Year 3 (15, n = 100), Year 4 (16, 17, n = 242), Post-Outbreak (15, n = 88).

(a) *Leschenaultia exul*



(b) *Patelloa pachypyga*

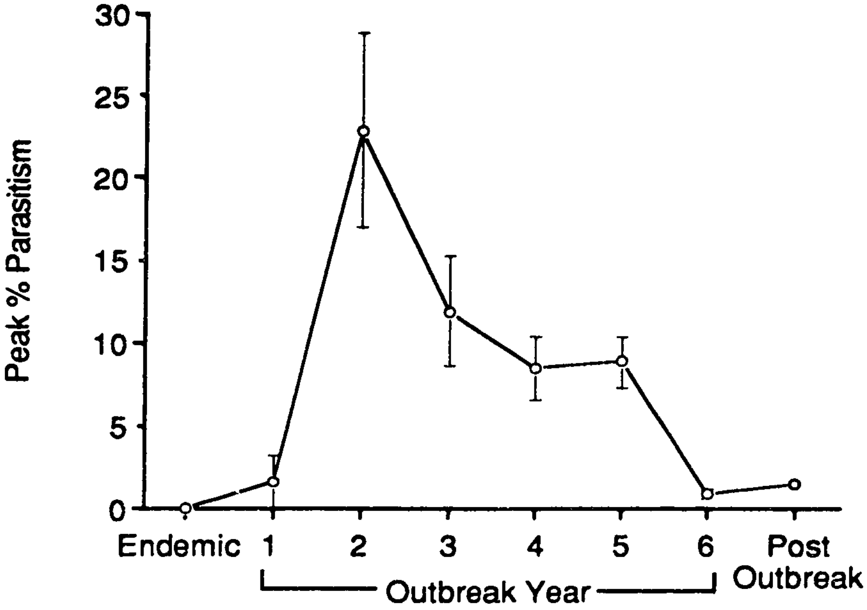
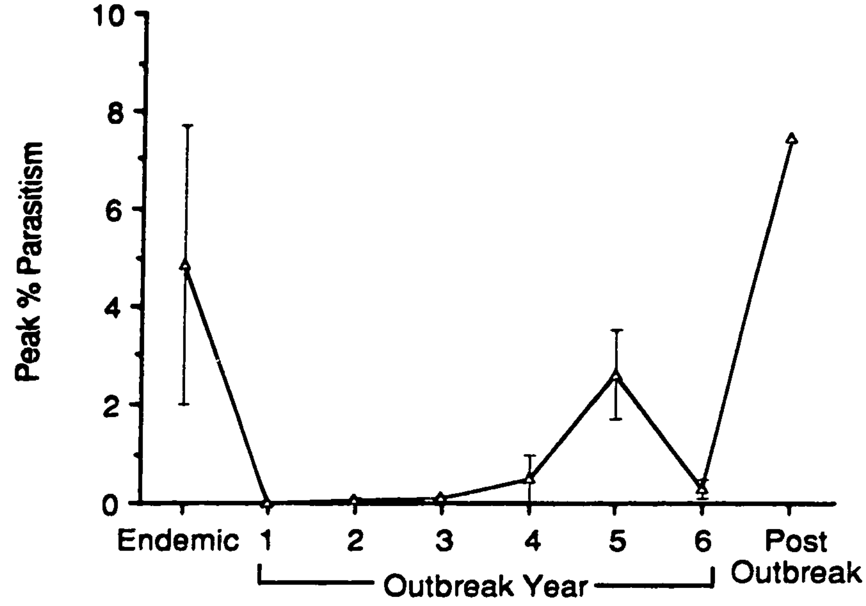


Fig. 2.3. Percentage parasitism (+/- SE) by *L. exul* and *P. pachypyga* in relation to different population phases of the forest tent caterpillar.
Sites collected: Endemic (14), Year 1 (5, 14), Year 2 (15, 16, 17, 18), Year 3 (3, 15, 16, 17, 18, 19), Year 4 (1, 3, 6, 9, 10, 12), Year 5 (1, 3, 4, 6, 8, 13), Year 6 (1, 2, 3, 4), Post-Outbreak (6) for *P. pachypyga* and (6, 15) for *L. exul*.

(a) *Carcelia malacosomae*



(b) *Lespesia frenchii*

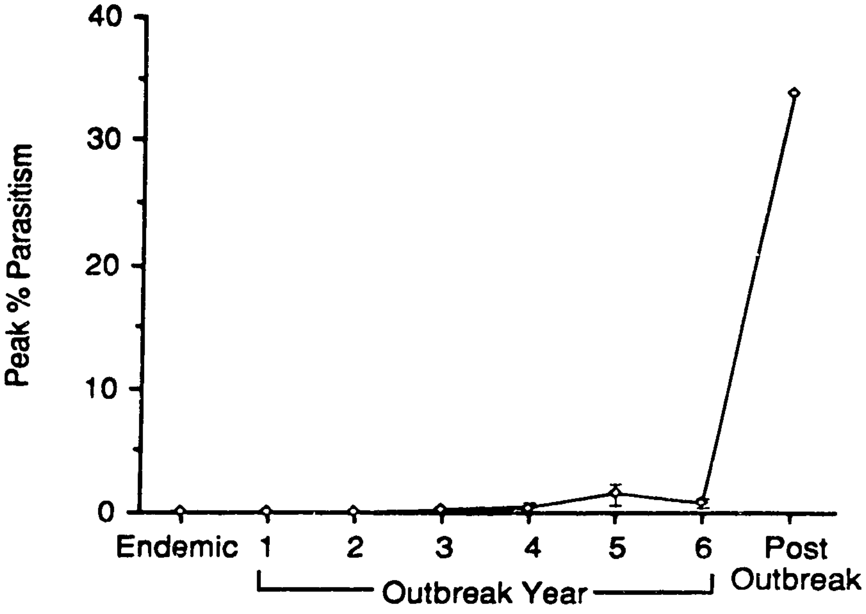
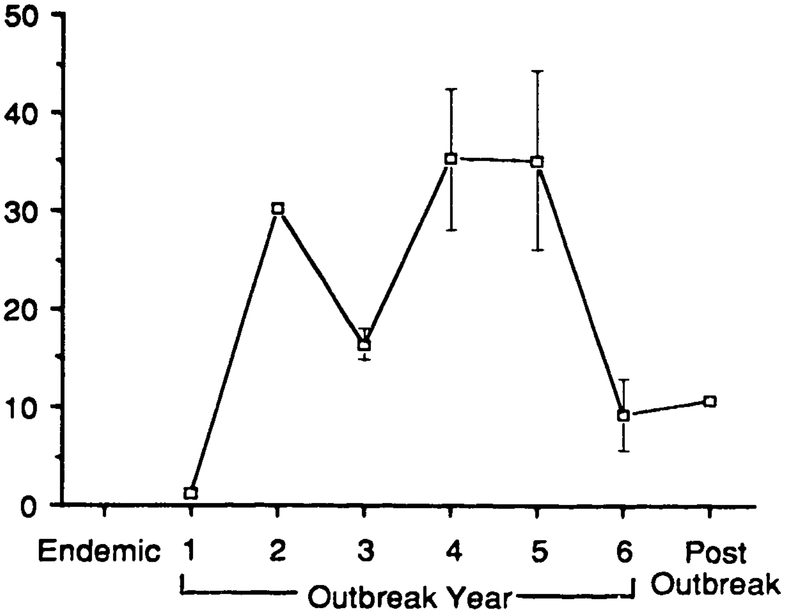


Fig. 2.4. Percentage parasitism (+/- SE) by *C. malacosomae* and *L. frenchii* in relation to different population phases of the forest tent caterpillar. **Sites collected:** Endemic (14), Year 1 (5, 14), Year 2 (15, 16, 17, 18), Year 3 (3, 15, 16, 17, 18, 19), Year 4 (1, 3, 6, 9, 10, 12), Year 5 (1, 3, 4, 6, 8, 13), Year 6 (1, 2, 3, 4), Post-Outbreak (6).

(a) *Arachnidomyia aldrichi*



(b) *Agria housei*

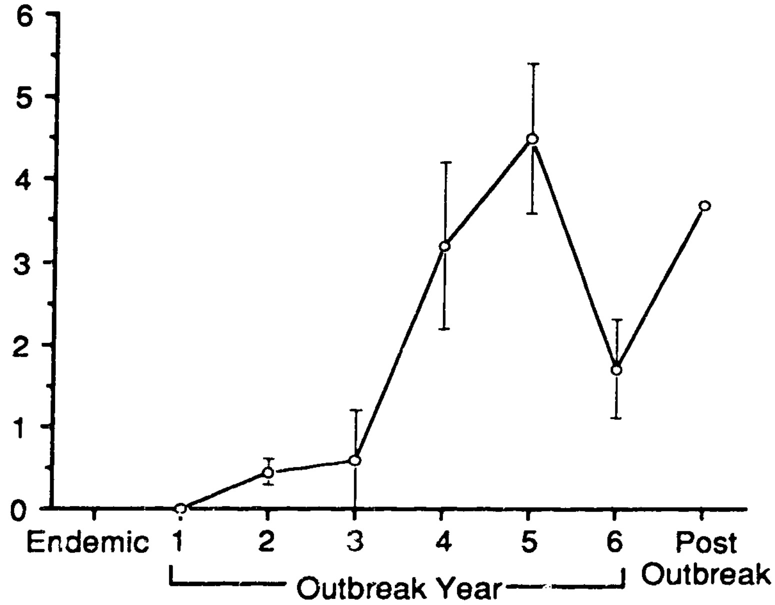
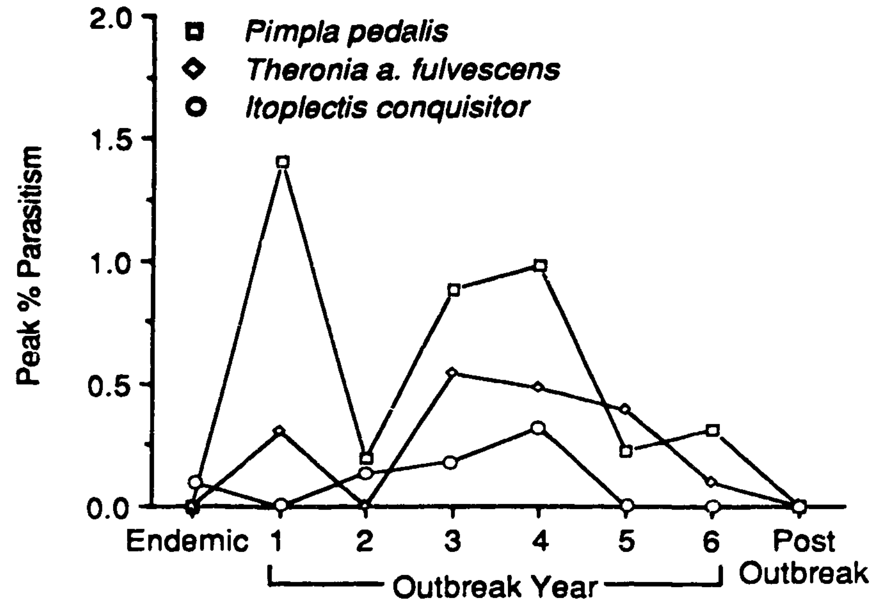


Fig. 2.5. Percentage parasitism (+/- SE) by *A. aldrichi* and *A. housei* in relation to different population phases of the forest tent caterpillar.

Sites collected: Year 1 (5), Year 2 (15, 16), Year 3 (15, 16, 17), Year 4 (1, 3, 6, 9, 10, 11), Year 5 (1, 2, 3, 6), Year 6 (1, 2, 3, 4), Post-Outbreak (6).


(a) Ichneumonidae

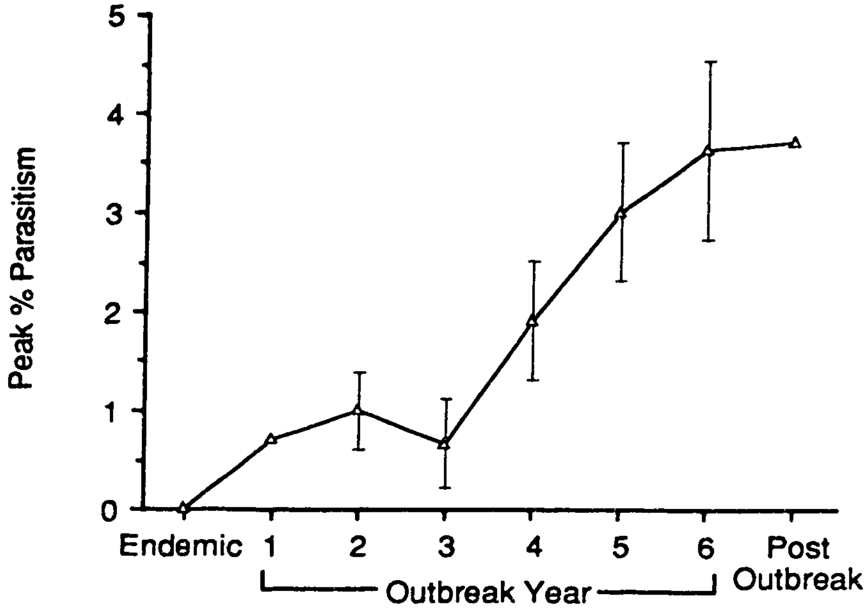

(b) *Aprostocetus esurus*

Fig. 2.6. Percentage parasitism (+/- SE) by three species of ichneumonid and *A. esurus* in relation to different population phases of the forest tent caterpillar. **Sites collected:** Year 1 (5), Year 2 (15, 16), Year 3 (15, 16, 17, 20), Year 4 (1, 3, 6, 9, 10, 11), Year 5 (1, 2, 3, 6), Year 6 (1, 2, 3, 4), Post-Outbreak (6).

