

Seasonal Life History, Abundance and Biology of the
Parasitoids of the Pea Aphid, Acyrtosiphon pisum (Harris)
in Manitoba.

By

© Frank Oliver Matheson

A thesis
presented to the University of Manitoba
in partial fulfillment of the
requirements of the degree of
Master of Science

Department of Entomology

1988

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SEASONAL LIFE HISTORY, ABUNDANCE AND BIOLOGY OF THE
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ABSTRACT

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Seasonal life history, abundance and biology of the parasitoids of the pea aphid, Acyrtosiphon pisum (Harris) in Manitoba.

A survey of the parasitoids of the pea aphid was conducted in alfalfa and field peas in the Red River Valley area of Manitoba during 1981-85. Five primary parasitoids and twelve secondary parasitoids were collected. The five primary parasitoids, all aphidiids, were: Praon occidentale Baker, Praon pequodorum Viereck, Aphidius ervi Haliday, Aphidius pisivorus Smith and Aphidius smithi Sharma and Subba Rao. P. pequodorum and A. ervi comprised most of the primary parasitoids each year. A. smithi was not found prior to the introduction of this parasitoid in Manitoba in 1983.

The twelve secondary parasitoids, including 8 identified to the species level, were: five pteromalids, Asaphes lucens (Provancher), Coruna clavata Walker, Pachycrepoideus vindemiae (Rondani), Pachyneuron siphonophorae (Ashmead), Pachyneuron sp.; three alloxystids, Alloxysta victrix (Westwood), Alloxysta megourae complex, Phaenoglyphis ambrosiae (Ashmead); three megaspilids, Dendrocercus carpenteri (Curtis), Dendrocercus sp. A, Dendrocercus sp. and one encyrtid, Aphidencyrtus aphidivorus (Mayr). A. lucens was the most abundant secondary parasitoid collected each year.

The percentage parasitism of the pea aphid by the primaries was determined for 1983-85 by both rearing and dissecting aphids collected from stem samples in the field. The relative abundance of the adult primary parasitoids for 1981-85 was determined from D-Vac collections, and for both the primary and secondary species from emergence from field-collected mummies. Seasonal changes in the abundance of the parasitoids are discussed.

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**Dedicated to my wife, Lori, and our children
Heather, Gail and Amanda**

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1. INTRODUCTION

The pea aphid, Acyrtosiphon pisum (Harris) (Homoptera:Aphididae) is the most important insect pest of field peas, Pisum sativum (L.), an annual crop grown in the Red River Valley of Manitoba (Lamb and Maiteki 1985) and is also a common pest of fababeans (Harper and Kaldy 1978) and of perennial crops such as alfalfa, Medicago sativa L. and clover, Trifolium spp. (Ali-Khan 1980). Insecticides are commonly used on field peas to control pea aphid populations. The dynamics of pea aphid populations depend upon weather conditions such as temperature and rainfall, the presence of parasitoids, predators and disease, and the time of maturation of the crop (Dunn and Wright 1955; Harper et al. 1978; Maiteki et al. 1986). In Manitoba, parasitoids are common from pea aphids on field peas (Lamb and Maiteki 1985) but details of the parasitoid complex on both annual and perennial crops are unknown.

The objective of this study was to identify the primary and secondary parasitoids of the pea aphid on field peas and alfalfa in the Red River Valley and to provide information on the seasonal life history, abundance and biology of the different parasitoids on both crops. Apart from its scientific value, the results would provide baseline information for a project involving the release of an exotic pea aphid parasitoid, Aphidius smithi Sharma and Subba Rao, in Manitoba.

A preliminary survey in 1981 and 1982 to evaluate collection methods and to verify if A. smithi was present in Manitoba was part of this study. A more detailed study of the pea aphid parasitoids was conducted during the field seasons of 1983, 1984 and 1985 and involved collections and rearings of pea aphids and their parasitoids from alfalfa and field peas.

2. LITERATURE REVIEW

2.1 The Pea Aphid

The pea aphid is considered to be of Palearctic-Oriental origin (Mackauer 1971) and is now cosmopolitan (Hill 1975). It is believed to have been introduced into North America from Europe on infested clover and peas (Harper et al. 1978) and populations causing economic damage were observed in the late 1800's (Hagen et al. 1976). Campbell (1926) recorded the pea aphid as well distributed over the United States, southern Canada and the west coast of Mexico.

The pea aphid usually infests the tips of growing plants and sucks sap from leaves, stems, blossoms, and seed pods. The plant is deprived of essential nutrients for normal growth as aphid feeding creates extra sinks for the products of photosynthesis. Maiteki (1985) found that aphid feeding causes pod shedding and reduces both the number of seeds per pod and seed size. The infested plants are often covered with the excrement of aphids, honeydew, on which sooty mold and other fungal diseases frequently develop and hinder assimilation by the leaves. Severe infestations of pea aphids can kill plants (Bardner and Fletcher 1974).

The pea aphid is known to vector 20 plant viruses (Kennedy et al. 1962) including alfalfa mosaic, alsike clover mosaic, bean yellow mosaic, pea enation mosaic, pea mosaic, pea streak and red clover vein mosaic (Harper et al. 1978).

The seasonal life history of the pea aphid in Manitoba begins with the fundatrices that emerge from eggs in the spring. These are apterous viviparae that give birth to other apterous viviparae. Depending on rearing conditions, the second and subsequent generations may be alate or apterous (Harper et al. 1978). Alata production can depend upon the host plant, including the species, stage of maturity and water content, as well as environmental conditions, such as temperature and photoperiod, physical conditions such as crowding, and intrinsic factors such as biotype (Harper et al. 1978) or maternal age effects (MacKay 1977).

Beginning in late May or early June, some aphids, as alate viviparae, migrate and infest peas, fababeans (Vicia faba L.) or other annual hosts and parthenogenetic generations are produced throughout the summer. The pea aphid is monoecious (MacKay et al. 1983) and some aphids reproduce on hosts such as alfalfa, clover and perennial wild legumes throughout the growing season.

In July the numbers of pea aphids increase rapidly and reach a peak in late July or early August. The peak is followed by a collapse in the population by about the middle of August. The sexual morphs appear late in the summer and early in the fall, mate, and the females oviposit on a winter host plant (Harper et al. 1978). The eggs overwinter to complete the cycle. MacKay et al. (1983) describe the overall pattern of sexual morph determination, for apterae and alatae of the pea aphid, during the change in day length and temperature from summer to winter.

2.2 Primary Parasitoids

2.2.1 Species

Mackauer and Stary (1967) reported that twenty species, belonging to the hymenopterous families Aphidiidae and Encyrtidae, are recorded in the world literature as primary parasitoids of the pea aphid. Mertins (1985) listed eleven aphidiids and two encyrtids from the literature as parasitoids of pea aphid in North America. The aphidiids include Ephedrus californicus Baker, Ephedrus plagiator (Nees), Praon barbatum Mackauer, Praon occidentale Baker, Praon pequodorum Viereck, Praon simulans (Provancher)(=Praon aguti Smith), Praon volucre (Haliday), Aphidius ervi Haliday, Aphidius pisivorus Smith, Aphidius smithi Sharma and Subba Rao and Monoctonus nervosus Haliday. A. ervi and A. smithi were introduced from Eurasia in the 1950's and became established; E. plagiator, P. barbatum and P. volucre were introduced but have not been confirmed as established; and the other six aphidiids were considered to be indigenous to North America. Both of the encyrtids, Aphelinus semiflavus Howard and Aphelinus howardii Dalla Torre, are indigenous. Mertins (1985) found only two of the listed species, Aphidius ervi and Praon pequodorum, during his field studies in Iowa. A. ervi and P. pequodorum were also the only species recorded in Manitoba (Maiteki 1985), and the only species, along with P. occidentale, in Wisconsin (Hutchison and Hogg 1985); and A. ervi was the only pea aphid parasitoid recorded in New Jersey (Matejko and Sullivan 1984). One other aphidiid, Aphidius eadyi (Stary, Gonzales and Hall)(=urticae Hal.), which is the dominant parasitoid of the pea aphid in some areas of Europe (Stary

1974), was introduced into California against the blue-green alfalfa aphid, Acyrtosiphon kondoi Shinja in the late 1970's (Stary et al. 1980). Aphidius eadyi (as urticae) was recorded in 1981 in California (Oatman et al. 1983) as a parasitoid of Macrosiphum euphorbiae (Thomas). Whether it became established in the late 1970's, or was already present before releases started as described by Eady (1969) is unknown.

Aphidius ervi (= A. ervi ervi of some authors) was imported into the United States from France in 1959 to establish a laboratory colony. Liberations from this colony were made in New Jersey and Delaware in 1959; Arizona, Idaho, Maine, Oregon, and Washington during 1962 and 1963; and again in New Jersey and Delaware during 1967 and 1968 (Angalet and Fuester 1977). It was also released in California in 1959 from France and in 1965 from Lebanon (Mackauer and Campbell 1972). By 1966 A. ervi had apparently become established in Oregon (Halfhill et al. 1972) and had spread from the northwestern United States to British Columbia where it was collected in 1970 (Mackauer and Campbell 1972). It was found in southern Ontario in 1972 (Campbell and Mackauer 1973). However, the status of A. ervi is not clear because no pre-release studies were done to verify that the species did not already occur in North America. In fact, A. ervi was recorded commonly in Nova Scotia in 1965 (Stary 1974). Thus, A. ervi may have occurred in North America prior to these releases, either by spread from Europe via Iceland or from the East Palearctic via the Aleutian Islands, or by accidental introduction (Stary 1974). In addition to being the most effective parasitoid of the pea aphid on

alfalfa in eastern North America (Mertins 1985), A. ervi also parasitizes other widely-distributed aphids such as Myzus persicae Sulz. and Macrosiphum euphorbiae (Krombein et al. 1979).