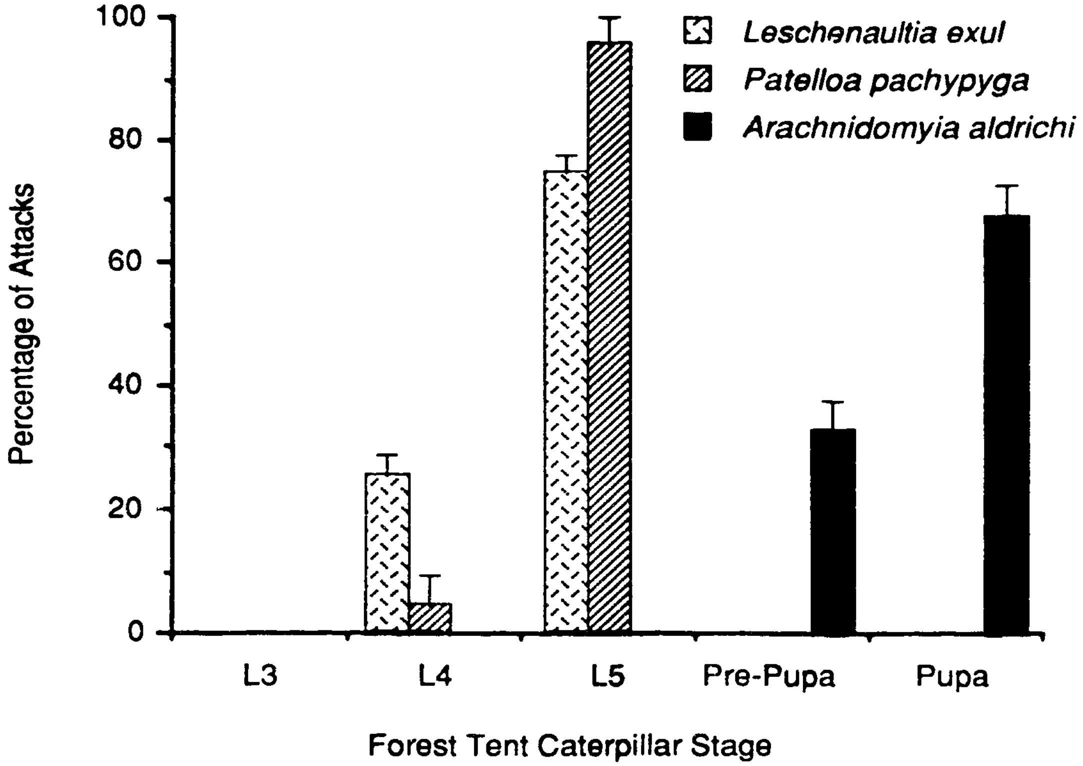


Fig. 2.7. Percentage of the total parasitism (+/- SE) by each species that occurred at each forest tent caterpillar developmental stage. The attack phenology was estimated from two outbreak populations for the larval parasitoids *L. exul* and *P. pachypyga* and four outbreak populations for the pupal parasitoid *A. aldrichi*.

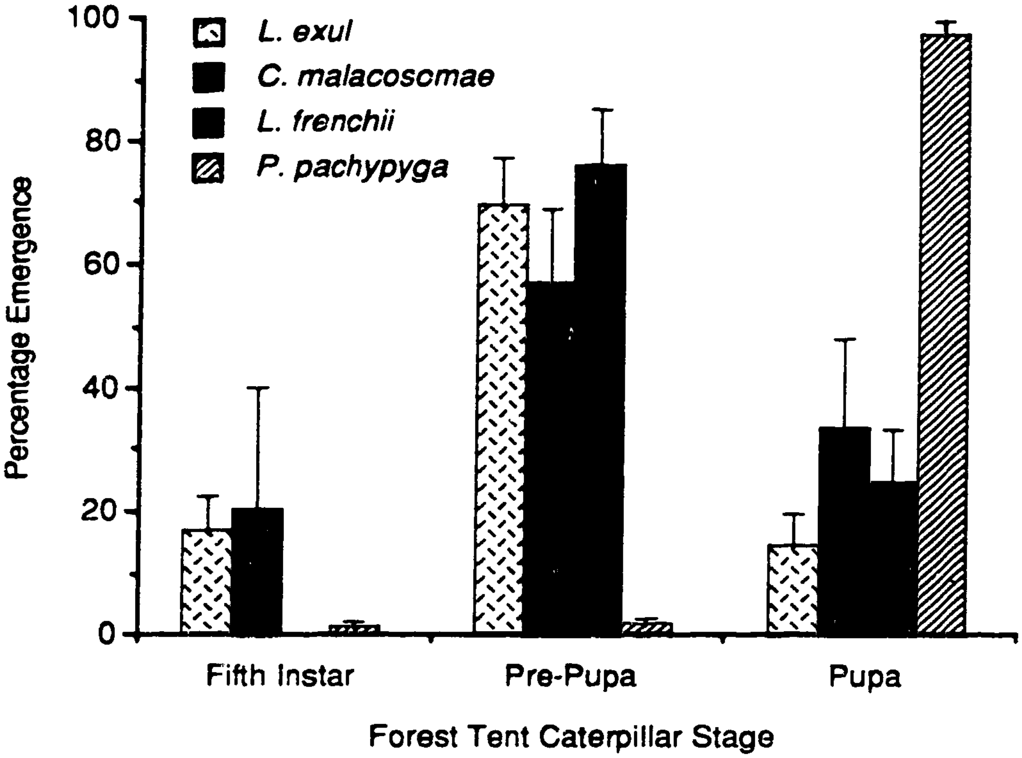
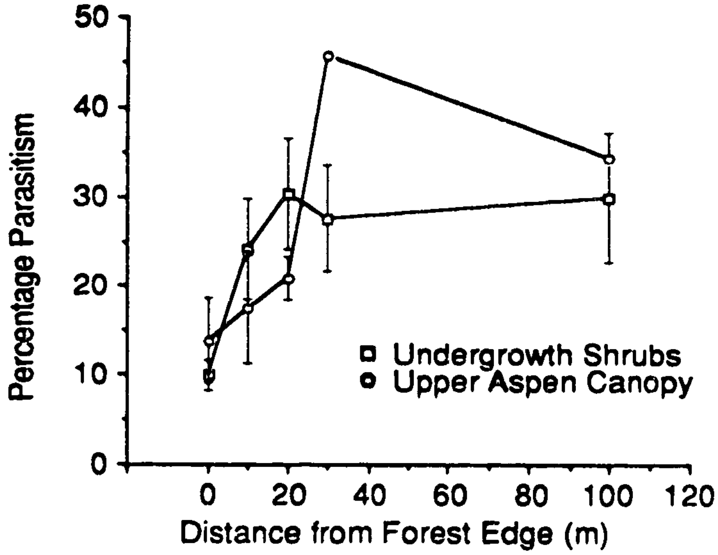


Fig. 2.8. Percentage of total emergence (+/- SE) by each species of tachinid that occurred at each forest tent caterpillar developmental stage.

(a) Tachinid parasitism of pupae.



(b) Sarcophagid parasitism of pupae.

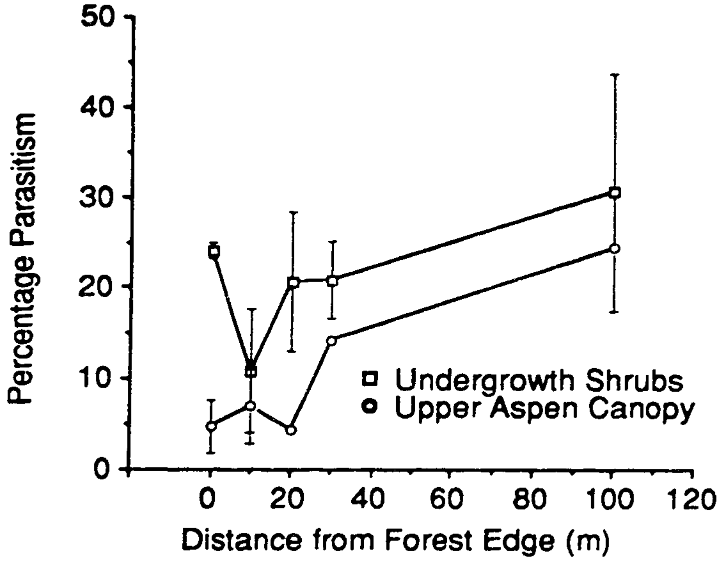
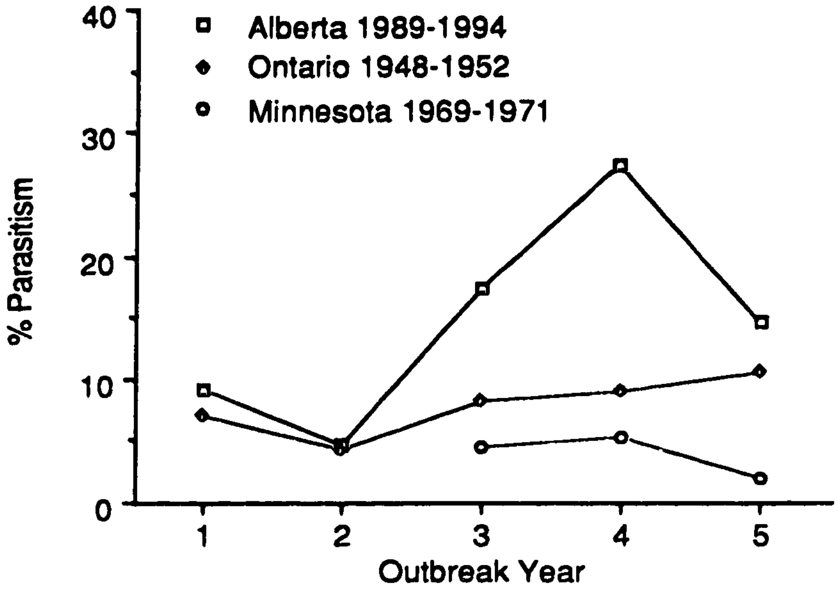


Fig. 2.9. Parasitism (+/- SE) of forest tent caterpillar cocoons along two 100 m transects by tachinid and sarcophagid flies. At each point on the transect, cocoons were collected from two stata, the canopy higher than 10 m and undergrowth shrubs below 1.5 m. Data for 30 m and 100 m in the upper canopy came from only one transect.

(a) *Leschenaultia exul*



(b) *Patelloa pachypyga*

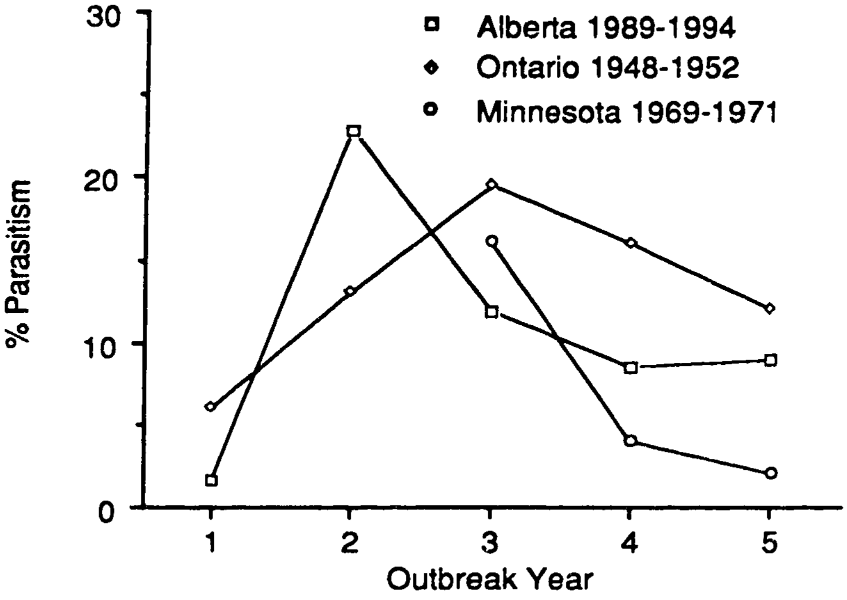


Fig. 2.10. Geographic variation in parasitism of forest tent caterpillar larvae by *L. exul* and *P. pachypyga*. The dynamics recorded in this study are compared with data from Ontario (Sippell 1957) and Minnesota (Witter & Kulman 1979).

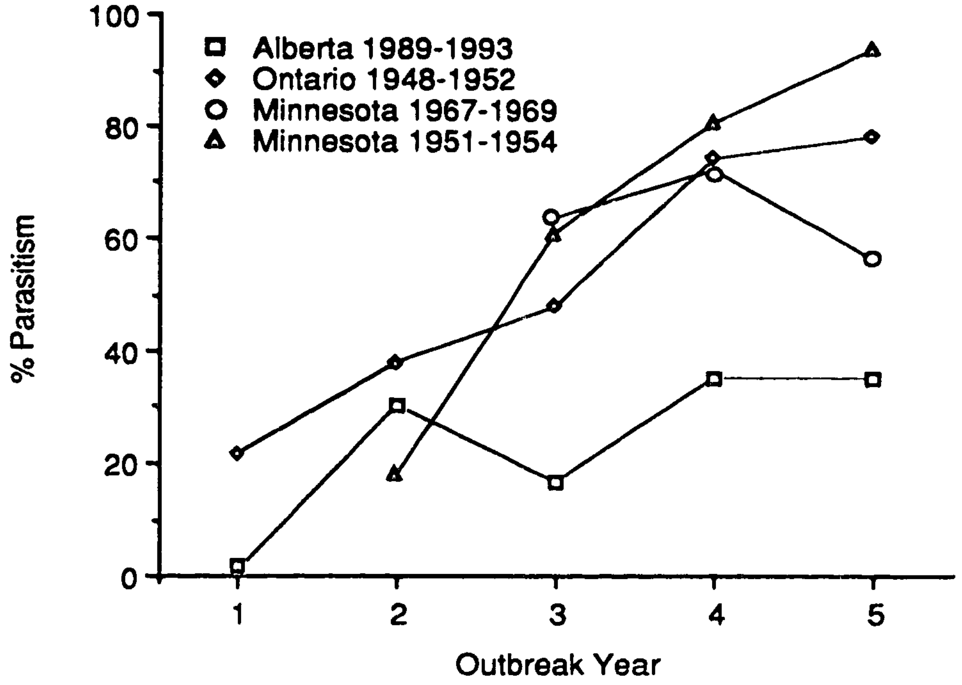


Fig. 2.11. Geographic variation in parasitism of forest tent caterpillar pupae by *Arachnidomyia aldrichi*. The dynamics recorded from Alberta are compared with data from Ontario (Sippell 1957) and two studies in Minnesota (Hodson 1977; Witter & Kulman 1979).

3. THE RESPONSE OF NATURAL ENEMIES TO EXPERIMENTALLY CREATED FOREST TENT CATERPILLAR POPULATIONS

3.1 INTRODUCTION

The forest tent caterpillar (FTC), *Malacosoma disstria* Hübner, is one of the most important defoliators of deciduous trees in North America. Outbreaks have been recorded on a variety of hosts, but over its northern range, the primary host of FTC is trembling aspen, *Populus tremuloides* Michx. In western Canada, vast outbreaks occur at approximately ten year intervals (Hildahl & Reeks 1960). The duration of outbreaks is variable but generally last less than five years at any particular locality (Sippell 1962). Many agents have been implicated in the collapse of outbreaks including disease (Stairs 1964), starvation (Hodson 1941; Sippell 1957), parasitoids (Hodson 1941, 1977) and weather (Blais et al. 1955; Prentice 1954; Gatreau 1964).

There have been several long term studies of FTC population dynamics although all have concentrated on epidemic populations (e.g., Hodson 1941; Sippell 1957; Ives 1971; Witter & Kulman 1979). Following outbreaks, FTC populations subside to endemic levels and may persist at very low densities for many years. Low population densities have prevented detailed studies on regulatory processes acting between outbreaks (Hodson 1941). Little information has been published about mortality agents and other factors acting on endemic populations (Witter et al. 1975; Witter 1979) even though Sippell (1957) and Witter & Kulman (1979) speculated that parasitoids could be important in their regulation.

Predation generally constitutes a relatively minor component of outbreak FTC mortality (Witter et al. 1972) but the role of predators in endemic populations is unknown. Research on other major defoliators such as gypsy moth, (*Lymantria dispar* L.), Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough) and the coniferaphagous budworms (*Choristoneura* spp.) indicates that both vertebrate and invertebrate predation can be important in maintaining sparse populations (e.g., Campbell & Sloan 1977; Miller &

Renault 1981; Furuta 1982; Campbell & Torgersen 1983; Mason & Torgersen 1983; Torgersen et al. 1983).

Localized spatial variation in susceptibility to mortality agents may be important in the low density dynamics of FTC populations. Harmsen & Rose (1983) suggested that endemic FTC populations may persist in low lying moist forest types and experience decreased rates of parasitism in these habitats. In other defoliators such as the gypsy moth, low level populations can be associated with susceptible forest types. Mortality from natural enemies may be reduced in these forests creating refugia or foci where incipient outbreaks can begin (Skinner et al. 1993).

The role of natural enemies in population regulation depends on the strength of density-dependent responses across a variety of prey densities. These responses can determine whether a population is stable, cyclic or fluctuates randomly (May 1986). Regulation of insect populations by density-dependent mortality has long been debated (e.g., Dempster 1983; Hassell 1985, 1987; Murdoch & Reeve 1987; Mountford 1988; Stiling 1988; Hassell et al. 1989; Turchin 1990). Many arguments have focused on the detection of density-dependent processes operating between generations. Hassell (1985) suggested that time lags or natural stochasticity could obscure density dependent trends in temporal life table data. Furthermore, life table studies where mortalities are averaged for each generation can overlook important population regulation processes occurring as the result of spatial heterogeneity within a generation (Hassell 1987).

Inherent difficulties in detecting density dependence from conventional life table studies have led some recent authors to suggest population manipulations as an alternative strategy (Hassell 1987; Murdoch & Reeve 1987; Price 1987). This approach also circumvents some logistical problems associated with sampling low density populations. Manipulative population studies have clearly shown that spatially density-dependent parasitism can indeed suppress localized increases in gypsy moth populations (Liebhold & Elkinton 1989; Gould et al. 1990).

In this chapter I describe results of an experimental approach to ascertain the response of natural enemies to patches of FTC at different densities in two forest types. These experiments were conducted in previously defoliated forests where natural FTC populations were so low as to be virtually undetectable. My goal was to elucidate whether parasitoids have the potential to play a significant regulatory role in endemic FTC populations or if other factors are more important.

3.2 MATERIALS AND METHODS

3.2.1 Site description.

The study was conducted at the George Lake Field Site (114 °06'W, 53°57'N) in north central Alberta, Canada (Fig. 3.1). Following ten years of moderate to severe defoliation, FTC populations in this area collapsed in 1989 and from 1990-1993, egg bands were rare or absent in the surrounding forest. Preliminary work began in 1992 and was followed by the main study in 1993. No naturally occurring egg bands were found in any of the plots used in 1992 or 1993.

Six plots were established in both upland and lowland aspen forests. The lowland forest was co-dominated by ca. 60 year old trembling aspen and balsam poplar (*Populus balsamifera* L.) and was characterized by a diverse understory of saskatoon (*Amelanchier alnifolia* Nutt.), pin cherry (*Prunus pensylvanica* (L.f.)), choke cherry (*Prunus virginiana* L.), wild rose (*Rosa acicularis* Lind.), green alder (*Alnus crispa* (Ait.) Pursh), Bebb willow (*Salix bebbiana* Sarg.), red osier dogwood (*Cornus stolonifera* Michx.) and paper birch (*Betula papyrifera* Marsh). The upland forest was on a low ridge top, dominated by 25 year old aspen originating from a burn. There was a sparse understory of wild rose, beaked hazelnut (*Corylus cornuta* Marsh), red osier dogwood and saskatoon.

3.2.2 Plot design and stocking.

Observations on natural, low-density FTC populations near Edmonton, Alberta indicated that small numbers of egg bands were concentrated in groves of aspen on south-facing slopes. I attempted to emulate this distribution with the design and stocking of my plots. Plots were located at least 50 m from each other. Each plot measured ca. 7 m X 5 m. and included 15 aspen trees and associated undergrowth. The trees were approximately equal in height (4-5 m) and dbh (6-9 cm). A 50 cm high polythene fence supported by 2" X 2" wood stakes was erected around the perimeter of each plot. Removal of overhanging branches and Tangletrap® (Tanglefoot, Grand Rapids, MI) barriers applied to the upper surface of the fence prevented escape of FTC larvae.

Egg bands for stocking were collected from an outbreak population near South Cooking Lake, Alberta. In order to be consistent and to minimize potential disease mortality, only large, regularly shaped egg bands with complete spumaline coverings were selected. Each egg band and a 5 cm portion of attached twig was placed in a 5% sodium hypochlorite solution for three minutes and then rinsed thoroughly with distilled water to remove viable nuclear polyhedrosis virus (NPV) from the egg surface as described by Grisdale (1968). As an assay for % hatch, 100 egg bands were selected from the above collection and were allowed to hatch in mesh bags near one of the plots Following hatch, these egg bands were collected and used to estimate the mean number of first instars that emerged / egg band.

Stocking was accomplished by attaching collected egg bands to the terminal twigs of aspen trees in each plot using thin copper wire. A low density treatment of 30 egg bands / plot, a medium density treatment of 60 egg bands / plot and a high density treatment of 120 egg bands / plot was replicated twice in each forest type. The highest stocking density is sufficient to cause moderate to severe defoliation of trees of this size in natural populations (Hodson 1941). Five aspen trees in each plot were left free of egg bands to insure adequate foliage for wandering late instar larvae.

Following hatch, family groups of first instar larvae remained close to the egg band they hatched from, feeding on expanding buds and new foliage. Two to three days after hatch, each tree was carefully examined to see how many family groups had become established. The number of visible family groups in each plot was multiplied by the mean observed hatch / egg band (123.0 ± 4.0) (mean ± SE), established as described above, to estimate initial larval densities in each plot (Table 3.1). In 1992, larval populations became established in only five of the twelve plots apparently due to poor synchrony with host plant phenology. In 1993, egg bands were warmed in the laboratory until approximately 24 hours before hatch. By monitoring individual tree phenology, it was possible to place egg bands on trees as the buds began to break. This method resulted in larvae becoming established in all of the lowland plots and in four of the six upland plots. In the two plots where larvae did not become established, all first instar larvae had disappeared from the trees within four days of hatch. Subsequent observations on other larvae released in these two plots suggested that very high ant predation may have been responsible for the termination of these populations.

3.2.3 Estimating larval mortality.

In 1992, a single sample of 100 fifth instar larvae was collected from each plot. Larvae were reared individually to estimate mortality rates. A time-specific analysis where mortality is measured over short, contiguous time intervals rather than stages (Gould et al. 1992) was used in 1993. Larvae were sampled at five day intervals from the second instar until pupation. Thirty larvae were randomly selected from each plot on each sampling day. These were individually reared at ambient temperature on fresh aspen foliage in 150 ml wax paper cups (Lily Cups Inc., Scarborough, Ontario). Larvae were checked every two days until death or emergence of moths or parasitoids. Moribund and dead larvae were examined for NPV, pathogenic fungi or parasitoids that failed to complete development. Parasitoids were collected, preserved and subsequently identified using the keys of Sippell (1961), Ross (1953) and D.J.M. Williams et al. (unpublished manuscript).

3.2.4 Marginal attack rates and density dependence.

The estimation of marginal attack rates is an important new method of assessing mortality which has increased the accuracy of life table studies (Royama 1981; Buonaccorsi & Elkinton 1990; Elkinton et al. 1992). Marginal attack rates estimate mortality due to a particular agent in the absence of competing contemporaneous agents. These were estimated according to the methods of Elkinton et al. (1992) using the observed proportions of sampled larvae dying as the basis of calculations (Appendix 1).

No attempt was made to assess density effects on parasitism in 1992. To detect density dependence in the 1993 generation, *k*-values (Varley &

Gradwell 1960) were calculated from the marginal attack rate for each five day period (Gould et al. 1990). These were summed over the season to produce *k*-values for each mortality agent in each plot (Table 3.2). The sum of all *k*-values provides the total generational mortality or *K* (Varley et al. 1973).

To test for the possibility of density dependence, the seasonal *k*-values for each agent in each plot were regressed against the log of initial larval densities ($\mathrm{Log}_{10}N_i$) in that plot (Varley & Gradwell 1968). Several authors have tried to address problems associated with using this method to detect density dependence (e.g., Eberhart 1970; Slade 1977). Both variates contain measurement error, inherent variability or both. Thus, an important assumption of ordinary least squares regression is violated, that is that all error should lie in the dependent variable. While recent ecological papers advocate Bartlett's (1949) triple group regression technique (Hassell 1987; Gould et al. 1990), others have suggested that this method is biased except in rare instances (Madansky 1959; Ricker 1973; Kuhry & Marcus 1977).

Reduced major axis (RMA) techniques have recently gained popularity as a possible solution for biased slopes (Ricker 1973, 1975; McArdle 1987), although McGororty et al. (1990) suggested that there is no completely satisfactory method to deal with the problem. The slope of a RMA regression line is the geometric mean of the linear regression coefficient of Y on X and the reciprocal of the regression coefficient of X on Y (Sokal & Rohlf 1981). RMA has been criticized by Jolicoeur (1975) but Slade (1977) showed that RMA was more reliable particularly with small sample sizes. RMA was used to generate slopes for all regressions in this study. Unlike other methods of calculating slope, a conventional test of significance with the null hypothesis H_0: $\beta = 0$ is inappropriate with RMA slopes (Sokal & Rohlf 1981). Instead, I tested for non-zero correlation coefficients using a one tailed t-test with n-2 degrees of freedom (Sachs 1982).

Because FTC densities were different in the two forest types, analysis of covariance (ANCOVA) with initial larval densities ($\mathrm{Log}_{10}N_i$) as the covariate, was used to compare mortalities between the two forest types in 1993 (PROC GLM in SAS) (SAS Institute 1992). If significant differences in mortality due to particular agents were detected between the two forest types, the possibility of density dependence was examined separately for the upland and lowland plots.