Aphidius smithi is indigenous to several countries in Central Asia (Stary 1979) and was introduced from northern India to California and to the Eastern United States in 1958 (Mackauer 1971; Angalet and Coles 1966). It became established in both areas. In the East it spread to southern Ontario by 1964 (Mackauer and Bisdee 1965). This establishment is classified as temporary, for A. smithi practically disappeared in Ontario by 1972 (Stary 1974) and in the Eastern United States by 1970 (Angalet and Fuester 1977). The temporary establishment of A. smithi was probably the result of a progressive displacement of this parasitoid by A. ervi as seen in the Eastern United States by Angalet and Fuester (1977). A. smithi was released in Nova Scotia during 1964-67 but did not become established (Mackauer 1971). From the East, A. smithi spread to the Mid-West, where it was the most abundant parasitoid of the pea aphid in Minnesota, Nebraska and South Dakota in 1970 (Angalet and Fuester 1977). In the West, it spread over much of California by 1960 and was considered to be important in controlling the pea aphid in coastal valleys (Hagen and Schlinger 1960). It spread from California to central Mexico by 1967 (Clancy 1967). Colonies were released in Idaho, Oregon and Washington during 1959-64 (Halfhill et al. 1972). By 1971 A. smithi was the most common parasitoid of the pea aphid in the interior of British Columbia where it presumably emigrated from the north-western United States (Mackauer and Campbell

1972). It emerged from pea aphids collected in southern Alberta in 1970, 1971 and 1974, and probably had spread there from Idaho or Washington (Harper 1976). A. smithi overwintered in Alberta after being released in 1975 (Harper, pers. comm.). A. smithi adults were first released in Manitoba in 1983.

Aphidius pisivorus (= A. ervi pulcher of some authors) may be indigenous to North America and secondarily adapted to the pea aphid, or may have spread to North America from the East Palearctic since the complex of Aphidius in the East Palearctic is unclear (Stary 1974). It was first described from Utah in 1937 and 1938 as a parasitoid of pea aphid (Smith 1941), and was considered to be widely-distributed in North America though unknown in Manitoba (Krombein et al. 1979).

Stary (1974), on the basis of characters proposed by Eady (1969), claimed that species of Aphidius can be distinguished by differences in the anterolateral area of tergite 1. Marsh (1977) accepted these diagnostic features and prepared a key to the North American species. However, Pungertl (1983) illustrated the difficulty in identifying the various Aphidius species because of intraspecific variation occurring in these various characters, particularly the number of costulae on tergite 1. For example, the ranges for the number of costulae overlap for A. eadyi, A. smithi and A. pisivorus. Because of the overlapping ranges, Pungertl (1983) concluded that the morphological basis upon which a number of nominal species are distinguished is unsatisfactory, and believed that some records of Aphidius species as parasitoids of pea and cereal aphids may be

misidentifications. Pending a possible revision of the genus, systematists continue using the characters described by Marsh (1977) to separate the various species.

Praon peguodorum, the only other common pea aphid parasitoid in North America, is found in the United States and southern Canada (Krombein et al. 1979), including Manitoba (Maiteki 1985) and is of primary economic importance as a parasitoid of the pea aphid in southern Ontario (Mackauer and Bisdee 1965). Shands et al. (1965) recorded P. peguodorum from Myzus persicae, Macrosiphum euphorbiae and Acyrtosiphon solani (Kaltenbach) but it may prefer species in the genus Acyrtosiphon (Mackauer and Finlayson 1967).

Praon simulans (= aguti) has a number of aphid hosts including A. pisum and its range includes New Brunswick and Ontario south to Virginia; Michigan, Idaho and California (Krombein et al. 1979). Sekhar (1960) noted that P. simulans (as aguti) preferred Macrosiphum rosae (L.) over A. pisum.

Praon occidentale has a number of aphid hosts including A. pisum in Canada and northern United States (Krombein et al. 1979); however it was not recorded in Manitoba. Mackauer and Bisdee (1965) noted that P. occidentale was of minor economic importance as a parasitoid of the pea aphid in southern Ontario.

Ephedrus californicus parasitizes A. pisum but prefers species of Macrosiphum and of related genera (Mackauer and Finlayson 1967). The range of E. californicus includes New Brunswick, Quebec, Ontario, Maryland, Michigan, Alberta, Idaho, Utah, Arizona, British Columbia, Oregon and California (Krombein et al. 1979).

Monoctonus nervosus (= paulensis Ashmead) is Holarctic in distribution and from North America has been recorded in Michigan, Oregon, California and Alaska (Krombein et al. 1979). It is believed to have spread from the East Palearctic to the Nearctic region via the Aleutian Islands (Stary 1974). Its hosts include eight aphid species and it is considered to be a minor parasitoid of A. pisum in California (Calvert and van den Bosch 1972).

Aphelinus semiflavus is an encyrtid with a cosmopolitan distribution including Manitoba (Batulla and Robinson 1984) and a wide host range (Krombein et al. 1979). It does not attack A. pisum readily and is not likely to be encountered commonly as a pea aphid parasitoid (Mertins 1985).

Aphelinus howardii can be considered rare as a pea aphid parasitoid as only two specimens have been reared from A. pisum (Gutierrez and van den Bosch 1970).

2.2.2 Habits of the Adults

All of the aphidiids and encyrtids that parasitize A. pisum in North America are considered to be solitary endoparasitoids. The parasitoid adults emerge from cocoons made by the larvae inside the mummified aphids or, in the case of Praon spp. from cocoons made under the mummy after the parasitoid larvae emerge (Hagen and van den Bosch 1968). The parasitoid adults are mature and will mate soon after emerging. Females mate only once whereas each male can inseminate several females. A female can oviposit after a short preoviposition period regardless of whether she is inseminated and uninseminated females produce only males (Stary 1970).

Host finding is by antennal contact for most aphidiids including species of Aphidius (Fox et al. 1967), Praon (Schlinger and Hall 1960), and Monoctonus (Calvert 1973). Aphidius nigripes Ashmead responds to contact kairomones in aphid honeydew but does not detect the honeydew of the host Macrosiphum euphorbiae from a distance (Bouchard and Cloutier 1984). Similarly, A. smithi lacks a long-range ability to detect hosts, and chemoreception is more important than vision in eliciting oviposition (Fox et al. 1967).

Newly-emerged aphidiids need water within several hours of emergence to survive, and honeydew seems to be their main source of food in nature (Stary 1970). In contrast, encyrtid females that parasitize pea aphids feed at an ovipositional puncture on the host and often kill the aphid and their own progeny by sucking the aphid dry (Hagen and van den Bosch 1968).

Aphidiids commonly fly between different parts of the same plant or between adjacent plants, and disperse long distances by windborne flight (Stary 1970). In contrast, encyrtids that parasitize pea aphids are rather sluggish and are not active fliers, but jump readily (Hagen and van den Bosch 1968).

Oviposition behaviour is similar for all aphidiids that have been studied. After locating an aphid, the female bends the abdomen beneath the thorax and between the legs, pierces the host with the ovipositor and deposits an egg immediately. The female then removes her ovipositor from the aphid and straightens her abdomen to the normal position (Stary 1970). In contrast, Aphelinus females that find a host turn quickly and insert the ovipositor by lunging

backwards. The ovipositor may remain inserted for as long as fifteen minutes to deposit one egg (Hagen and van den Bosch 1968). Whereas aphidiids only oviposit in light, encyrtids oviposit in darkness or in light (Stary 1970). Most aphidiids oviposit in the abdomen, but some attack other body areas (Stary 1970).

Host acceptance by aphidiids may depend on the host's stage of development (Fox et al. 1967; Stary 1970). Each of the aphidiid species that parasitize the pea aphid prefers one host instar, usually an intermediate one, but will oviposit in other instars as well (Stary 1970). A. smithi prefers second over first, third or fourth instar pea aphids (Mackauer 1973) and accepts reproductive adults but rejects post-reproductive adults (Fox et al. 1967). Pea aphids parasitized in the third instar by A. ervi never mature to the parturitional stage and very few aphids parasitized as fourth instars or young adults produce progeny. Larvae from eggs of A. ervi laid in adult aphids do not mature (Hagen and van den Bosch 1968). Dispersal of the parasitoid may be affected by the instar of aphid preferred for oviposition; a preference for a smaller instar instead of a larger one increases the probability that the aphid will mummify before reaching maturity, and will therefore be unable to disperse as an alate adult (Stary 1970). Host acceptance also depends on whether the host is parasitized. Female Praon palitans distinguish parasitized Therioaphis maculata (Buckton) from unparasitized ones on the basis of chemical stimuli received by the parasitoid's antennae (Schlinger and Hall 1960). Usually aphidiid females ovipositing under natural conditions ignore a host aphid that contains third

instar or later developmental stages of the parasitoid (Stary 1966, 1970). Chow and Mackauer (1986) found that Ephedrus californicus could discriminate between parasitized and unparasitized pea aphids and suggest that host discrimination is time-dependent and can be induced by a pheromone-like external marker left by a first-attacking female (0-9h) or by changes in host quality associated with parasitoid development (≥ 14 h).

With the exception of a Monoctonus species (Griffiths 1960) and some Praon species (Stary 1970) which use their front legs to grasp the aphid, most aphidiid and encyrtid females do not restrain their hosts. A. pisum resists attacks by female parasitoids by pulling the rostrum out of the plant, running away and sometimes falling from the plant. These defensive reactions are most frequent at warmer temperatures and are generally less frequent in the smaller aphid instars and during rainy or windy weather, as the aphids try to stay on the plants (Stary 1970). Each mated aphidiid female lays both fertilized and unfertilized eggs (arrhenotoky) until all the sperm she contains have been used; thereafter, she lays only unfertilized eggs, which produce males. Environmental factors appear to be responsible for stimulating the spermatheca to discharge spermatozoa into the oviduct, and since environmental factors are inconstant the sex ratio is variable (Stary 1970).

Mackauer (1971) reported that unmated females of A. smithi laid an average of 774 eggs (range 381-1812) as compared with 567 (109-1011) for A. ervi, 316 (90-597) for A. pisivorus (as pulcher), 199 (84-369) for P. piquorodum and 312 (123-537) for Aphelinus

semiflavus when the females were provided daily throughout life with 60 aphid larvae 3 to 4 days old at 20°C and 55% relative humidity. Females of A. smithi searched more efficiently than the other species, and immatures developed more rapidly.

2.2.3 Immature Stages

Oviposited eggs of aphidiids increase in size in suitable hosts and when the eggs hatch the larvae feed on the haemolymph, tissues and organs of the host. Only one larvae survives in each host; supernumeraries are killed in combat or by physiological suppression (Soldan and Stary 1981). In superparasitized hosts a mandibulate first instar parasitoid larva generally eliminates eggs and older larvae by direct attack, but late first instar and older larvae may eliminate eggs by some physiological means. In multiparasitized pea aphids, the first instar P. peguodorum is intrinsically superior to all larval stages of A. smithi in contest-type competition (Chow and Mackauer 1984, 1985) and Aphidius sp. and Praon sp. are both intrinsically superior to Aphelinus semiflavus (Hartley 1922; Force and Messenger 1965).

Chorney and Mackauer (1979) concluded that all aphidiids have four larval instars, and described the four instars of A. smithi. With the exception of specific details of the mouthparts there is considerable uniformity among instars in the external and internal morphology, including the number and shape of cuticular spines and the cauda.

Chow (1982) noted that the first-instar larva of P. peguodorum has a posteriorly-directed cauda and two ventrally-directed processes on the caudal segment. These ventral processes are typical for first-instar Praon and Ephedrus (Wheeler 1923) and distinguish them from first instars of Aphidius or Aphelinus. Larvae of Aphelinus are hymenopteriform in the early instars and globular in the later instars, and thus are easily separable in the later instars from the more elongate larvae of the aphidiids (Hagen and van den Bosch 1968).

The first to third larval instars of aphidiids feed on the haemolymph, with the first instar diffusing a cytolytic secretion into the haemolymph which prevents encapsulation by the host. The fourth larval instar of aphidiids is mandibulate and attacks all the organs and tissues of the host (Stary 1970). Degenerative changes become apparent in the reproductive organs of the pea aphid four to five days after parasitization by A. smithi, though mature embryos may survive in older aphids and be born (Soldan and Stary 1981). Eventually, the fourth-instar larva fills the aphid skin.

The mature Aphidius larva makes a hole in the ventral side of the mummified aphid and attaches the mummy to the surface of the plant with a secretion of the silk glands. The larva then spins a cocoon inside the mummy (Stary 1970). In contrast, the fourth-instar Praon exits from the ventral side of the mummy and spins a skirt-like cocoon and attaches both the mummy and cocoon to the plant underneath the empty skin (Chow 1982). The host of Aphelinus semiflavus turns black, then the mature parasitoid larva cuts a small hole in the ventral side of the aphid skin and attaches the skin to the plant with silk as it spins the cocoon (Schlinger and Hall 1959).

Aphidiids are multivoltine and in the temperate zone enter diapause as prepupae within the mummified aphids, in the late spring, summer or in the fall (Stary 1970). Short days and low temperature induce hibernal diapause by affecting the host plant and host aphid (Schlinger and Hall 1959). Schlinger and Hall (1960) reported once the diapause is induced in late spring or early summer, the parasitoid remains in diapause until the following spring. For Praon and Aphidius the thickness of cocoons varies with the season, those containing diapausing parasitoids being darker in colour and more heavily-built with several silk layers instead of one (Stary 1970). Mummies with diapausing parasitoids probably overwinter in the duff after the leaves to which they are attached fall to the ground.

Parr and Pass (1969) found that the time from oviposition to adult emergence for non-diapausing A. smithi was 10.7 days (range 9-12) at $78 \pm 2^\circ\text{F}$ (26.6°C) and 36.6 days at $50 \pm 2^\circ\text{F}$ (10.0°C).

Chow (1982) reported that at 21.1°C the development time for P. pequodorum was approximately 13 days.

Aphidiid adults emerge by cutting a circular chink in the cocoon and, if Aphidius, in the mummy as well. With the exception of those specimens that have overwintered in a field that in the previous year was sowed to an annual crop, all pea aphid parasitoids that emerge in the spring are in a habitat that is likely to contain hosts.

2.3 Hyperparasitoids

Secondary parasitoids commonly attack aphidiids that are developing inside living aphids or mummies. These species are in the hymenopterous families Pteromalidae, Encyrtidae, Eulophidae,

Megaspilidae (Ceraphronidae) and Cynipidae (Hagen and van den Bosch 1968). Some of these secondary parasitoids occasionally act as tertiary parasitoids, attacking individuals of their own species or other species of secondary parasitoids (Bennett and Sullivan 1978). Although they usually prefer a particular species of primary parasitoid, most secondary parasitoids accept a larger host range than primary parasitoids do (Shands et al. 1965). Hyperparasitoids may comprise over 50% of all parasitoids reared from a pea aphid population (Angalet and Fuester 1977) and probably reduce the effectiveness of primary parasitoids as biocontrol agents. Mackauer (1971) believed that secondary species prevented establishment of Aphidius smithi in Nova Scotia by eliminating small founder colonies.

Mertins (1985) listed twelve secondary parasitoids of pea aphid that have been recorded in North America. These include six pteromalids, Asaphes californicus Girault, A. lucens (Provancher), A. rufipes Brues, A. vulgaris Walker, Coruna clavata Walker, and Pachyneuron siphonophorae (Ashmead); one encyrtid, Aphidencyrtus aphidivorus (Mayr); three alloxystids, Alloxysta victrix (Westwood), Phaenoglyphis ambrosiae (Ashmead), and P. americana Baker; and two megaspilids, Dendrocercus attentus (Muesebeck) and D. carpenteri (Curtis). The pteromalids and megaspilids are direct secondary parasitoids and are ectoparasitic, that is, they attack the primary parasitoid directly by ovipositing on the primary larva or pupa inside the mummy or in the case of Praon sp. inside the cocoon beneath the mummy and the secondary larva feeds externally on the primary parasitoid. The encyrtid and alloxystids are indirect

secondary parasitoids and are endoparasitic, that is, they attack the host aphid and indirectly the primary parasitoid by ovipositing inside the larva of the primary parasitoid, which they locate after piercing the pea aphid with the ovipositor and the larva of the secondary feeds inside the larva of the primary parasitoid (Sullivan 1987).

Mertins (1985) noted that Asaphes vulgaris is a very common and consistent hyperparasitoid of aphids in Greenland and the Palearctic, but its occurrence on the North American continent has not been verified despite numerous literature citations. Mertins (1985) also published keys to adults of the hyperparasitoids of pea aphid in North America, and to the primary and secondary parasitoids based on evidence left on or in vacated pea aphid mummies. Batulla and Robinson (1984) gave host records for some of the hyperparasitoids of pea aphid in Manitoba.

The bionomics of some hyperparasitoids of aphids were described by Hagen and van den Bosch (1968) and Shands et al. (1965). Matejko and Sullivan (1979) described the bionomics and behaviour of Alloxysta megourae (Ashmead) (Hymenoptera:Alloxystidae), a factitious pea aphid hyperparasitoid through A. smithi.

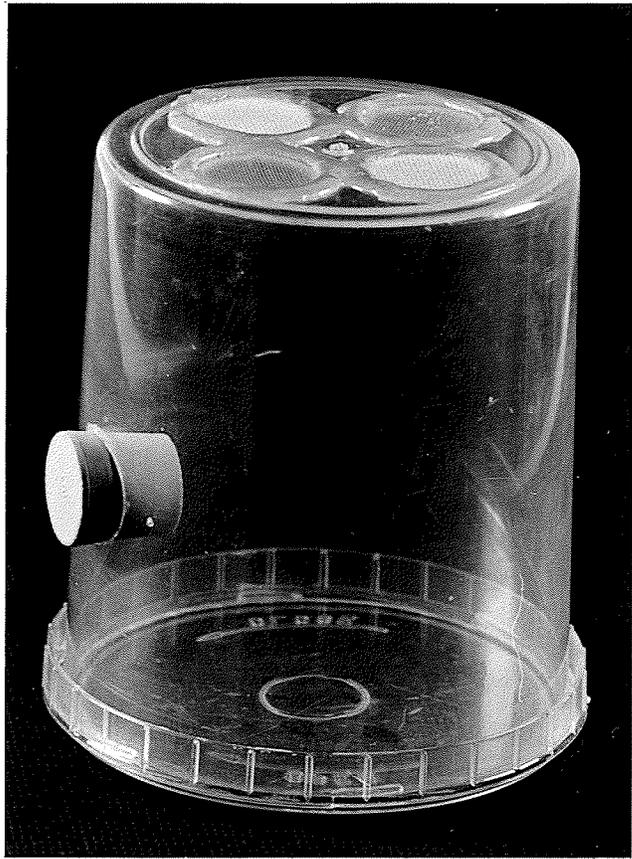
3. MATERIALS AND METHODS

3.1 Preliminary Studies, 1981-1982

In 1981 and 1982 pea aphids and mummies were collected from field peas and alfalfa and were held for parasitoid emergence. Six collection methods were tested to determine the most suitable: D-Vac Vacuum Insect Net (D-Vac Co., Riverside, California, U.S.A.) and sweepnet to collect aphids and parasitoid adults; paintbrush to collect aphids by gently brushing the aphids from the plants; mouth aspirator to collect aphids; hand picking leaves with pea aphid colonies; hand-picking 20 cm stems including the growing tips to collect aphids and mummies.

In 1981 aphids were collected weekly (16 June - 7 August) from field peas in a plot at the Agriculture Canada Winnipeg Research Station and weekly (16 June - 3 July and 17 August - 15 September) from a forage alfalfa field at Glenlea. Most of the aphids were collected with a D-Vac, 50 D-Vac contacts being taken per field or plot on each day [1 contact = lowering the nozzle (0.0285m²) of the D-Vac over the plants to the ground and then raising the nozzle off the plants). The collected insects were transported in a D-Vac net to the laboratory. Additional aphids, collected in a sweepnet or by using a paintbrush, were taken to the laboratory in plastic containers of two sizes, depending on the number of insects collected. The larger size (Fig. 1) was 14 cm high and 11 cm in diameter with a removeable bottom and four holes, each 2.5 cm in diameter, drilled in the top and covered with Nytex screen (7/cm). A

Figure 1: Large plastic container for holding aphids, parasitoids and other insects.