3.2.5 Defoliation and parasitism.

Since there is no reliable technique for estimating field densities of late instar FTC, *k*-values were also regressed on the mean defoliation level of each plot. As the majority of feeding is done by fifth instar larvae (Hodson 1941, Parry & Spence, unpublished data), defoliation provides a reasonable estimate of relative final instar densities. Values ranging from zero to five were assigned to each tree in each plot (Table 3.3), using an arbitrary scale (0 = no visible defoliation, 1= 10-30% , 2= 30-50%, 3= 50-70% 4= 70-90%, 5= complete defoliation). The mean percentage defoliation was calculated for each plot. Arcsine transformation was used because some plots had greater than 70% defoliation (Sokal & Rohlf 1981). Plot defoliation was regressed against the *k*-values for foliage ovipositing parasitoids and against total larval parasitism. Slopes and probabilities were calculated using the above methods.

3.2.6 Estimating pupal mortality.

No pupae were recovered in any plots in 1992. In 1993, two methods were used to assess pupal mortality. First, all cocoons that were spun in the plots were collected shortly before adult emergence. Secondly, to determine if pupal mortality observed in the plots was an artifact of the plot design, I deployed 179 pupae on the periphery of three lowland and three upland plots and compared mortalities with 92 pupae deployed at four other sites at least 1 km from the nearest plot.

In order to emulate natural pupation in the deployed treatments, cage reared final instar larvae were placed in fine mesh pollination bags (Kleen Test Products, Brown Deer, Wisconsin) just prior to pupation. The bags were placed over branches and the larvae allowed to spin cocoons in the enclosed foliage. Bags were removed, exposing the pupae for twelve days. Four host plants (aspen, balsam poplar, paper birch and saskatoon) commonly used as cocooning locations were used at each site.

All pupae were returned to the laboratory shortly before adult emergence, reared individually and moths and parasitoids allowed to emerge. Pupal parasitoids were identified using the keys of Ross (1953), Sippell (1961), and D.J.M. Williams et al. (unpublished manuscript). Pupal predation was easily quantified because the cocoon remains after the pupa is removed. Avian predators leave a characteristic hole in the silk cocoon (Sippell 1957; Stark & Harper 1982). The χ^2 statistic was used to detect differences between the treatments.

3.3 RESULTS

3.3.1 Larval mortality.

3.3.1.1 Parasitoid complex and phenology of attack.

In 1992 a braconid wasp, *Aleiodes* (= *Rogas*) *malacosomatos* (Mason), and three tachinid flies, *Leschenaultia exul* (Townsend), *Patelloa pachypyga* (A & W) and *Carcelia malacosomae* (Sellers), were reared from FTC larvae collected from the plots. *Aleiodes malacosomatos*, *L. exul* and *P. pachypyga* occurred in all five plots whereas *C. malacosomae* was found only in two upland plots. An additional tachinid, *Lespesia frenchii* (Williston), was reared from larvae in two upland plots in 1993. *Aleiodes malacosomatos*, *L. exul* and *P. pachypyga* were again abundant in 1993. In 1993, *C. malacosomae* was recovered from only one upland and one lowland plot.

The influence of forest type on parasitism rates in 1992 (Fig. 3.2a) was difficult to analyze because of uncertain larval density effects and the small number of plots in which larvae became established. Therefore the results must be viewed with some caution. However, a t-test suggested that *P. pachypyga* parasitism was higher in the lowland plots ($t = 3.698$, d.f. = 3, $P < 0.03$). Although not statistically significant ($t = 2.645$, d.f. = 3, $P = 0.08$), parasitism by *L. exul* was higher in the upland forest. *Aleiodes malacosomatos* parasitism did not vary between habitats and *C. malacosomae* was found only in the upland plots.

Distinct habitat associations were exhibited by two parasitoid species in 1993 (Fig. 3.2b). Analysis of covariance showed that *A. malacosomatos* parasitism was significantly higher in the upland plots in 1993 ($F = 8.54$, d.f.

= 9. $P < 0.02$). Mortality attributable to *P. pachypyga* was significantly higher in the lowland plots in 1993 ($F = 9.01$, d.f. = 9, $P < 0.01$) as it was in 1992. On the other hand, parasitism by *L. exul* and *C. malacosomae* were very similar in both forest types. *Lespesia frenchii* was reared from two upland plots but was not found in the lowland habitat. Although higher in the lowland plots, total larval parasitism was not significantly different ($F = 4.48$, d.f. = 9, $P = 0.06$) from the upland plots. Higher levels of parasitism in the lowland plots is primarily due to the dominance of *P. pachypyga* in this habitat.

Although the magnitudes were different, the relative abundance of the species in the two forest types was consistent between years despite the use of different sampling methods. The exception was parasitism by *L. exul* which was higher in the upland plots than in the lowland plots in 1992 although the difference was not significant. This pattern was not seen for *L. exul* in 1993.

Parasitoid phenology was estimated by plotting percentage parasitism (mean ± SE) against sampling date (Calendar day) and FTC development. Periods of attack varied with species (Fig. 3.3). The only parasitoid of early instar larvae was *A. malacosomatos* which initiated attack on late second instars. *Leschenaultia exul* was the first tachinid to parasitize larvae and its impact gradually increased until the end of the larval period. Both *C. malacosomae* and *L. frenchii* were not recovered until late in the final instar. Although *P. pachypyga* initiated oviposition when larvae were in the fourth instar, the majority of the parasitism occurred in the last two sampling dates at the end of the larval period.

3.3.1.2 Density-dependent parasitism.

The response of different parasitoid species to FTC density was variable. Although a significant relationship with density was not evident in the lowland plots (Fig. 3.4a), *A. malacosomatos* exhibited a striking density-dependent response in the upland plots ($r = 0.940$, d.f. = 2, $p < 0.05$) (Fig. 4b). Neither *L. frenchii* nor *C. malacosomae* had significant density-dependent responses (Fig. 3.4c & 3.4d). Surprisingly, parasitism by the ubiquitous *L. exul* was not significantly correlated with density (Fig. 3.5a).

Parasitism by *P. pachypyga* was strongly correlated with FTC density in the lowland plots ($r = 0.900$, d.f. = 4, $p < 0.01$) (Fig. 3.5b) but this relationship did not hold in the upland plots (Fig. 5c). Total larval parasitism was significantly density dependent in the lowland plots ($r = 0.791$, d.f. = 4, $p < 0.05$) (Fig. 3.6a) but a significant correlation could not be demonstrated in the upland forest (Fig. 3.6b).

Initial larval density and mean plot defoliation were significantly correlated ($r = 0.721$, d.f. = 8, $p < 0.01$) although the relationship explained only about half of the variation in defoliation. Individual trees in the upland plots carried more foliage than those in the lowland plots because upland stand density was lower. More foliage on each tree likely contributed to the lower defoliation levels observed in the upland plots.

The two tachinids that lay microtype eggs on foliage had rather different responses to defoliation. Parasitism by *L. exul* was not significantly correlated with defoliation (Fig. 3.7a). Conversely, parasitism by *P. pachypyga* was significantly correlated with defoliation in lowland plots ($r = 0.901$, d.f. = 4, $p < 0.05$) (Fig. 3.7b) and although rates of parasitism were much lower in the upland plots, the relationship to defoliation was also significant ($r = 0.891$, d.f. = 2,) $p < 0.05$) (Fig. 3.7c).

Total larval parasitism was not significantly correlated with defoliation in the lowland plots although a positive slope was suggested by the data (Fig. 3.8a). These variables were strongly correlated in the upland forest ($r = 0.989$, d.f. = 2, $p < 0.01$) (Fig. 3.8b). The relationship between total larval parasitism and defoliation mainly reflects the response of *P. pachypyga* because it was the dominant parasitoid in all but two of the plots.

3.3.1.3 Other sources of larval mortality.

It was not possible to make quantitative estimates of invertebrate and vertebrate predation on larvae although observations suggested that it was important. *Calosoma frigidum* Kirby, a carabid beetle, was found attacking third instar larvae in three plots. As well, the predacious pentatomid, *Podisus brevispinus* Phillips, was observed attacking larvae on numerous occasions from the second through final instars. Mortality caused by this hemipteran can be quite high, particularly in the early instars (D. Parry unpublished data).

Least flycatchers (*Empydonax minimus* (Baird & Baird)), rose- breasted grosbeaks (*Pheuciticus ludovicianus* (L.)), yellow warblers (*Dendroica petechia* L.) and northern orioles (*Icterus galbula* (L.)) depredated late instar larvae. Observations of avian predation and high numbers of eviscerated final instar FTC found in the plots after the final larval molt, suggested that birds were more important larval predators in the lowland plots than in the upland plots.

Despite the precaution of bleaching all egg bands, nuclear polyhedrosis virus (NPV) occurred in all plots. Contamination or stressful conditions in the rearing facility led to an overestimation of NPV mortality as more larvae died from this disease in the rearing room than in the plots. For this reason it was not possible to assess disease mortality separately from other sources of non-parasitoid mortality in the plots.

Pooled estimates of mortality from sources other than parasitoids were not significantly different in the two forest types, although there was a marked reduction in this type of mortality in the upland plots. These residual sources of mortality were not significantly correlated with either initial larval density or defoliation (Fig. 3.9a & 3.9b).

3.3.2 Pupal mortality.

3.3.2.1 Parasitism.

Surprisingly few (< 2%) pupae with in the plots were parasitized by the sarcophagid flies *Arachnidomyia* (= *Sarcophaga*) *aldrichi* (Parker) and *Agria housei* (Shewell), both of which are abundant in FTC outbreaks (see Chapter 2). Because sarcophagids characteristically stain cocoons with exudates of proteolytic enzymes and few depredated cocoons showed this symptom, it is unlikely that bird predation obscured higher levels of parasitism by these flies. A few parasitized pupae were opened and abandoned with the maggot still inside, suggesting that birds may prefer pupae not parasitized by sarcophagids.

In addition to the sarcophagids, two species of generalist ichneumonid, *Itoplectis conquisitor* (Say) and *Gambrus canadensis canadensis*

(Provancher), were recovered in very low numbers from pupae. A single specimen of *Exorista mella* (Walker), a polyphagous tachinid parasitoid of lepidopteran larvae, also emerged from a pupa. This species did not appear in larval samples.

None of the deployed pupae in either treatment were attacked by pupal parasitoids. This suggests that the pupal parasitoids were attacking pupae only at the highest densities and ignoring pupae even at the edge of the plots.

3.3.2.2 Predation.

Total pupal mortality was very high in the three upland plots containing large numbers of pupae. Predators killed 90.8 ± 4.7% (mean ± SE) of the pupae and were the dominant source of pupal mortality (Fig. 3.10). Few caterpillars survived to pupation and no moths emerged in the lowland plots. Northern orioles were observed pulling the pupae out of the cocoons and all depredated cocoons showed similar damage. However, other bird species were also suspected of attacking pupae, particularly in the undergrowth where orioles were not observed foraging.

Predation was also the dominant source of mortality in the deployed treatments with 97.6 ± 1.8% and 94.7 ± 3.1% (mean ± SE) of the peripherally and distantly deployed pupae dying from predation (Fig. 3.10). There was no difference in survival between pupae on the plot peripheries and the pupae distantly deployed from the plots ($\chi^2 = 2.17$, d.f. = 1, $p = 0.10$). A comparison of mortalities in plot and peripherally deployed pupae indicated that bird predation was significantly higher on plot peripheries than within the plots, ($\chi^2 = 6.81$, d.f. = 1, $p = 0.01$). A significant difference was not found between the distantly deployed and plot pupal mortalities or between the four host plant species used in the deployed treatments.

Pupal predation had a deleterious effect on the survival of larval parasitoids such as *P. pachypyga* that emerge from FTC pupae. Only 3.3% of pupae recovered from the plots yielded this species. This is a considerable reduction from the observed 14.4% *P. pachypyga* parasitism on the final larval sampling day, suggesting that birds were not discriminating between pupae containing tachinids and unparasitized pupae and may even favor them.

3.3.3 Total generational mortality.

The combined action of mortality agents reduced the experimental populations to very low levels. From an initial density of approximately 82 000 first instar larvae in ten plots, 33 adults emerged, all in the upland forest. Although far more larvae survived to pupation in the upland forests, avian predation compensated for this difference with the result that forest type had no significant impact on total mortality. Total mortality was not dependent on density and was not significantly correlated with defoliation (Fig 3.11a & 3.11b) although both relationships had strong positive slopes.

3.4 DISCUSSION

3.4.1 Parasitoids.

The density-dependent response by *A. malacosomatos* in the upland plots and its abundance in natural low density populations (Chapter 2) suggest that this species may be relatively important in the dynamics of endemic FTC populations. As well, its early attack phenology allowed *A. malacosomatos* to avoid competition with mortality factors that come in to play in the later instars. Reduced levels of parasitism in lowland forests was not caused by standing water drowning parasitoids as was suggested for this species in Ontario (Harmsen & Rose 1983). *A. malacosomatos* pupates inside the mummified host's body, cemented to branches and silk in the canopy (Sippell 1957; Chapter 2) and would not usually be affected by hydrological conditions on the forest floor. The results of this study and Harmsen & Rose (1983) suggest that *A. malacosomatos* may prefer drier upland aspen forests.