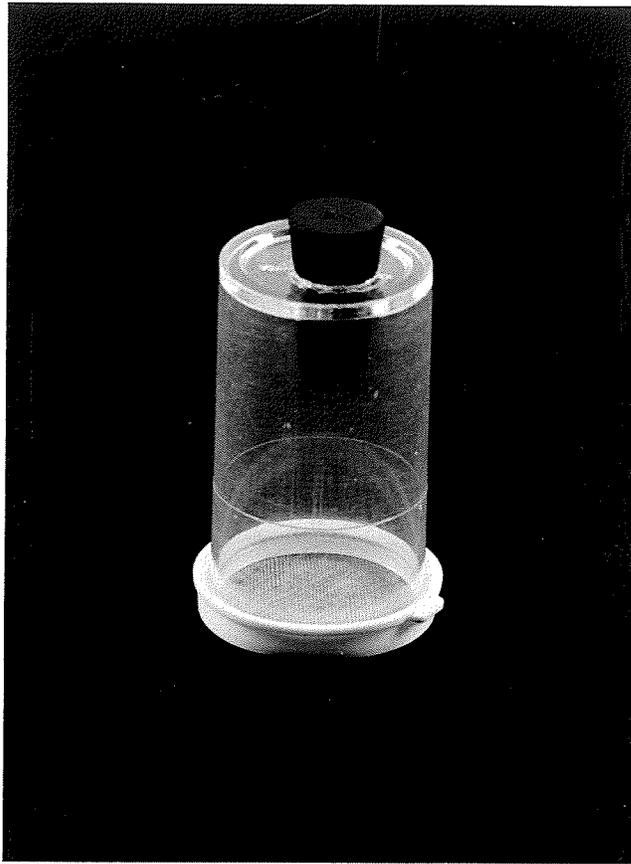


hole 2.5 cm in diameter was drilled in the side of the container and plugged with a cork. The smaller cages (Fig. 2) were 6 cm long and 3.5 cm in diameter with a mesh screen (24/cm) at one end and a cork at the other. In 1981, mummies were collected twice weekly, during 3 July to 4 August by a visual search of the plants in a plot of field peas at the Winnipeg Research Station, and taken to the laboratory using the small cages.

In 1982, pea aphids and mummies were collected on 25 May from a field of forage alfalfa near Glenlea, and twice weekly during 10 June to 6 August from an experimental field pea plot at the Winnipeg Research Station. Aphids were collected with a mouth aspirator, a D-Vac, by picking leaves with colonies, and by picking stem samples. Mummies were collected by a visual search of plants and from stem samples. The aphids from the mouth aspirator and those in colonies on leaves were transferred to the small plastic cages and then taken to the laboratory. Individual stem samples were placed in plastic bags, transferred to a cooler containing ice, and then taken to the laboratory.

In the laboratory, aphids from half of the stem samples (the odd numbered stems) were pooled, as were small numbers collected with the D-Vac and both groups were preserved (Weaver and Thomas 1956) and set aside for dissection. All other aphids, pooled by field and collection technique, were held in groups of up to 50 in petri dishes, with filter paper moistened with distilled water, for 13 days. Excised leaves of fababeans were added daily as food and mummies that formed in the dishes were harvested every 2 to 3 days. These mummies and those collected in the field were held individually

Figure 2: Small plastic container for holding aphids and mummies.



in shell vials with a cotton plug. All holdings were at 20°C, 70-80% R.H. and a 18h:6h L:D cycle. Parasitoid adults that emerged were preserved and later pinned for identification. All the parasitoids obtained in 1981 were identified by systematists at the Agriculture Canada Biosystematic Research Centre, Ottawa (BRC). In 1982, the most common primary parasitoids were identified by the author, based on diagnostic characters recommended by the systematists at BRC, and the remaining parasitoids were identified at BRC.

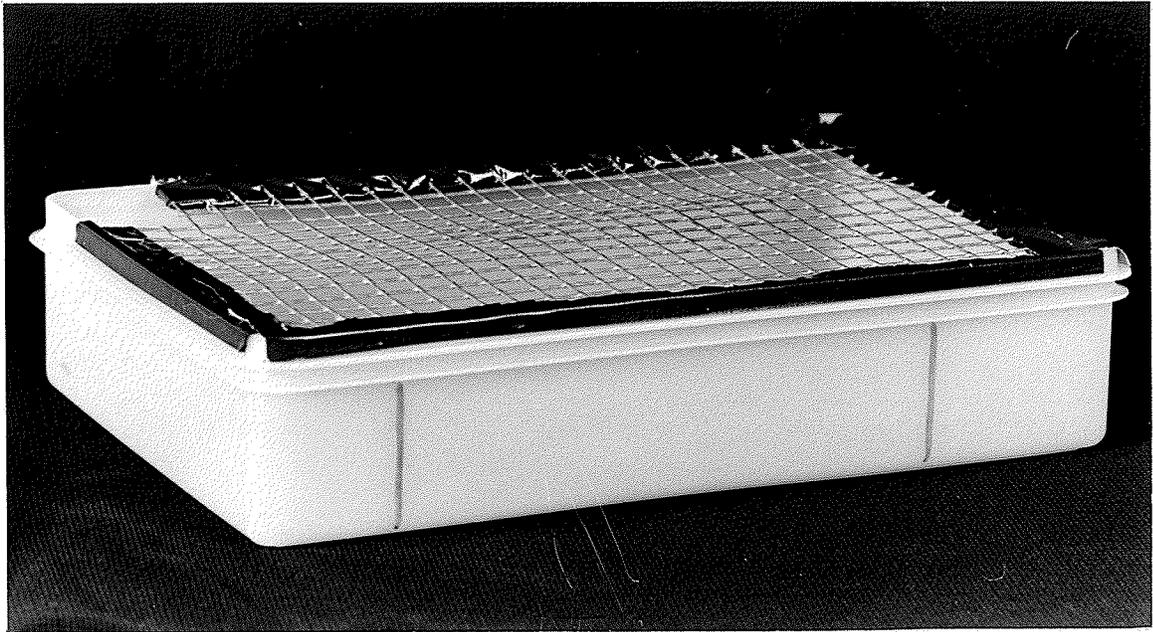
Additional information about the abundance and seasonal occurrence of the parasitoid species was obtained by taking 50 D-Vac contacts per field or plot on a number of dates each year. In 1981, adults were collected on 20 July in seven fields of field peas [Morris, Kane, Myrtle (2), Morden (3)] and on 13 August in eight fields [Morris (2), Kane, Myrtle (2), Morden (3)]. In 1982, parasitoid adults were collected weekly from 24 June to 9 August in nine fields of field peas [Kane (2), Myrtle, Roland (2), Morden, Winkler, Plum Coulee, St. Jean Baptiste], two of fababeans [Morris, St. Jean Baptiste] and one of forage alfalfa [Glenlea]. The aspirated material (aphids, parasitoids and other insects) was pooled by field and transported to the laboratory in the large plastic containers and frozen, and the adult primary parasitoid species identical to those already recorded from the pea aphid and mummy collections were later identified and tabulated.

3.2 Studies in 1983-85

3.2.1 Stem Samples

Stems were sampled in each of the 3 years in two commercial fields of forage alfalfa and two of field peas located in the St. Adolphe-Ste. Agathe area; and in two fields at the Agriculture Canada Glenlea field station, one of alfalfa seeded in 1983 and one of field peas seeded each year. Stems were collected weekly in each crop, beginning in late-June or early-July when the pea plants were tall enough to take a 20 cm length of the growing tip and ending in mid-August each year when the peas were senescing. Sampling was suspended in each alfalfa field after the crop in the field was cut, and resumed 1-2 weeks later, when 20-cm stems could again be taken. Usually, 100 stems were collected in each field on each sampling date. Two persons collected, one taking the odd-numbered samples, the aphids from which were reared, and the other the even-numbered samples, the aphids from which were preserved and dissected, and these categories were alternated in successive fields. Sampling began approximately 20 m inside each field, 5 stems/person being taken at each of 10 stations 10 m apart along a transect. The two transects were parallel and approximately 10 m apart. The aphids were removed from each stem by tapping the stem 5-10 times against the cover of a modified "beat container" (Fig. 3) (Bishop and MacKenzie 1982). This was a plastic container 33 cm x 21 cm x 7 cm deep with a wire mesh (1.3/cm) cover and a 20 cm scale on the side for measuring the stems. The aphids from each stem were counted in the container and aspirated into one of two labelled plastic cages

Figure 3: Beat container used in stem sampling.



for each field, one for even-numbered samples which were preserved and the other for odd-numbered ones which were reared. The mummies on each stem were then counted and transferred on pieces of stem or leaf to a labelled plastic cage, one for each field. The cages with aphids and mummies were placed on ice in a cooler and taken to the laboratory.

In the laboratory, aphids from the odd-numbered samples from each field were held in groups of up to 50 in petri dishes on excised fababean leaves, as described for the 1981-82 studies. Mummies that formed in the petri dishes were harvested every 2-3 days. In 1983 and 1984, these mummies were held in shell vials with a cotton plug, and in 1985 in gelatin capsules (Parke-Davis and Company Limited, No. 0), for parasitoid emergence. The aphids from the even-numbered samples of each field were preserved, frozen and later thawed, immersed in distilled water with a small amount of detergent added to reduce surface tension, separated under a binocular microscope by stage and instar (Hutchison and Hogg 1985) and dissected.

Mummies collected on stems and leaves in the field were held for emergence as described above. Parasitoid adults that emerged from these mummies and from mummies that formed in the laboratory were identified and the identifications confirmed by specialists at BRC as necessary. All mummies and cocoons that were held in the laboratory and from which there was no emergence were dissected and details of the type of mummy and developing parasitoid were noted. Mummies from which parasitoids had emerged in the field were categorized as field-emerged.

3.2.2 Additional Mummy Collections

After taking the stem samples in each field, both investigators made a 5-minute visual search for additional mummies by scanning the plants along the transect. Any mummies located in this visual search were also taken to the laboratory and held as described above for parasitoid emergence.

In 1984, additional mummies were obtained, from St. Adolphe and Glenlea, by visually examining whole plants in fifteen $1/2\text{m}^2$ quadrats (1 m x .5 m) of forage alfalfa. Leaves with attached mummies were removed and handled as in previous years. In 1985, additional mummies were collected by 30 minute visual searches in a seed alfalfa field near Oakbank, Manitoba on 11, 17 and 25 July and a forage alfalfa field near St. Adolphe on 30 July.

3.2.3 D-Vac Collections

To provide additional information on the seasonal abundance of the various parasitoid species, adults were collected from alfalfa with the D-Vac. In 1983, two forage alfalfa fields, one at St. Adolphe and one at Ste. Agathe, were surveyed weekly from 31 May to 12 July (50 contacts/field/date). In 1984, three forage alfalfa fields were surveyed: two (St. Adolphe, Ste. Agathe) from 5 June to 27 June and one (Glenlea) from 24 May to 10 July (250 contacts/field/date). In 1985, fields in four locations were surveyed: St. Adolphe and Ste. Agathe from 16 May to 2 July, Glenlea from 16 May to 15 August with one additional collection 12 September, and Lowe Farm from 16 May to 3 August (250 contacts/field/date). All D-Vac collections in 1985 were on forage alfalfa except those made at

Lowe Farm during 16 May to 24 July, which were on seed alfalfa. The parasitoids collected in the three years were handled the same way as those collected with the D-Vac in 1981-82.

4. RESULTS

4.1 Preliminary Studies 1981-1982

The results of the preliminary studies are summarized in Table 1. Four species of primary parasitoids, all aphidiids, were recorded from 9490 pea aphids and 158 pea aphid mummies collected from alfalfa and peas and held in the laboratory. The indigenous species Praon occidentale, Praon peguodorum, Aphidius pisivorus and the introduced species Aphidius ervi were found. These four species were also recorded from 4500 D-Vac contacts taken in alfalfa, peas and fababeans. The introduced species, Aphidius smithi, was not found. The secondary parasitoids collected during the preliminary study are discussed in section 4.2.4 .

In 1981, from 9115 aphids collected on peas and alfalfa, P. peguodorum (N=118) comprised 53.6% of the total primary parasitoid emergence, followed by 37.3% for A. ervi (N=82) and 9.1% for P. occidentale (N=20). In 1982, based on 375 aphids from peas and alfalfa, P. peguodorum was again the most abundant primary parasitoid (61.5%;N=24) followed by A. ervi (28.2%;N=11), P. occidentale (7.7%;N=3) and A. pisivorus (2.6%;N=1).

The four primary parasitoids were recorded in D-Vac contacts taken in 1981, with P. peguodorum and A. ervi the most abundant species (Table 1). From 50 D-Vac contacts taken in each field the mean numbers of adult P. peguodorum and A. ervi collected per field from seven pea fields on 20 July were $2.71 \pm .99$ (mean \pm S.E.) and

Table 1. Primary and secondary parasitoid species composition (% of total) based on parasitoid adults reared from field-collected Acyrtosiphon pisum (Harris), emerged from field collected A. pisum mummies, and collected by D-Vac, in 1981-82. Aphids and mummies were collected from alfalfa and peas, and D-Vac contacts were from alfalfa, peas and fababeans.

Parasitoid Species	1981			1982		
	9115 aphids reared	121 field collected mummies	900 D-Vac contacts	375 aphids reared	37 field collected mummies	3600 D-Vac contacts
Primary						
Aphidiidae						
<u>Praon occidentale</u> Baker	6.0	4.1	3.8	6.4	5.4	1.4
<u>Praon peguodorum</u> Viereck	35.6	18.2	60.4	51.1	10.8	20.3
<u>Aphidius ervi</u> Haliday	24.7	10.7	35.8	23.4	24.3	76.9
<u>Aphidius pisivorus</u> Smith	0.0	0.0	0.0	2.1	0.0	1.4
Secondary						
Pteromalidae						
<u>Asaphes lucens</u> (Provancher)	0.0	32.2			18.9	
<u>Coruna clavata</u> Walker	0.0	2.5		0.0	0.0	
<u>Pachycrepoideus vindemiae</u> (Rondani)	0.0	0.0		0.0	13.5	
<u>Pachyneuron siphonophorae</u> (Ashmead)	0.0	1.7		0.0	0.0	
<u>Pachyneuron</u> sp.	0.0	0.0		0.0	8.1	
Alloxystidae						
<u>Alloxysta victrix</u> (Westwood)	0.0	0.0		4.2	0.0	
<u>Phaenoglyphis ambrosiae</u> (Ashmead)	0.6	0.0		0.0	0.0	
Megaspilidae						
<u>Dendrocerus carpenteri</u> (Curtis)	0.0	0.8		0.0	0.0	
Unemerged (dead or in diapause)	33.1	29.8		12.8	19.0	
(N)	(332)	(121)	(106)	(47)	(37)	(1452)

2.00 \pm .90 respectively and from eight pea fields on 13 August were 2.63 \pm 1.29 and 0.50 \pm .27, respectively. In addition, 50 D-Vac contacts taken from a plot of peas at the Winnipeg Research Station on each of 22 June, 3 July and 10 July, yielded a total of 4 P. occidentale, 24 P. pequodorum and 20 A. ervi.

In 1982, 50 D-Vac contacts taken in each of nine pea fields on six dates from 24 June to 9 August showed that A. ervi predominated throughout the season followed by A. pequodorum (Table 2). Very few primary parasitoid adults (N=34) were collected from fababeans and as only one alfalfa field was sampled, the results of these collections are presented only in the summary of primary parasitoids from D-Vac collections given in Table 1. In 1982, A. ervi and P. pequodorum made up 76.9% and 20.3%, respectively, of the adult primary parasitoids collected by D-Vac.

From the preliminary study, when the amount of relevant material, time expended and ease of collection were considered, the following three methods were found to be best for collecting pea aphids, mummies and adult aphidiids for the main study of 1983-1985: stem samples, for pea aphids and mummies; a visual search of plants for additional mummies; and the D-Vac to collect adult aphidiids. Stems proved to be a more practical sampling unit than individual leaves, and stem sampling was less injurious to the aphids than the D-Vac or sweepnet and less time-consuming than collecting with a paintbrush or mouth aspirator. To collect additional mummies, a visual search was less time-consuming than picking and examining additional stems. The D-Vac was the best method for collecting parasitoid adults, since a large number of contacts could be taken in a short time.

Table 2. Mean number of each parasitoid species collected per pea field per sampling date, 1982. Fifty D-Vac contacts were taken in each of nine fields on each date.

Date	No. of Contacts	Mean number of adults collected per field			
		Praon occidentale	Praon pequodorum	Aphidius ervi	Aphidius pisivorus
		$\bar{X} \pm$ S.E.	$\bar{X} \pm$ S.E.	$\bar{X} \pm$ S.E.	$\bar{X} \pm$ S.E.
24 June	450	0	0	0	0
28 June	450	0	0	0	0
21 July	450	0.67±0.37	7.89±2.04	45.89±5.92	1.33±0.58
30 July	450	0.78±0.36	9.44±2.03	30.11±4.94	0.56±0.18
4 August	450	0.56±0.24	7.78±2.61	10.78±3.18	0.22±0.22
9 August	450	0	0.33±0.17	0.89±0.39	0
TOTAL	(2700)	(18)	(229)	(789)	(19)

4.2 Studies in 1983-85

4.2.1 Aphid Species

In addition to A. pisum, small numbers of three other aphid species, Myzus persicae, Therioaphis sp. and Macrosiphum euphorbiae, were recorded on peas and alfalfa. Adults of M. persicae and Therioaphis sp., which are easily distinguished from those of A. pisum (Richards 1965, MacGillivray 1979) were observed each year on collected stems in the field and were discarded. Immature M. persicae and Therioaphis sp. are more difficult to recognize in the field; however, few were brought to the laboratory, because no adults of either species were found after 13 days holding, and there were <100 immatures of these two species among 22362 dissected aphids. Adults of M. euphorbiae, which can be distinguished from those of A. pisum only by microscopic examination of the cornicles (A.G. Robinson, pers. comm.) were collected on both crops in three of the six fields sampled in 1985 (Table 3) and were brought to the laboratory. All of the M. euphorbiae were alate adults, suggesting that only winged individuals reached peas or alfalfa from their main food hosts such as potato (Metcalf and Flint 1962). The winged adults probably did not reproduce on peas or alfalfa, because the immature aphids collected on both crops and held in the laboratory did not produce the parastoid Aphidius nigripes (Ashmead). This species commonly parasitizes M. euphorbiae (Shands et al. 1965) but is not known to parasitize pea aphid. Adults of A. nigripes were collected periodically with the D-Vac on both crops, including the alfalfa field sampled at Glenlea in 1985 (Table 3).

Table 3. Relative abundance of Macrosiphum euphorbiae and Acyrtosiphon pisum in three fields in which Macrosiphum euphorbiae was found in 1985.

Location and Crop	Date	% <u>Macrosiphum euphorbiae</u>	Total number of aphids collected
Glenlea - peas	August 7	5.6	1616
	August 15	28.41	630
*Glenlea - alfalfa	August 15	2.29	350
Ste. Agathe - peas	August 15	0.54	921

*55 Aphidius nigripes, a parasitoid of M. euphorbiae were collected from 250 D-Vac contacts in this field on August 15.
No D-Vac contacts were taken in the Glenlea peas on this date.

4.2.2 Pea Aphid Abundance

Aphid population statistics obtained from stem samples taken at three sites each of forage alfalfa and field peas each year 1983-85 are given in Appendix 1. The seasonal population trends of pea aphid (mean number of aphids per stem sample) were examined only in fields of forage alfalfa that were uncut during July-August and in fields of unsprayed field peas, since alfalfa cutting and insecticide spraying on peas both temporarily reduce aphid densities (Cooke 1963; Maiteki and Lamb 1985). The results are in line with those of Maiteki et al. (1986): populations in the one uncut alfalfa field sampled each year during 1983-85 and in six of the seven unsprayed pea fields increased in July and reached maximum densities in late July or in August (Table 4). The maximum densities were higher on both crops in 1985 than in 1983 or 1984, possibly due to the longer growing season: cool, damp weather in 1985 delayed senescence on peas until the end of August, whereas in 1983 and 1984 75% of the foliage senesced by the first and second weeks of August, respectively. In 1983 and 1984, pea aphid densities on peas were higher than those in the one alfalfa field that could be sampled throughout July and August, whereas in 1985 the densities were similar on the two crops (Table 4).

4.2.3 Primary Parasitoids

Five aphidiids, Praon occidentale, Praon piquodorum, Aphidius ervi, Aphidius pisivorus and Aphidius smithi, were recorded from 19,333 pea aphids and 1812 pea aphid mummies collected and held in

Table 4. Mean number of *Acyrtosiphon pisum* in 20-cm stem samples (n=100) from one uncut alfalfa and two unsprayed pea fields each year, 1983-85.