Some authors have speculated that both *L. frenchii* and *C. malacosomae* could be important in endemic populations (Sippell 1957; Witter & Kulman 1979; Chapter 2.). However, parasitism by these flies was low in my plots. Because the polyphagous *L. frenchii* is bivoltine, it depends on a secondary host and low population densities of other hosts could explain the minimal impact observed in this study. *Carcelia malacosomae* may be a low density specialist (Chapter 2) but this species appeared only sporadically in both 1992 and 1993. These results suggest that neither *L. frenchii* nor *C. malacosomae* are capable of regulating low density FTC populations.

Parasitism by *L. exul* was much lower in the upland plots in 1993 than in 1992. Background FTC levels were very low in 1992 and *L. exul* may have become concentrated in the plots. Subsequent sampling and predation of larvae removed the progeny of flies attracted to the plots and could have depleted the pool of *L. exul* available to parasitize larvae in 1993.

The lack of an aggregative response to spatial variations in host density by *L. exul* was unexpected as it is the most abundant tachinid in natural low density populations in Alberta (Chapter 2). *Leschenaultia exul* requires several generations to become common in outbreak FTC populations and these dynamics may have been mirrored in the results from the plots.

Leschenaultia exul selectively oviposits microtype eggs very near feeding groups of larvae, often on the underside of leaves that are actively being consumed by caterpillars (personal observation). This strategy is particularly effective at endemic densities where defoliation is minimal because it insures that some of its eggs will be ingested. Because of the selectivity in oviposition behavior, *L. exul* does not depend on high levels of defoliation for its eggs to be consumed. This may account for the absence of an association with defoliation in the plots.

High rates of parasitism observed for *P. pachypyga* may have been an artifact of the plot design as this species is generally rare in low density FTC populations, becoming abundant only after the first year of outbreaks (Sippell 1957; Witter & Kulman 1979; Chapter 2). Plot barriers prevented larval wandering which normally occurs after the fourth molt in natural low density populations. The phenology of *P. pachypyga* observed in this and other studies (e.g., Chapter 2) suggests that oviposition peaks late in the final instar. The solitary nature of the dispersed final instars and *P. pachypyga*'s reliance on high levels of defoliation for its eggs to be consumed, result in the negligible impact observed in natural endemic populations. However, the high rates of parasitism observed in the experimental plots do suggest that *P. pachypyga* was very effective in finding small patches of FTC at high density. They also indicate that this tachinid is relatively abundant even four years after natural FTC populations crashed in the study area.

Despite the very low background FTC population, both *A. malacosomatos* and *P. pachypyga* responded strongly to increased host densities in the plots although these responses were restricted to particular habitats. Unlike similar manipulative studies with gypsy moth (Liebhold & Elkinton 1989; Gould et al. 1990), mortality from parasitoids was not high enough to suppress the experimental host populations within a single generation.

Although the results of this study suggest that parasitoids may play a relatively minor role in low density FTC populations, use of an incorrect spatial scale could have obscured the true nature of density-dependent responses by parasitoids. Both Heads & Lawton (1983) and Hassell et al. (1987) showed that the ability to detect density dependence changed depending on the spatial scale used. Density dependence may have occurred at the level of trees within plots for smaller species such as *A. malacosomatos*. For the large tachinids with good dispersal capabilities, all of the plots in one forest type may be evaluated as a single patch and density dependence could occur across patches distributed as were my plots. It is also possible that the unnaturally high caterpillar densities concentrated within the small area of the plots overwhelmed the parasitoids capability to suppress the populations.

Although not addressed in this study, recent work has indicated that traditional analyses test only for direct density dependence and may overlook lags (Turchin 1990; Turchin & Taylor 1992). The possibility of delayed density dependence is a concern particularly for the parasitoids *L. exul* and *A. malacosomatos* which are so prevalent in endemic FTC populations. Further investigation is required to address the possibility of delayed density-dependent regulation of FTC populations.

3.4.2 Predation.

Although at least sixty species of birds are predators of tent caterpillars (Witter & Kulman 1972), it is generally thought that most birds favor smaller individuals over the hairy last instar larvae (Fashingbauer et al. 1957). However, noticeable bird predation did not occur until after the fourth molt in the plots. Although Heinrich (1979, 1993) suggested that the conspicuous large larvae of FTC are relatively immune to avian attack, high rates of predation observed in this study suggest that birds can cause biologically significant mortality in low density populations. Predation occurred despite the concurrent abundance of several species of aspen feeding lepidopterans which are not protected by setae or other obvious defences. Bird predation on FTC larvae coincided with nesting season for many song birds in this region and hungry nestlings may expand the range of prey taken by the birds. This could also account for the apparent lack of predation on smaller larvae earlier in the season.

Northern orioles, least fly catchers and yellow warblers were observed seizing large tent caterpillars in their beaks and rupturing them by banging them on branches. Viscera was eaten while the head capsule and integument were discarded. Previous researchers have observed orioles and other bird species using similar methods to circumvent the defensive setae of *Malacosoma* spp. (Forbush 1896; McAtee 1926; Grant 1959; Root 1966). Forbush (1896) also suggested that stomach content analysis would overlook larvae eaten in this manner, a point that has been ignored by many subsequent researchers.

During outbreaks, impact of avian predators on FTC pupae generally accounts for only a fraction of the observed mortality and is considered a sporadic occurrence (Hodson 1943, Hardy 1943; Stark & Harper 1979). In contrast, high mortality of both plot and distantly deployed pupae indicates that they are a preferred food item and are actively sought by birds over a range of densities when FTC populations are low. Orioles appeared to be the primary source of pupal predation in this study. In eastern North America, McAtee (1926) also observed orioles feeding hundreds of FTC pupae to their young, providing further evidence that pupae may be a common food source for this bird.

Late larval and pupal predation may help explain some enigmatic behaviors exhibited by FTC larvae. Extensive wandering by final instars has long been considered a response to starvation (Hodson 1941; Sippell

1957), but caterpillars also disperse independently of conspecific density or food abundance suggesting that an alternative mechanism is acting (D. Parry & J.R. Spence unpublished data). I hypothesize that predation on late instars and pupae in endemic populations has selected not only for FTC to develop quickly, but also to undertake their characteristic movements. Because handling time for hairy larvae is greater, it may be profitable for generalist predators to exploit FTC larvae only when they are aggregated. Aggregated larvae are also associated with conspicuous defoliation and are relatively easy to discover whereas locating the dispersed final instars may require extensive search time.

Southwood & Comins (1976) suggested that prey populations have a stable lower equilibrium that is far below the carrying capacity of their environment. Functional and numerical responses by generalist predators create a "natural enemy ravine" that maintains prey populations at this equilibrium. Natural variation in predator numbers and spatial heterogeneity can change the "depth" of the ravine allowing populations to move to higher equilibria. Models published by Ludwig et al. (1978) and Clark et al. (1979) and applied to eastern and western spruce budworm populations support the idea of a "natural enemy ravine" or "predator pit" where the action of generalist predators, in particular birds, maintain populations of budworm at a low density (Campbell 1993). Beddington et al. (1978) referred to systems where polyphagous predators maintain prey populations at low levels as "complex density dependence". They predict that any reduction in the efficiency of these polyphagous predators due to natural fluctuations in the system will result in periodic outbreaks.

The results from this study suggest that FTC populations may have more than one stable equilibrium point. At low densities, FTC may be held in check by bird predation augmented by parasitism. Small perturbations may favor the rapid increase of FTC populations in forest types with reduced natural enemy complexes. Once past a certain threshold, the response of natural enemies will be insufficient to prevent the population from moving to a less stable outbreak equilibrium where intra-specific competition for foliage may be the limiting factor.

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Table 3.1. Estimated first instar density in the plots at George Lake, Alberta, 1993.

Location	**Plot**	**Initial Density**	**Log Initial Density**
Lowland	1	14761	4.169
"	2	14761	4.169
"	3	3690	3.567
"	4	4428	3.646
"	5	2952	3.470
"	6	738	2.868
Upland	1	0	-
"	2	7381	3.868
"	3	0	-
"	4	14761	4.169
"	5	3690	3.567
"	6	14761	4.169

Initial density = (123.0 first instars / eggband) X (# family groups / plot)

Table 3.2. k-values for all mortality sources acting on FTC in the experimental plots at George Lake, 1993

			Lowland Forest Plots			
Source	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6
A. malacosomatos	0.2231	0.0000	0.1249	0.0164	0.0000	0.0591
L. exul	0.0212	0.0322	0.0507	0.1263	0.2508	0.0000
P. pachypyga	0.5936	0.4894	0.2846	0.5242	0.3678	0.0530
C. malacosomae	0.0300	0.0000	0.0000	0.0000	0.0000	0.0000
L. frenchii	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Larval Parasitism	0.8679	0.5215	0.4602	0.6689	0.6186	0.1122
Larval Residual	2.3470	2.8694	2.6297	2.5002	1.9484	2.4556
All Larval Mortality	3.2149	3.3910	3.0899	3.1691	2.5671	2.5671
All Pupal Mortality	0.9542	0.7782	0.4771	0.4771	0.9031	0.3010
Total Mortality	4.1691	4.1691	3.5671	3.6463	3.4702	2.8688

			Upland Forest Plots			
Source	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6
A. malacosomatos	0	0.2096	0	0.2432	0.1409	0.2978
L. exul	0	0.0743	0	0.0582	0.0669	0.1163
P. pachypyga	0	0.3235	0	0.0746	0.0177	0.0929
C. malacosomae	0	0.0000	0	0.0000	0.0000	0.2228
L. frenchii	0	0.0000	0	0.0483	0.0000	0.0458
Larval Parasitism	0	0.6074	0	0.4244	0.2256	0.5750
Larval Residual	0	0.4275	0	1.5220	3.0404	1.3019
All Larval Mortality	0	1.0349	0	1.9465	3.2660	1.8769
All Pupal Mortality	0	1.6027	0	1.0186	0.3010	2.2923
Total Mortality	0	2.6377	0	2.9650	3.5671	4.1691

Table 3.3. Estimated defoliation of 15 trembling aspen in each experimental plot at George Lake, Alberta, 1993.

			Lowland Plots			
Tree #	1	2	3	4	5	6
1	5	5	3	4	4	4
2	4	5	4	3	4	4
3	4	5	4	4	5	3
4	5	5	3	4	3	2
5	3	5	3	4	2	2
6	3	5	2	3	2	2
7	3	4	2	3	1	1
8	4	4	3	2	2	1
9	4	4	2	2	2	2
10	5	5	2	2	1	2
11	5	5	1	4	3	1
12	3	4	1	2	3	1
13	4	4	2	2	2	1
14	4	4	1	1	2	0
15	4	5	2	2	2	0
Mean	4	4.6	2.333	2.800	2.533	1.733
%	80	92	46.667	56.000	50.667	34.667
Arcsine Transform	0.927	1.168	0.486	0.594	0.531	0.354

			Upland Plots			
Tree #	1	2	3	4	5	6
1	0	4	0	2	3	3
2	0	4	0	2	3	3
3	0	3	0	2	3	2
4	0	3	0	3	2	3
5	0	5	0	4	3	3
6	0	3	0	3	2	3
7	0	4	0	3	5	2
8	0	3	0	3	2	2
9	0	3	0	4	2	2
10	0	3	0	3	1	2
11	0	3	0	3	0	2
12	0	2	0	3	4	4
13	0	3	0	3	0	4
14	0	4	0	2	1	4
15	0	4	0	3	0	2
Mean	0.000	3.400	0.000	2.867	2.067	2.733
%	0	68.000	0.000	57.333	41.333	54.667
Arcsine Transform	0	0.748	0	0.611	0.426	0.578

0 = no defoliation, 1 = 10-30%, 2 = 30-50%, 50-70%, 4 = 70-90%, 5 = complete defoliation