Year	Date	Peas		
		Alfalfa Glenlea	Ste. Agathe	Glenlea
		$\bar{X} \pm$ S.E.	$\bar{X} \pm$ S.E.	$\bar{X} \pm$ S.E.
1983	5 July	0.53±0.09	1.64±0.32	4.91±0.70
	12	5.89±0.65	6.13±0.89	9.34±1.20
	21	4.10±0.43	8.91±0.94	10.49±1.34
	26	2.40±0.37	6.24±1.01	7.87±1.15
	2 August	5.05±0.39	9.21±0.99	8.79±0.88
	8	1.72±0.18	-	1.64±0.27
	16	0.01±0.01	-	-
		Ste. Agathe	Ste. Agathe (1)	Glenlea
1984	4 July	-	9.12±0.88	0.37±0.09
	10	-	6.60±0.71	1.08±0.18
	17	0.09±0.03	5.83±0.83	0.52±0.15
	24	1.88±0.23	3.12±0.50	2.52±0.44
	1 August	2.67±0.32	8.55±1.17	3.28±0.50
	8	0.42±0.09	6.10±0.67	2.87±0.34
	14	0.11±0.05	3.05±0.41	1.92±0.22
		Glenlea	Ste. Agathe	Glenlea
1985	3 July	-	6.23±0.87	0.66±0.18
	9	0.38±0.08	13.22±1.88	1.58±0.30
	16	2.65±0.41	7.00±0.82	2.65±0.78
	24	6.51±0.62	2.75±0.45	4.91±1.01
	30	16.23±1.70	6.52±0.87	15.38±2.42
	7 August	31.76±3.54*	24.56±2.45*	24.57±2.76
	15	33.60±2.02**	57.50±8.18**	18.94±1.77*

*n = 50

**n = 20

(1) - Pea Field number 1, 1984

the laboratory. A. smithi was recorded only in 1984 and 1985 after releases started in Manitoba in 1983. All five of the species emerged from aphids or mummies from both alfalfa and peas.

4.2.3.1 Incidence of Parasitism

The incidence of parasitism for reared and dissected pea aphids collected from stem samples at three sites each of alfalfa and peas for each year 1983 to 1985 are shown in Appendix 2. Analysis of variance using the transformation of $\log(1+y)$ (ANOVA-split plot design) (Statistical Analysis Systems Institute 1985) showed that the parasitism of aphids each year from alfalfa was significantly higher ($p < .01$) than the corresponding values from peas. A summary of the mean percentage parasitism for alfalfa is given in Table 5 and for peas in Table 6. In 1983, $10.73 \pm 4.27\%$ (mean \pm S.E.) of the reared and $4.97 \pm 1.73\%$ of the dissected pea aphids from alfalfa were parasitized (Table 5). Corresponding values in 1984 were $9.47 \pm 3.36\%$ and $9.23 \pm 2.57\%$, but for 1985, only $0.90 \pm 0.35\%$ and $1.03 \pm 0.60\%$. The low level of parasitism on alfalfa in 1985 is similar to the low levels for aphids on peas in all three years, 1983-1985 (Table 6). The lower levels of parasitism in both the aphids from the 1985 alfalfa and the aphids from the pea fields in all three years corresponds to aphid population levels that are 2.5 to 5.0 times greater than aphid population levels in the 1983 and 1984 alfalfa fields (Tables 5 and 6). There was no direct relationship between parasitism and aphid density, however the highest levels of parasitism in alfalfa (Table 5) occurred in late July or early August

Table 5. Mean percentage parasitism of *Acyrtosiphon pisum*, based on rearings and dissections of aphids from 20-cm stem samples from alfalfa, 1983-1985.

Year	Date	No. of fields sampled (N)	Aphids reared		Aphids dissected	
			No.	Mean % parasitism $\bar{X} \pm \text{S.E.}$	No.	Mean % parasitism $\bar{X} \pm \text{S.E.}$
1983	28 June	2	30	33.50±29.00	12	0.00
	5 July	3	84	8.10±1.75	118	3.53±2.14
	12	1	193	6.20	348	5.50
	21	3	246	5.53±1.90	230	1.60±1.60
	26	3	302	11.83±7.10	251	3.87±2.67
	2 August	3	337	11.10±3.55	327	8.33±7.60
	8	3	54	24.50±14.44	58	23.73±14.49
	Season total	3	1246	10.73±4.27	1344	4.97±1.73
1984	4 July	1	39	2.50	45	2.20
	10	1	214	0.00	140	0.00
	17	3	95	15.27±9.71	70	2.37±2.37
	24	2	265	7.85±5.05	219	2.30±2.30
	1 August	3	441	14.27±2.34	762	13.37±3.63
	8	2	63	9.45±0.35	59	12.40±1.90
	14	2	7	16.65±16.65	7	0.00
	Season total	3	1124	9.47±3.36	1302	9.23±2.57
1985	9 July	1	27	0.00	17	5.90
	16	3	211	1.70±0.98	320	0.17±0.17
	24	3	1771	2.20±0.98	1156	3.83±3.10
	30	2	849	1.40±0.50	1086	1.85±1.85
	7 August*	2	926	0.70±0.70	1163	1.30±0.60
	15*	1	277	0.00	342	0.30
	Season total	3	4061	0.90±0.35	4084	1.03±0.60

*high mortality among reared aphids due to entomophoran fungi

Table 6. Mean percentage parasitism of *Acyrtosiphon pisum*, based on rearings and dissections of aphids from 20-cm stem samples from peas, 1983-85.

Year	Date	No. of fields sampled (N)	Aphids reared		Aphids dissected	
			No.	Mean % parasitism $\bar{X} \pm \text{S.E.}$	No.	Mean % parasitism $\bar{X} \pm \text{S.E.}$
1983	28 June	1	0	0.00	2	0.00
	5 July	3	401	0.27±0.27	308	0.00
	12	3	1139	0.17±0.17	1244	0.17±0.09
	21	3	642	0.33±0.18	1064	0.20±0.12
	26	3	569	0.67±0.67	854	0.37±0.23
	2 August	3	715	1.60±0.82	809	0.93±0.47
	8	2	80	4.15±4.15	67	1.70±1.70
	Season total	3	3546	0.80±0.40	4348	0.43±0.15
1984	4 July	3	841	0.07±0.07	849	0.00
	10	3	704	0.30±0.15	1050	0.00
	17	3	458	0.53±0.53	541	0.00
	24	3	325	2.30±1.22	261	1.70±1.37
	1 August	3	707	2.30±0.49	603	0.60±0.35
	8	3	614	0.93±0.48	553	3.57±1.34
	14	3	323	2.67±1.12	289	5.50±1.44
	Season total	3	3972	1.13±0.34	4146	1.07±0.19
1985	3 July	3	190	0.00	481	0.00
	9	3	614	0.00	856	0.70±0.65
	16	3	438	0.00	572	0.00
	24	3	499	0.00	539	0.00
	30	3	1567	0.13±0.09	1288	0.27±0.18
	7 August*	3	1387	0.13±0.13	2005	0.33±0.18
	15 August*	2	649	0.00	1367	1.60±0.90
	Season total	3	5344	0.08±0.06	7108	0.40±0.23

*high mortality among reared aphids due to entomophoran fungi

when aphid population levels were highest. In peas the response of the parasitoids appeared to be delayed and the highest levels of parasitism (Table 6) occurred after the peak in aphid populations.

A. ervi was responsible for the highest incidence of parasitism of all the primary species each year, followed by P. peguodorum. Together, the two primary species comprised most of the parasitism of pea aphids collected on the two crops and held in the laboratory: 1983, 98.0% and 92.0% on alfalfa and peas respectively; 1984, 94.9% and 91.4%; 1985, 100% and 100% (Tables 7 and 8). A. pisivorus, A. smithi and P. occidentale were recorded occasionally in 1983-84.

First-instar larvae of, Aphidius and Praon could be distinguished in dissected hosts primarily by the presence in Praon larvae of two ventrally-directed processes on the caudal segment (Chow 1982). On the basis of this difference, Praon spp. was determined to comprise 15% of the first instars found in dissected aphids, and Aphidius spp. the remainder. No diagnostic features were found for separating eggs or older larvae of the two genera, or for distinguishing immature stages of species from the same genus.

Immature parasitoids were found in all larval instars and in adults of the pea aphid (Table 9). Only one parasitoid was found in 8567 dissected first instars. The incidence of parasitism in the dissected aphids was always higher in third than in second instars and the incidence of parasitism in fourth instars was similar to or greater than that in third instars (Table 9). Finally, the incidence of parasitism in dissected adult aphids was similar to or lower than in dissected fourth instars (Table 9). Of all the parasitized aphids

Table 7. Percentage parasitism of *Acyrtosiphon pisum* by five primary parasitoids, based on adult emergence from reared aphids from 20-cm alfalfa stem samples, 1983-1985.

Year	Date	No. of aphids reared	% parasitism by					All spp. combined	
			<u>Praon</u> <u>occidentale</u>	<u>Praon</u> <u>pequodorum</u>	<u>Aphidius</u> <u>ervi</u>	<u>Aphidius</u> <u>pisivorus</u>	<u>Aphidius</u> <u>smithi</u>		
1983	28 June	30	-	10.0	3.3	-	-	13.3	
	5 July	84	-	2.4	4.8	-	-	7.2	
	12	193	-	-	6.2	-	-	6.2	
	21	246	-	0.4	3.3	-	-	3.7	
	26	302	-	-	7.9	0.7	-	8.6	
	2 August	337	-	1.5	8.3	-	-	9.8	
	8	54	-	7.4	11.1	-	-	18.5	
	Season total	1246	-	1.2 (N=15)	6.7 (N=83)	0.2 (N=2)	-	8.1 (N=100)	
	1984	4 July	39	-	-	2.6	-	-	2.6
		10	214	-	-	-	-	-	0.0
17		95	-	-	4.2	-	-	4.2	
24		265	0.8	0.4	6.4	-	-	7.6	
1 August		441	0.2	0.9	9.1	0.2	-	10.4	
8		63	-	-	7.9	-	-	7.9	
14		7	-	-	28.6	-	-	28.6	
Season total		1124	0.3 (N=3)	0.4 (N=5)	6.1 (N=69)	0.1 (N=1)	-	6.9 (N=78)	
1985	9 July	27	-	-	-	-	-	0.0	
	16	211	-	-	1.9	-	-	1.9	
	24	1771	-	0.4	0.3	-	-	0.7	
	30	849	-	0.5	0.7	-	-	1.2	
	7 August*	926	-	-	0.9	-	-	0.9	
	15*	277	-	-	-	-	-	0.0	
	Season total	4061	-	0.3 (N=11)	0.6 (N=24)	-	-	0.9 (N=35)	

*high mortality among reared aphids due to entomophthoran fungi

Table 8. Percentage parasitism of *Acyrtosiphon pisum* by five primary parasitoids based on adult emergence from reared aphids from 20-cm pea stem samples, 1983-1985.