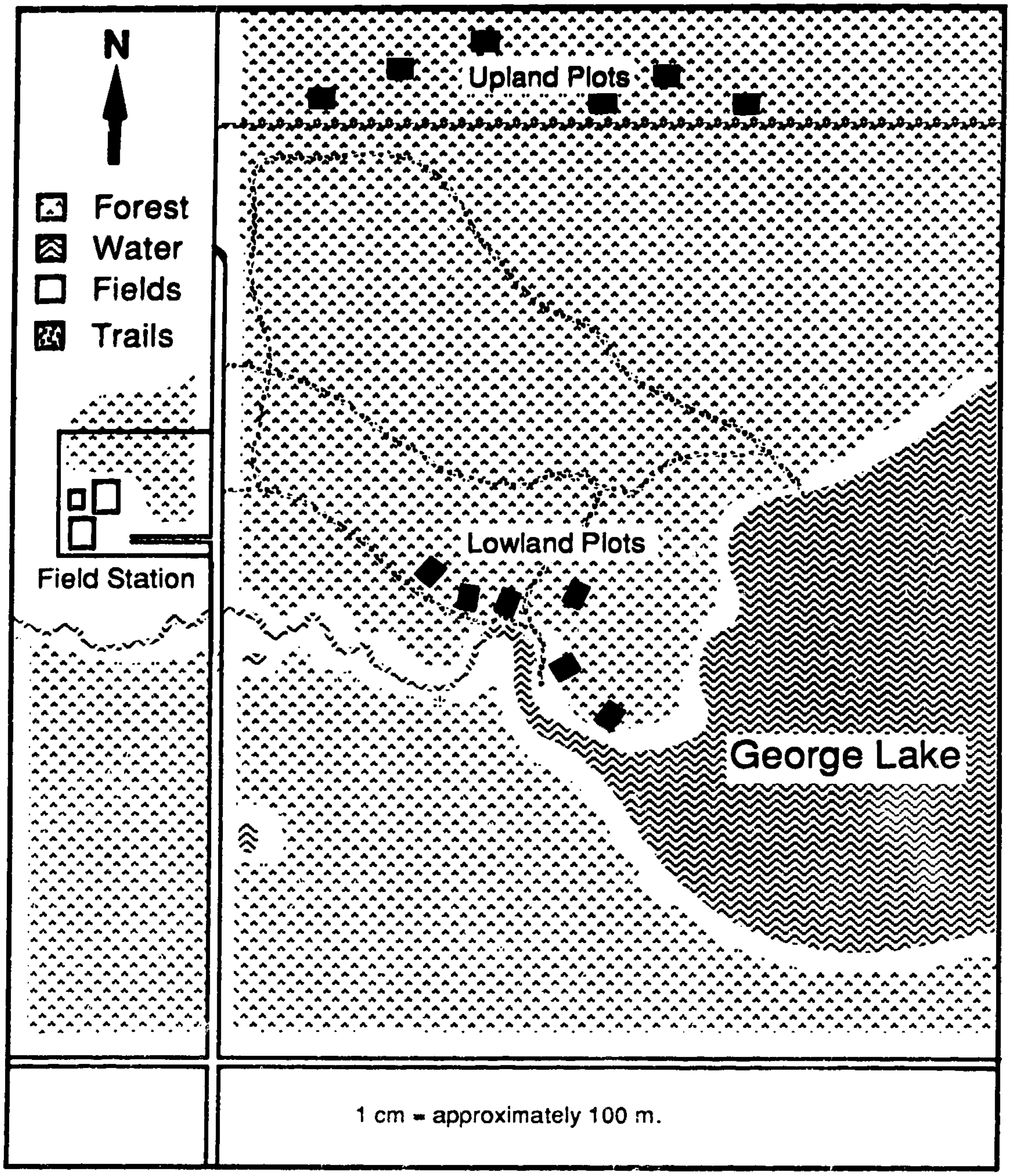
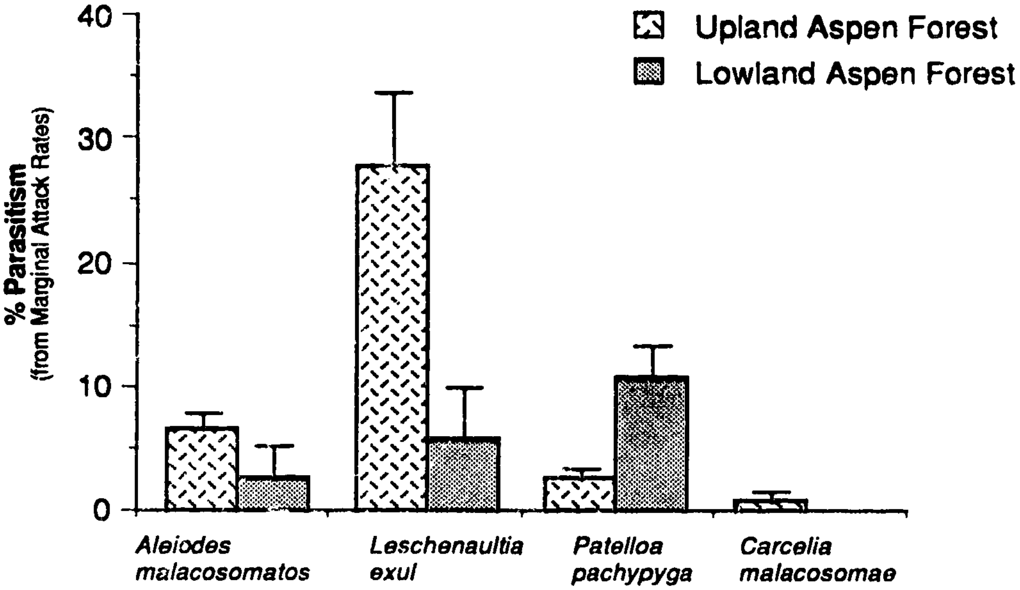
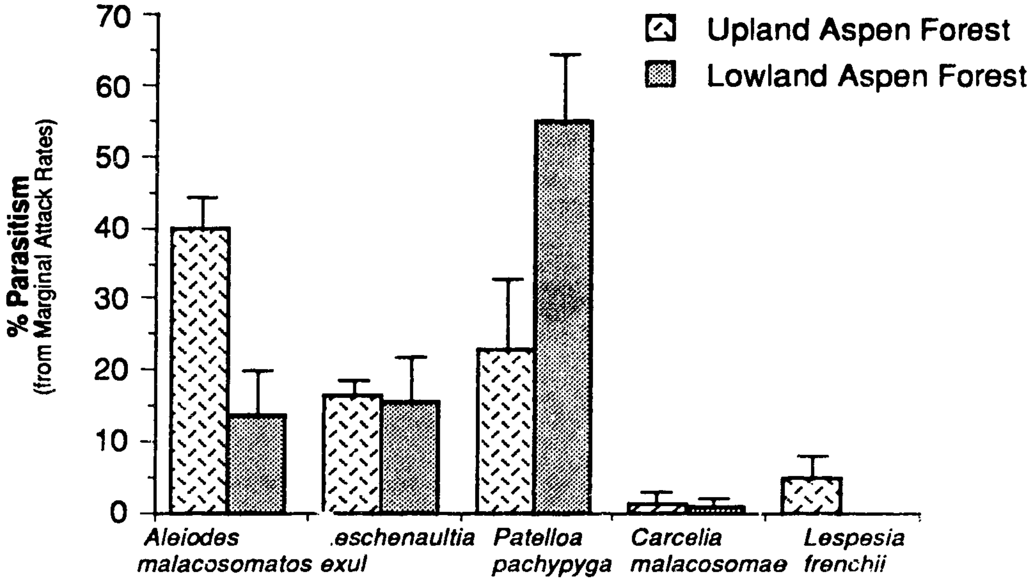


Fig. 3.1. Location of experimental plots at George Lake, Alberta. Located approximately 100 km North of Edmonton, Alberta, Canada.



(a) Parasitoids reared in 1992.



(b) Parasitoids reared in 1993.

Fig. 3.2. The impact of parasitoids (mean + / - SE) reared from forest tent caterpillar larvae sampled in the experimental plots, 1992 and 1993.

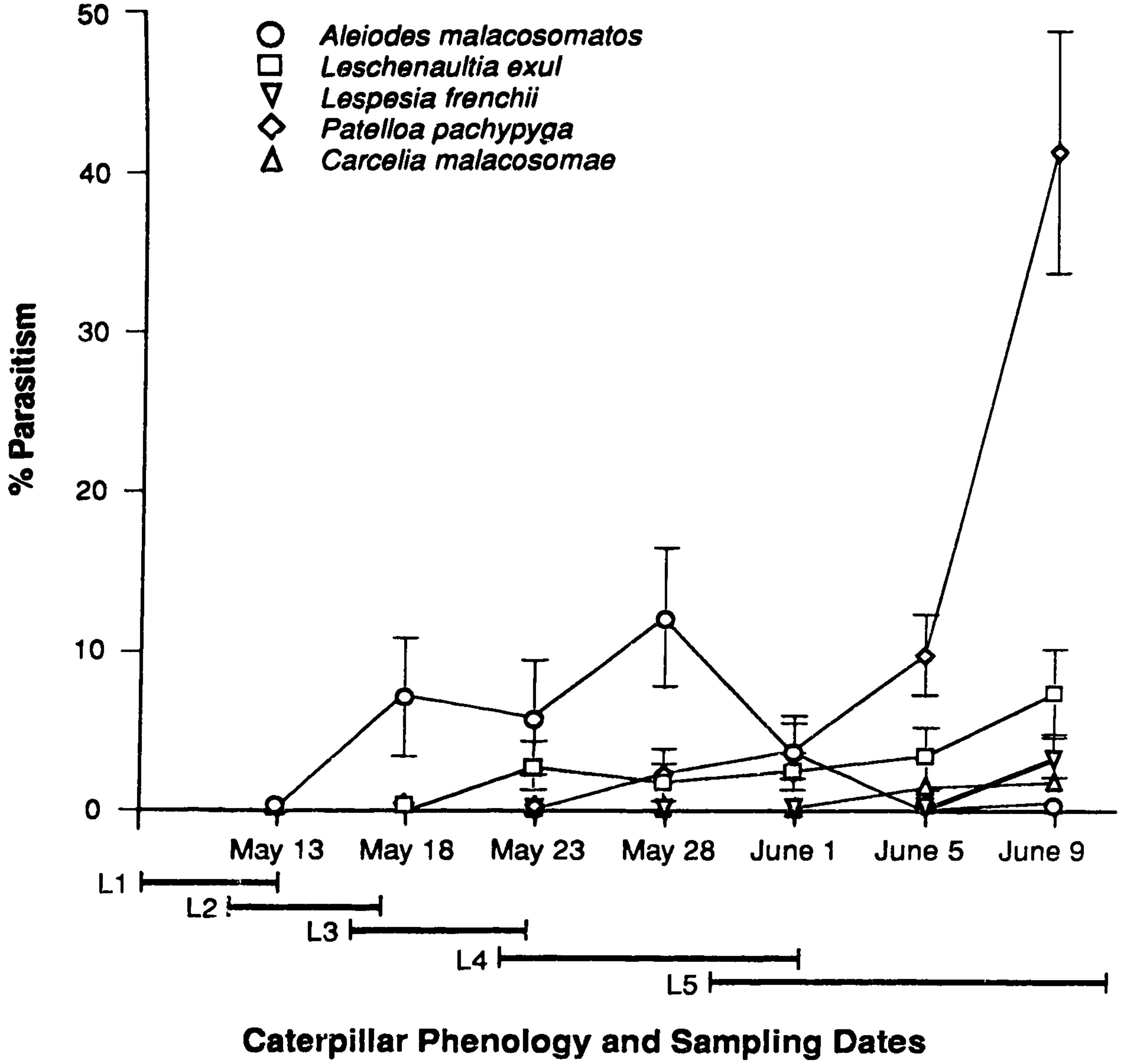
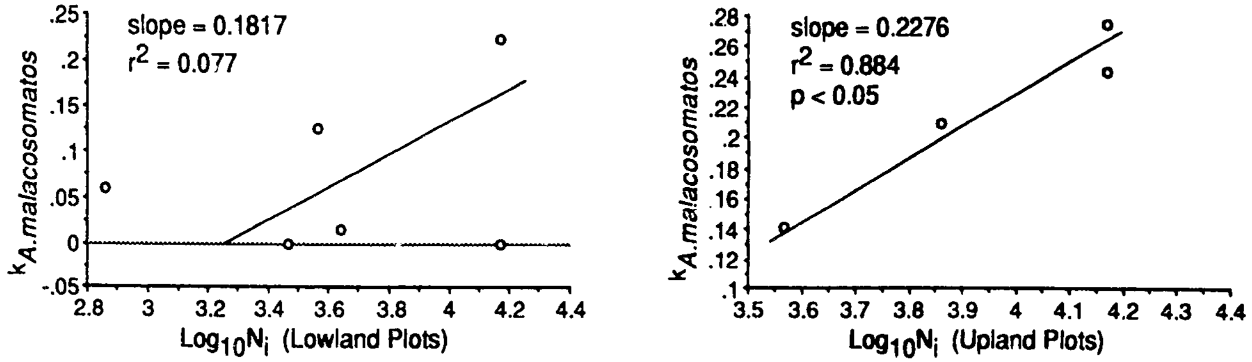
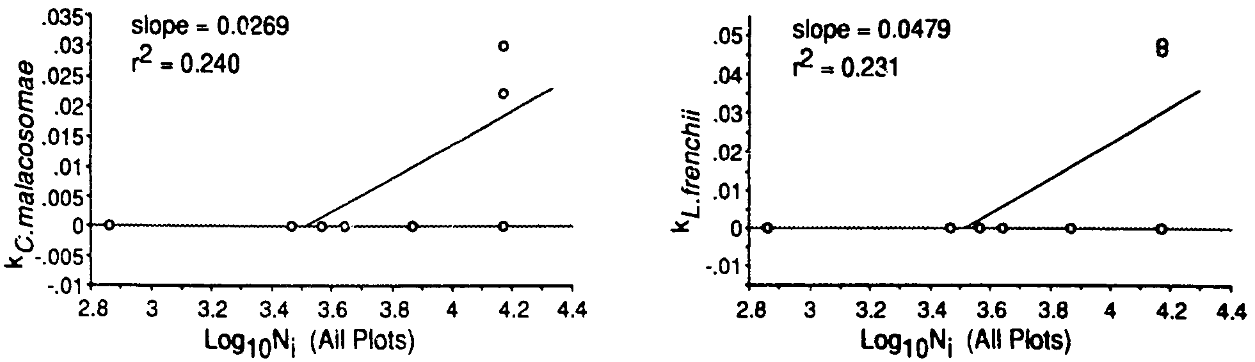


Fig. 3.3. Seasonal distribution of parasitoid attacks (mean +/- SE) in relation to forest tent caterpillar phenology and sampling date in the experimental plots (1993).