Year Date	No. of aphids	% parasitism by . . .					All spp. combined
		<u>Praon occidentale</u>	<u>Praon pinguicolum</u>	<u>Aphidius ervi</u>	<u>Aphidius pisivorus</u>	<u>Aphidius smithi</u>	
1983 28 June	0	-	-	-	-	-	0.0
5 July	401	-	0.3	-	-	-	0.3
12	1139	-	-	0.2	-	-	0.2
21	642	-	0.2	-	-	-	0.2
26	569	-	0.2	0.4	-	-	0.6
2 August	715	0.1	0.7	0.7	0.1	-	1.6
8	80	-	-	7.5	-	-	7.5
Season total	3546	0.03 (N=1)	0.2 (N=8)	0.4 (N=15)	0.03 (N=1)	-	0.66 (N=25)
1984 4 July	841	-	-	0.1	-	-	0.1
10	704	-	-	0.1	-	-	0.1
17	458	-	-	0.9	-	-	0.9
24	325	-	0.3	0.9	-	-	1.2
1 August	707	-	0.3	1.6	-	0.3	2.2
8	614	-	0.2	0.3	-	0.2	0.7
14	323	-	0.6	1.6	-	-	2.2
Season total	3972	-	0.2 (N=6)	0.7 (N=26)	-	0.1 (N=3)	1.0 (N=35)
1985 3 July	190	-	-	-	-	-	0.0
9	614	-	-	-	-	-	0.0
16	438	-	-	-	-	-	0.0
24	499	-	-	-	-	-	0.0
30	1567	-	0.06	0.06	-	-	0.1
7 August	1387	-	-	0.1	-	-	0.1
15	649	-	-	-	-	-	0.0
Season total	5344	-	0.02 (N=1)	0.06 (N=3)	-	-	0.1 (N=4)

*high mortality among reared aphids due to entomophthoran fungi

Table 9. Percentage parasitism with a comparison (chi² analysis) of parasitism in adjacent age classes of *Acyrtosiphon pisum* collected on alfalfa and peas, 1983-1985. Numbers of aphids in parentheses.

Instar Year	% Parasitism of Aphids on . . .											
	alfalfa						peas					
	Adult	4th	3rd	2nd	1st	Total	Adult	4th	3rd	2nd	1st	Total
1983	10.0 (200)	14.9 (134)	14.8 (155)	0.4 (233)	0.2 (622)	4.8	2.1 (380)	0.8 (638)	1.1 (799)	0 (1005)	0 (1526)	0.5
		ns	ns	**				ns	ns	**		
1984	17.6 (165)	31.9 (144)	22.8 (145)	1.8 (170)	0 (678)	8.5	1.8 (271)	4.5 (551)	1.6 (625)	0.3 (975)	0 (1724)	1.0
		**	ns	**				ns	**	**		
1985	3.1 (489)	6.4 (406)	3.5 (434)	0.7 (877)	0 (1878)	1.6	1.9 (639)	2.3 (1044)	0.5 (1029)	.05 (1855)	0 (2541)	0.6
		*	*	**				ns	**	*		

* significant difference (P<0.05) Chi² analysis

** significant difference (P<0.01) Chi² analysis

(N=347) 69.7% of the parasitoids were found in 3rd and 4th instar aphids. The incidence of parasitism among all the adult alate aphids dissected (N=410) and all the adult apterous aphids dissected (N=1761) was 3.7% and 4.3%, respectively.

4.2.3.2 Relative Abundance in Field-Collected Mummies

The mean number of mummies collected per stem from stem sampling in three alfalfa and three pea fields each year, 1983-1985, are given in Appendix 3. A summary of the mean number of mummies per 20-cm stem from alfalfa and peas each year, 1983-85, is given in Table 10. Each year the mean number of mummies per stem for the season was higher in alfalfa. In both crops the peak density of mummies per stem usually occurred in late July or early August. The primary and secondary species that emerged from stem-sampled mummies are shown in Table 11. A. ervi and P. pequodorum predominated each year in both crops. A. smithi was collected in 1984 from a plot of peas near a site where this parasitoid was released in 1983. The secondary parasitoid species reared are discussed in Section 4.2.4.

Statistics on mummies collected during weekly visual searches in three alfalfa and three pea fields each year, 1983-85 are given in Appendix 4. A summary of the mean number of mummies collected per minute per-person of visual search in alfalfa and peas each year 1983-1985 is given in Table 12. As with stem-sampled mummies, more mummies were found on alfalfa than on peas and consistently the peak in abundance in both crops was at the end of July or beginning of August. Parasitoids that emerged from mummies collected during the visual searches are shown in Table 13; again, A. ervi and

Table 10. Mean number of *Acyrtosiphon pisum* mummies per 20-cm stem collected from alfalfa and peas, 1983-1985.

Year	Date	Alfalfa			Peas		
		No. of fields sampled (N)	No. of stems	Mean Number of mummies/stem $\bar{X} \pm$ S.E.	No. of fields sampled (N)	No. of stems	Mean Number of mummies/stem $\bar{X} \pm$ S.E.
1983	28 June	2	200	0.02±0.01	1	100	0.01
	5&6 July	3	300	0.02±0.01	3	300	0.00
	12	1	100	0.00	3	300	0.01±0.00
	19&21	3	300	0.04±0.03	3	300	0.02±0.02
	26	3	300	0.03±0.01	3	300	0.02±0.02
	2 August	3	300	0.06±0.01	3	300	0.00
	8	3	300	0.01±0.01	2	200	0.00
	16	2	200	0.02±0.02	-	-	-
	Season total	3	2000	0.03±0.01	3	1800	0.01±0.01
1984	4 July	1	100	0.04	3	300	0.00
	10	1	100	0.03	3	300	0.00
	17	3	300	0.00	3	300	0.00
	24	2	200	0.07±0.03	3	300	0.03±0.01
	1 August	3	300	0.15±0.00	3	300	0.01±0.01
	8	2	200	0.17±0.15	3	300	0.05±0.02
	14	2	200	0.13±0.12	3	300	0.04±0.01
	Season total	3	1400	0.09±0.02	3	2100	0.02±0.01
1985	3 July	0	-	-	3	300	0.00
	9	1	100	0.02	3	300	0.00
	16	3	300	0.01±0.01	3	300	0.00
	24	3	300	0.02±0.01	3	300	0.00
	30	2	200	0.06±0.06	3	300	0.01±0.00
	7 August	2	80	0.49±0.09	3	250	0.01±0.01
	15	1	20	0.45	2	70	0.08±0.08
	Season total	3	1000	0.06±0.02	3	1820	0.01±0.00

Table 11. Primary and secondary parasitoid species composition (% of total) based on Acyrtosiphon pisum mummies collected from stem samples of alfalfa and peas, 1983-1985.

Parasitoid Species	1983		1984		1985	
	alfalfa	peas	alfalfa	peas	alfalfa	peas
Primary						
Aphidiidae						
<u>Praon occidentale</u>	0.0	0.0	1.6	0.0	0.0	0.0
<u>Praon pequodorum</u>	15.4	35.7	8.8	2.5	39.7	11.1
<u>Aphidius ervi</u>	32.7	21.5	39.2	35.0	19.1	22.2
<u>Aphidius pisivorus</u>	0.0	0.0	0.8	2.5	0.0	0.0
<u>Aphidius smithi</u>	0.0	0.0	0.0	2.5	0.0	0.0
Secondary						
Pteromalidae						
<u>Asaphes lucens</u>	0.0	0.0	0.0	5.0	7.4	0.0
Alloxystidae						
<u>Alloxysta victrix</u>	1.9	7.1	0.0	0.0	0.0	11.1
Megaspilidae						
<u>Dendrocercus</u> sp. "A"	0.0	0.0	0.0	0.0	1.5	0.0
Emerged in field, dead or in diapause	50.0	35.7	49.6	52.5	32.3	55.6
(N)	(52)	(14)	(125)	(40)	(68)	(9)

Table 12. Mean number of *Acyrtosiphon pisum* mummies collected per person per minute of visual search in alfalfa and peas, 1983-1985.

Year Date	Alfalfa			Peas		
	No. of fields sampled (N)	Length of search (min.)	Mean number of mummies/minute $\bar{X} \pm \text{S.E.}$	No. of fields sampled (N)	Length of search (min.)	Mean number of mummies/minute $\bar{X} \pm \text{S.E.}$
1983 28 June	2	20	0.00	1	10	0.00
5&6 July	3	30	0.10±0.06	3	30	0.07±0.07
12	1	10	0.60	2	20	0.00
19&21	3	30	2.53±2.28	3	30	0.37±0.20
26	3	30	0.90±0.65	3	30	0.23±0.15
2 August	3	30	1.13±0.33	3	30	0.13±0.13
8	2	20	0.60±0.60	1	10	0.00
Season total	3	170	0.89±0.62	3	160	0.15±0.07
1984 4 July	1	10	0.60	3	30	0.07±0.03
10	1	10	0.90	3	30	0.27±0.27
17	1	10	0.30	2	20	0.00
24	2	20	1.70±0.10	3	30	0.38±0.09
1 August	3	30	5.07±1.57	2	20	0.10±0.00
8	3	30	3.37±0.73	3	30	0.13±0.09
14	2	20	2.65±1.45	2	20	0.05±0.05
Season total	3	130	3.07±0.90	3	180	0.15±0.02
1985 3 July	0	-	-	0	-	-
9	1	10	3.20	0	-	-
16	3	30	1.03±0.67	1	10	0.00
24	3	30	3.00±1.76	3	30	0.00
30	3	30	4.80±2.53	3	30	0.00
7 August	2	20	7.14±0.55	3	30	0.10±0.10
15	1	10	5.00	2	20	0.55±0.55
Season total	3	130	3.64±0.87	3	120	0.09±0.09

Table 13. Primary and secondary parasitoid species composition (% of total) based on Acyrtosiphon pisum mummies collected during visual searches in alfalfa and peas, 1983-1985.