(a) *Aleiodes malacosomatos*

(b) *Aleiodes malacosomatos*

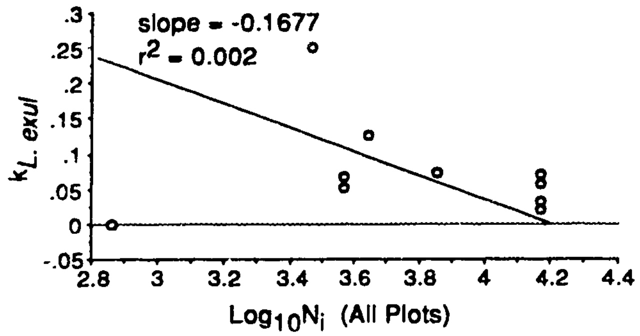


(c) *Carcelia malacosomae*

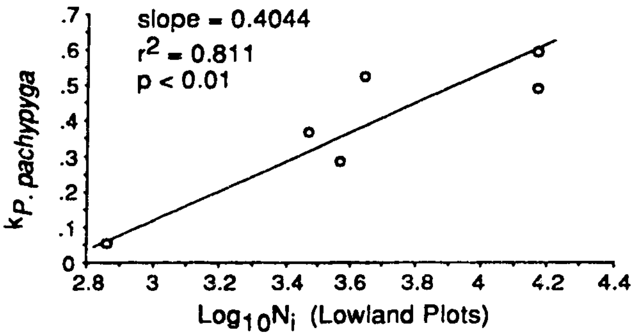
(d) *Lespesia frenchii*

Fig. 3.4. Density dependence of three parasitoids of forest tent caterpillar larvae in the experimental plots. Plots in the two forest types were pooled if parasitism rates were not significantly different between them. Probabilities are given for significant correlations.

(a) *Leschenaultia exul*



(b) *Patelloa pachypyga*



(c) *Patelloa pachypyga*

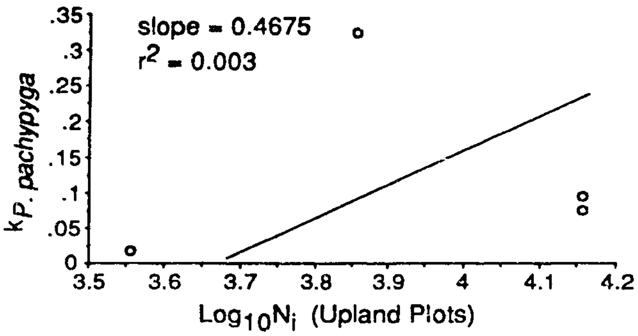
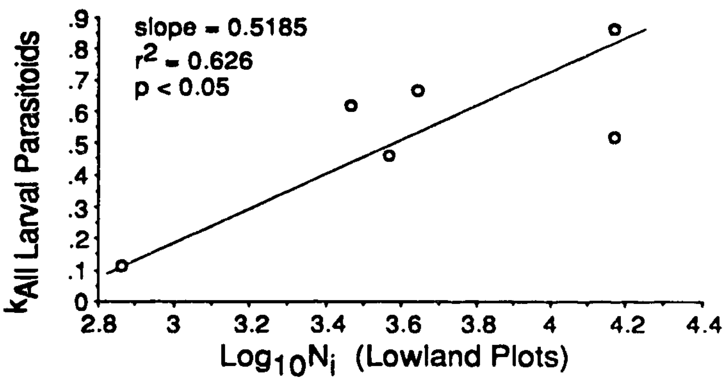


Fig. 3.5. Density dependence of two parasitcids of forest tent caterpillar larvae in the experimental plots. Plots in both forest types were pooled if parasitism rates were not significantly different between them. Probabilities are given for significant correlations.

(a) Total Larval Parasitism



(b) Total Larval Parasitism

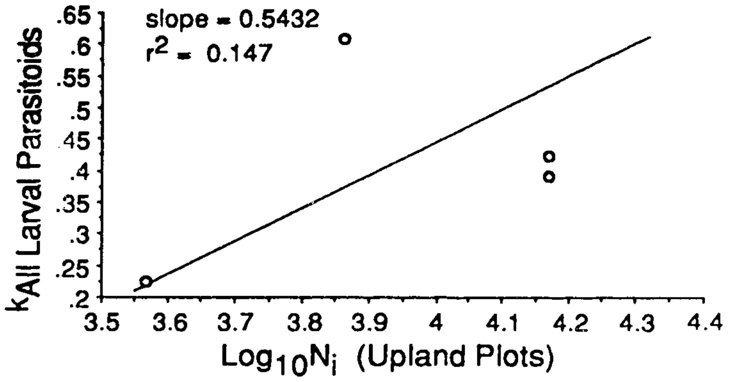
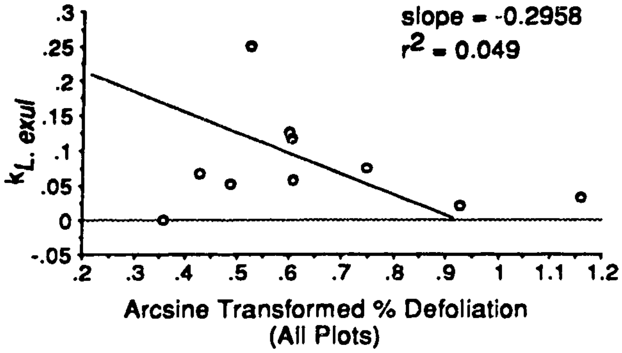
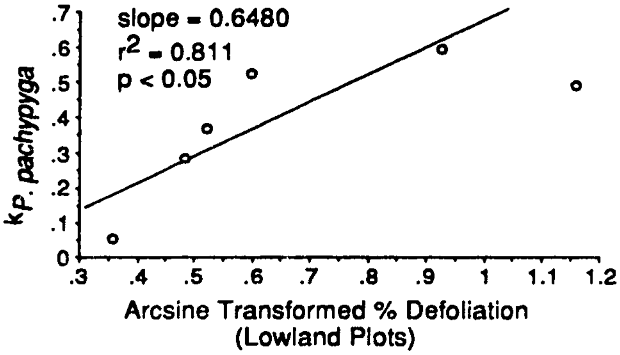


Fig. 3.6. Density dependence of total parasitism of forest tent caterpilla larvae in the experimental plots. Forest types are plotted seperately because parasitism rates were significantly different between them. Probabilities are given for significant correlations.

(a) *Leschenaultia exul*



(b) *Patelloa pachypyga*



(c) *Patelloa pachypyga*

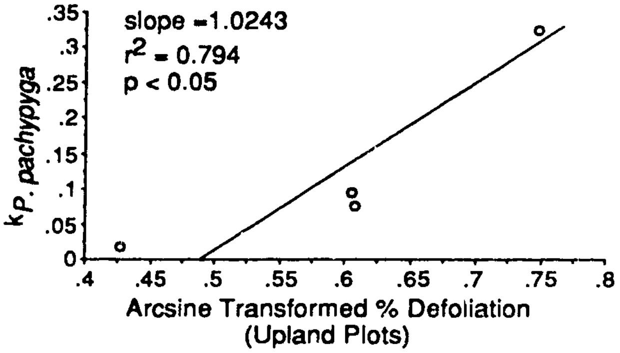
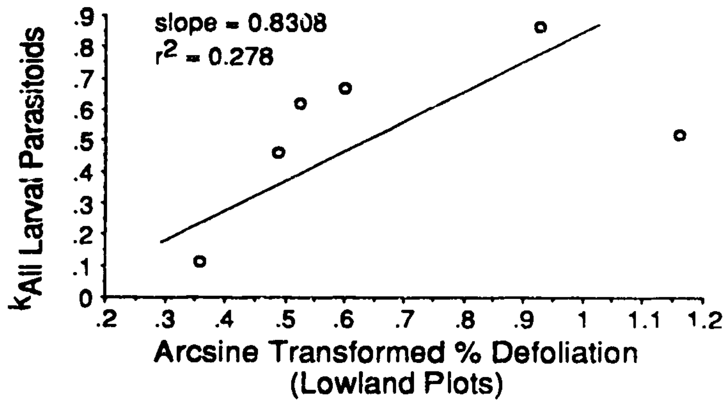


Fig. 3.7. Defoliation by forest tent caterpillar and parasitism by two larval parasitoids in the experimental plots. Plots in both forest types were pooled if parasitism rates were not significantly different between them. Probabilities are given for significant correlations.

(a) Total Larval Parasitism



(b) Total Larval Parasitism

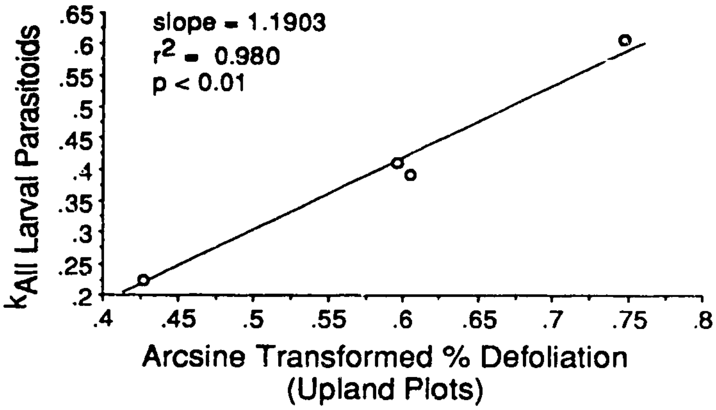
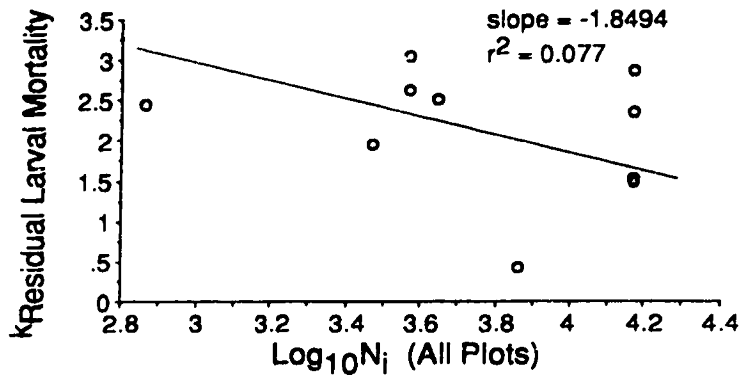
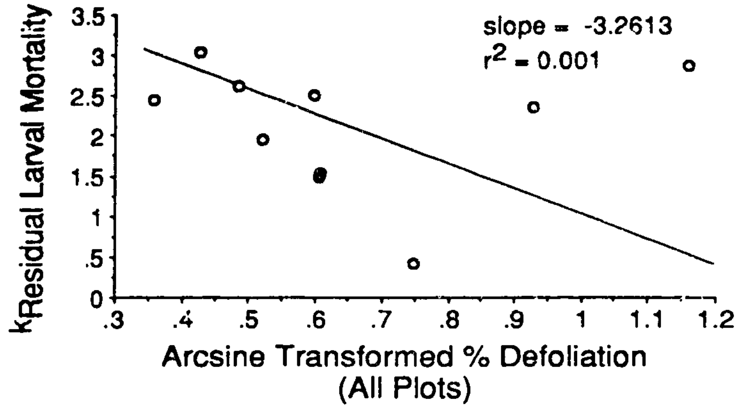


Fig. 3.8. Forest tent caterpillar defoliation in the experimental plots and total larval parasitism. Forest types are plotted seperately because parasitism rates were significantly different between them. Probabilities are given for significant correlations.



(a) Residual Larval Mortality



(b) Residual Larval Mortality

Fig. 3.9. Larval forest tent caterpillar mortality from all sources other than parasitoids in the experimental plots in relation to initial larval density and plot defoliation. Plots were pooled because there was no significant difference in residual mortality between the two forest types.

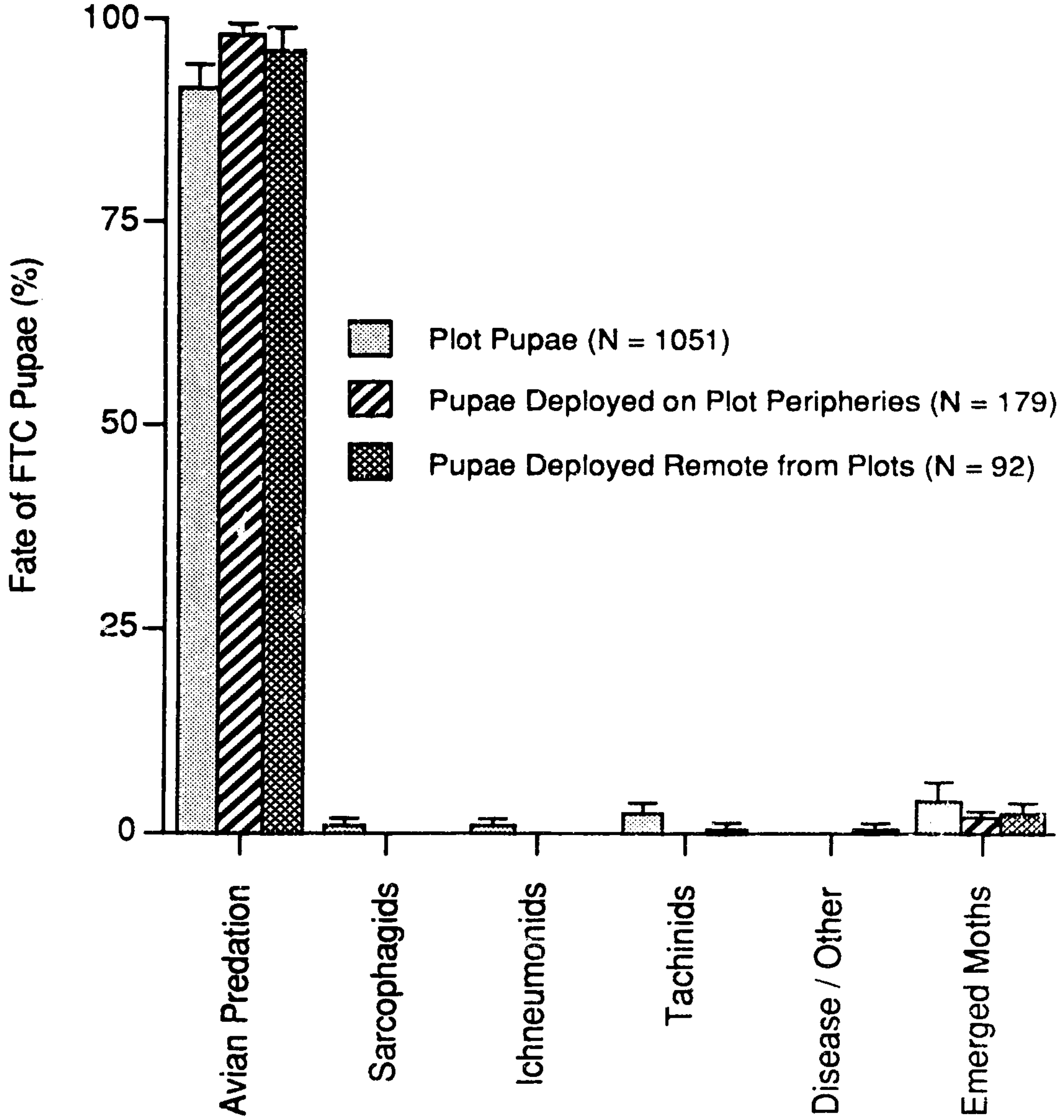
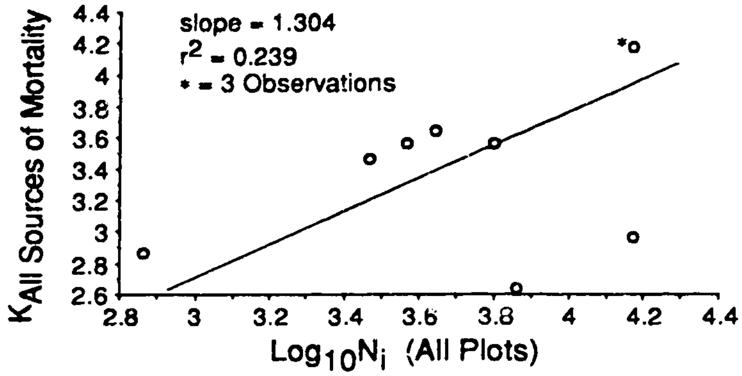


Fig. 3.10. The fate of all pupae (mean +/- SE) collected from the experimental plots and from the deployed treatments (1993).

(a) Total Seasonal Mortality



(b) Total Seasonal Mortality

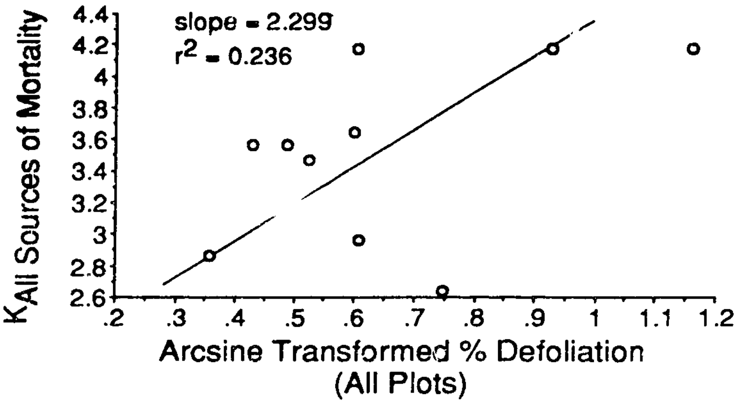


Fig. 3.11. Total seasonal mortality from all sources in relation to initial forest tent caterpillar density and defoliation in the experimental plots. Plots were pooled because there was no significant difference in total seasonal mortality between the two forest types.

4. CONCLUSIONS

4.1 SUMMARY

Predators and parasitoids can have a significant impact on forest tent caterpillar (FTC) populations. However, my work suggests that the importance of natural enemies varies with the population phase of FTC. In Chapter 2, I showed that although a large parasitoid complex is associated with FTC in Alberta, few are capable of causing biologically significant levels of mortality. Results from experimentally established populations in areas where natural FTC were at low density indicate that avian predators can be a more important source of mortality than parasitoids, at least in some situations.

Only *Aleiodes malacosomatos* (Hymenoptera: Braconidae) was reared from larvae prior to the third molt. This species was unimportant in outbreak populations but its abundance in endemic and first year outbreak populations suggested a potentially greater role in FTC populations at low density. In Chapter 3, I found that *A. malacosomatos* responded in a spatially density-dependent manner in the dryer, upland aspen forest.

The tachinid *Leschenaultia exul* (Townsend) was the most important parasitoid of late instar larvae in both outbreak and natural low density populations. Phenology leading to early attack contributes to the success of *L. exul* in low density host populations. At the time of oviposition, FTC are still feeding gregariously which greatly enhances the probability of eggs being ingested. During FTC outbreaks, abandonment of the host prior to pupation allows a portion of the *L. exul* population to avoid competitive pressure from aggressive pupal parasitoids. The dynamics obse[illegible] Chapter 2 suggested that *L. exul* could be important in low dens[illegible]TC populations but results from Chapter 3 showed that *L. exul* did not respond to spatial variations in host density.

Another important parasitoid of late instar larvae in outbreak populations was the tachinid *Patelloa pachypyga* (A & W). The dynamics of this species were characterized by a rapid increase early in outbreaks followed by a decline as the outbreak aged. Because of its prolonged development in larvae and pupae, I suspect that increasing competition from both pupal parasitoids and pathogens may explain the reduction in parasitism in older outbreaks. Although absent in natural low density populations, *P. pachypyga* was the most abundant parasitoid in my experimental plots (Chapter 3). Plot barriers artificially constrained the dispersal of final instar larvae raising densities to outbreak levels in some plots which may account for the high parasitism observed. However, it also suggest that *P. pachypyga* is extremely effective at locating patches of FTC at higher densities. *Pateiloa pachypyga* exhibited a strong density-dependent response in lowland aspen forest but not in the upland. Parasitism by *P. pachypyga* was better predicted by defoliation than density in both forest types.

The dynamics of the tachinids *Lespesia frenchii* and *Carcelia malacosomae* observed in Chapter 2 indicated that they could be important between outbreaks. However, results from Chapter 3 suggested otherwise, as both were reared only sporadically from larvae in my experimental plots.

Pupal parasitism by *Arachnidomyia aldrichi* was the dominant source of mortality in outbreak populations although at considerably lower levels than have been recorded in eastern North America. Clearly *A. aldrichi* is an outbreak specialist as pupal parasitism found in the experimental plots was less than 2%, similar to parasitism rates at the beginning of an outbreak. *Arachnidomyia aldrichi* parasitism was spatially variable with respect to vegetation height and distance from the forest edge. Parasitism of pupae at the forest edge was high and may reflect the movement of *A. aldrichi* between stands.

Other pupal parasitoids rarely caused more than 5% parasitism despite being more abundant in Alberta than elsewhere. Increased levels of parasitism by *Agria housei* (Shewell) and *Aprostocetus esurus* (Riley) in Alberta are probably related to lower levels of their major competitor, *A. aldrichi*. In Chapter 3, pupal parasitoids accounted for less than 3% of the pupal mortality in the experimental plots and deployed pupae treatments.

An surprising result from Chapter 3 was the tremendous impact that avian predators had on both larvae and pupae. Although difficult to quantify, birds were probably the largest source of final instar mortality in the lowland plots. In the upland plots, avian predation accounted for more than 90% of pupal mortality and reduced the experimental populations to very low levels. Avian predation was also the major source of mortality in pupae deployed at two distances from the plots. This suggests that birds can have a significant impact at a variety of densities and can potentially hold FTC populations at low levels in some forests.

4.2 GENERAL DISCUSSION.

The results of Chapter 2 suggest that parasitoids, exhibit a similar effect in FTC populations across a wide geographical area. Although the abundance of some species was higher than recorded in Ontario and Minnesota (Sippell 1957; Witter & Kulman 1979), the dynamics of the major parasitoids were similar in Alberta. The most important larval parasitoids in aspen feeding FTC populations appear to be the tachinids *L. exul*, *P. pachypyga*, *L. frenchii* and the braconid *A. malacosomatos*. Common pupal parasitoids are the sarcophagids *A. aldrichi* and *A. housei*.

Arachnidomyia aldrichi was considerably less abundant in Alberta outbreaks than has been recorded in other studies (Hodson 1941, 1977; Sippell 1957; Witter & Kulman 1979). Because this fly appears to be integral to the collapse of FTC populations in eastern North America (Witter 1979), reduced parasitism in Alberta outbreaks could increase their duration. On the other hand, higher parasitism by *A. housei* and *A. esurus* observed in Chapter 2 could partially compensate for lower levels of *A. aldrichi*. High levels of *A. aldrichi* found in some previous studies (Sippell 1957; Hodson 1977) may reflect a bias toward sampling only undergrowth cocoons. As described in Chapter 2, I found that parasitism of pupae in the undergrowth is significantly higher than in the canopy. Failure to account for this difference could lead to inflated estimates of parasitism.

Despite Sippell's (1957) assertion that generalist parasitoids could be important when FTC populations are endemic, the results of both Chapter 2 and Chapter 3 indicate that oligophagous *Malacosoma* specialists were the predominant parasitoids even at low FTC densities. When FTC are at low density, host-specific parasitoids are also likely to be at low density. As FTC populations increase populations of parasitoids may lag for a few years before increasing. As described in Chapter 3, *P. pachypyga* and *A. malacosomatos* exhibited spatial density dependence but the response was restricted to particular habitats. Mortality from parasitoids was not high enough to suppress the experimental FTC populations.

Differential mortality in the two forest types used suggests a possible mechanism for FTC survival between outbreaks. Reduced natural enemy impact in habitats such as upland forest may create partial refugia similar to those observed in other forest defoliators such as gypsy moth, *Lymantria dispar* L. (Skinner et al. 1993). With the favorable weather conditions suggested by Ives (1973), populations could expand from these habitats into less susceptible forest types, overwhelming natural enemies and creating large regional outbreaks. This could account for incipient FTC outbreaks spreading out from small patches of defoliated aspen (Shepherd 1977).

4.3 FUTURE RESEARCH

In addition to the suggestions made at the end of Chapter 2, there are several other problems that require investigation. The biology of several important parasitoids such as *P. pachypyga* and *A. malacosomatos* is poorly known. Although we can describe the dynamics of these species, with out sound knowledge of their life history, it is difficult to explain their responses. The results of transect studies in Chapter 2 and those by Batzer (1955) have indicated that horizontal spatial variation in parasitism can be important for *A. aldrichi* and some tachinid species. Both vertical and horizontal spatial variation must be incorporated into any sampling methodology used to determine the impact of parasitoids.

The experimental work that I did in Chapter 3 should be expanded to encompass a variety of different scales. To determine if the results obtained in Chapter 3 are general, experiments need to be conducted over a range of stand ages and forest types. Under these conditions, the impact of both avian predation and parasitism may either be enhanced or reduced. These experiments could result in the development of profiles of aspen stands susceptible to outbreak.

Finally as suggested in Chapter 2, the most pressing problem in the study of FTC population dynamics is our inability to accurately estimate late instar larval densities. Quantification of larval densities are necessary to couple the dynamics of parasitoids and other mortality factors with the dynamics of FTC. Until this is accomplished, the sophisticated techniques used in the analysis of population dynamics of other important defoliating insects can not be employed.

The search for regulating processes in FTC populations has historically concentrated on outbreaks. However, it is factors operating when forest insect populations are at low density that determine when and where outbreaks will occur (Mason & Torgersen 1987). I believe that this thesis has provided evidence that natural enemies can play an important role in suppressing low density FTC populations.

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Appendix 1.

Marginal attack rates for each parasitoid species were calculated using the following equations from Elkinton et al. (1992).

$$m_A = \frac{b-((b^2-4cd_A)^{1/2})}{2c}$$

$$m_B = d_B/(1-cm_A)$$

where: $b = c(d_A+d_B)+1-d_B$

and d_A = observed # dying from agent A

d_B = observed # dying from agent B

The value c is a competition coefficient which represents the proportion of each mortality factor that is obscured by other contemporaneously acting mortality agents. I assumed that all parasitoids were out competed in any host that was infected with nuclear polyhedrosis virus (NPV) or pathogenic fungus which is analagous to the case of a contemporaneous predator and parasitoid with c = 1 (Elkinton et al. 1992). The outcome of interactions between FTC larval parasitoids is unknown. I made the assumption that there was no competition between parasitoids based on their biologies. *Aleiodes malacosomatos* was temporally seperated from other parasitoids and each tachinid species can successfully complete development in multiparasitized hosts (Bess 1936; Sippel' 1957; personal observation). Thus, I assumed that each parasitoid species was only in competition with NPV and fungus.