Parasitoid Species	1983		1984		1985	
	alfalfa	peas	alfalfa	peas	alfalfa	peas
Primary						
Aphidiidae						
<u>Praon occidentale</u>	0.0	0.0	1.4	0.0	0.4	7.1
<u>Praon piquodorum</u>	6.3	33.3	5.5	3.7	18.0	35.8
<u>Aphidius ervi</u>	46.2	20.8	46.1	40.7	35.5	21.4
<u>Aphidius pisivorus</u>	0.0	4.2	0.0	0.0	0.0	0.0
<u>Aphidius smithi</u>	0.0	0.0	0.0	0.0	0.0	0.0
Secondary						
Pteromalidae						
<u>Asaphes lucens</u>	2.5	4.2	0.3	3.7	14.9	7.1
<u>Pachyneuron siphonophorae</u>	1.3	0.0	0.0	0.0	0.8	0.0
Alloxystidae						
<u>Alloxysta victrix</u>	0.0	0.0	0.0	0.0	0.2	0.0
<u>Alloxysta megourae</u> complex	0.0	0.0	0.0	0.0	0.2	0.0
Megaspilidae						
<u>Dendrocercus</u> sp. "A"	0.0	0.0	0.0	0.0	2.2	0.0
<u>Dendrocercus</u> sp.	0.0	0.0	0.6	0.0	0.0	0.0
Emerged in field, dead or in diapause	43.7	37.5	46.1	51.9	27.8	28.6
(N)	(158)	(24)	(358)	(27)	(490)	(14)

P. pequodorum predominated. The secondary parasitoids are discussed in Section 4.2.4.

In 1984, from whole plants examined in a total of fifteen 1/2m² quadrats of forage alfalfa at St. Adolphe and Glenlea, the mean number of mummies per quadrat area was as high as 25.0±3.4 (mean ± S.E.) (Table 14). The parasitoid species that emerged are listed in Table 15, A. ervi and P. pequodorum again predominated. Emergence of parasitoids decreased late in the season, but dissection of the mummies containing dead parasitoids did not reveal the reason for increased mortality late in the season.

The emergence from mummies obtained from 30 minute visual searches in a seed alfalfa field near Oakbank and a forage alfalfa field near St. Adolphe, in 1985, is given in Table 16. A. ervi and P. pequodorum predominated at both sites and at Oakbank, a release site for A. smithi in 1985, A. smithi was collected as well. The secondary parasitoids are discussed in Section 4.2.4.

A summary of the primary parasitoid emergence from field collected Acyrtosiphon pisum mummies, 1983-1985 is given in Table 17. Overall, the predominant parasitoid was A. ervi, followed by P. pequodorum.

4.2.3.3 Abundance in D-Vac Collections

In 1983, 550 D-Vac contacts taken on alfalfa yielded only 12 primary parasitoids, the relative abundance of which are given in Table 18.

Table 14. The mean number of mummies collected per 1/2m² quadrat of alfalfa at Glenlea and St. Adolphe in 1984.

Date	Location	No. of quadrats (N)	No. of mummies	Mean No. of mummies/quadrat $\bar{X} \pm \text{S.E.}$	% Emergence
2 August	Glenlea	5	47	9.4 \pm 7.0	80.9
	St. Adolphe	5	125	25.0 \pm 3.4	70.4
21 August	Glenlea	5	95	19.0 \pm 3.3	0

Table 15. Primary and secondary parasitoid species composition (% of total) based on Acyrtosiphon pisum mummies collected in 1/2m² quadrats of alfalfa at Glenlea and St. Adolphe in 1984.

Species	% of total
Primary	
<u>Praon occidentale</u>	0.4
<u>Praon peguodorum</u>	7.5
<u>Aphidius ervi</u>	36.9
Secondary	
Pteromalidae	
<u>Asaphes lucens</u>	3.2
Megaspilidae	
<u>Dendrocercus</u> sp.	0.4
Encyrtidae	
<u>Aphidencyrtus aphidivorus</u>	0.4
Emerged in field, dead or in diapause	51.2
(N)	(279)

Table 16. Primary and secondary parasitoid species composition (% of total) based on Acyrtosiphon pisum mummies collected by visual searches in alfalfa at Oakbank and St. Adolphe in July, 1985. Three 30 minute collections were made at Oakbank (11, 17 & 25 July) and one 30 minute collection at St. Adolphe (30 July).

Species	% of total	
	Oakbank	St. Adolphe
Primary		
Aphidiidae		
<u>Praon</u> <u>pequodorum</u>	14.3	10.7
<u>Aphidius</u> <u>ervi</u>	18.4	58.9
<u>Aphidius</u> <u>smithi</u>	5.1	0.0
Secondary		
Pteromalidae		
<u>Asaphes</u> <u>lucens</u>	20.4	10.7
Alloxystidae		
<u>Alloxysta</u> <u>victrix</u>	0.0	1.8
Megaspilidae		
<u>Dendrocerus</u> sp. "A"	12.2	0.0
Emerged in field, dead or in diapause	29.6	17.9
(N)	(98)	(56)

Table 17. Percentage of field-collected mummies of Acyrtosiphon pisum from which adults of each primary parasitoid emerged, 1983-1985. Number of collected mummies in parentheses.

Species of primary parasitoids	1983 (248)	1984 (829)	1985 (735)
<u>Praon occidentale</u>	0.0	0.3	0.4
<u>Praon pequodorum</u>	12.5	6.0	23.0
<u>Aphidius ervi</u>	39.5	40.7	29.7
<u>Aphidius pisivorus</u>	0.4	0.2	0.0
<u>Aphidius smithi</u>	0.0	0.1	0.8

Table 18. Relative abundance (%) of adults of primary parasitoids of Acyrtosiphon pisum collected with a D-Vac Vacuum Insect Net, 1983-1985. Number of adults in parentheses.

Parasitoid Species	1983 550 contacts (12)	1984 4000 contacts (104)	1985 11,500 contacts (1494)
<u>Praon occidentale</u>	8.3	7.7	0.0
<u>Praon pequodorum</u>	58.4	40.4	53.4
<u>Aphidius ervi</u>	33.3	51.0	46.3
<u>Aphidius pisivorus</u>	0.0	0.0	0.0
<u>Aphidius smithi</u>	0.0	0.9	0.3

In 1984, D-Vac collections were made from 24 May to 10 July and although a total of 4000 contacts were taken from three alfalfa fields, only 104 adult primary parasitoids were collected; their relative abundances are given in Table 18.

In 1985, D-Vac collections were used in a more extensive survey of alfalfa from 16 May to 12 September. For the whole season, P. pequodorum and A. ervi made up 53.4% and 46.3%, respectively, of the primary parasitoids collected (Table 18). The mean number of primary parasitoids per 250 contacts is given in Table 19.

P. pequodorum was the predominant parasitoid except when A. ervi peaked in abundance in the field at Glenlea on 8 to 15 August. The absolute abundance of each of these species (number of adults/D-Vac contact) from the alfalfa field at Glenlea fluctuated until mid-July, increased until mid-August, then decreased. This is shown by D-Vac data taken at approximately weekly intervals during 16 May - 12 September (Table 20). The number of P. pequodorum per contact was greater than that of A. ervi on each sampling date until late-July; thereafter, numbers of A. ervi were larger until both species peaked early in August.

4.2.4 Secondary Parasitoids

Eight of the twelve secondary species reared from pea aphids or pea aphid mummies were identified to the species level (Table 1, 11, 13, 15, 16). Two alloxystids, Alloxysta victrix (Westwood) and Phaenoglyphis ambrosiae (Ashm.) emerged from mummies that formed in the laboratory from field-collected aphids during the preliminary study (Table 1). This result confirms that both alloxystids are

Table 19. The mean number of primary parasitoid adults collected in 250 D-Vac contacts per alfalfa field on each sampling date, 1985.

Date	No. of fields	No. of contacts (N)	Mean no. of parasitoids/250 contacts				
			<u>Praon occidentale</u>	<u>Praon pequodorum</u> $\bar{X} \pm X.E.$	<u>Aphidius ervi</u> $\bar{X} \pm S.E.$	<u>Aphidius pisivorus</u>	<u>Aphidius smithi</u> $\bar{X} \pm S.E.$
16 May	4	1000	0	1.75±0.63	0.50±0.50	0	0
22	4	1000	0	8.25±3.20	1.00±0.58	0	0
28	4	1000	0	11.75±3.99	0.50±0.50	0	0
3&4 June	4	1000	0	6.75±2.95	0.50±0.50	0	0.25±0.25
7	2	500	0	5.50±0.50	0	0	0
11	4	1000	0	4.75±2.29	1.25±0.75	0	0.25±0.25
18	3	750	0	17.67±10.27	0.67±0.67	0	0
27	4	1000	0	4.75±1.65	1.00±0.58	0	0.25±0.25
2 July	4	1000	0	14.50±6.99	1.00±0.71	0	0
10	2	500	0	4.50±3.50	2.50±2.50	0	0.50±0.50
18	2	500	0	25.50±20.50	8.00±8.00	0	0
24	2	500	0	28.00±28.00	18.50±13.50	0	0.50±0.50
31	2	500	0	45.50±44.50	39.50±30.50	0	0
8 August	2	500	0	37.00±36.00	58.00±51.00	0	0
15	1	250	0	235.00	402.00	0	0
12 September	4	500	0	2.00±0.41	2.75±1.03	0	0
TOTAL	(4)	11500	(0)	(798)	(691)	(0)	(5)

Table 20. Number of parasitoid adults collected on alfalfa at Glenlea, Manitoba per D-Vac contact in each of 15 collections in 1985.

Date	Number of Adults/250 D-Vac Contacts			Number of Adults/D-Vac contact		
	<u>Praon</u> <u>pequodorum</u>	<u>Aphidius</u> <u>ervi</u>	<u>Aphidius</u> <u>smithi</u>	<u>Praon</u> <u>pequodorum</u>	<u>Aphidius</u> <u>ervi</u>	<u>Aphidius</u> <u>smithi</u>
16 May	3	2	0	0.012	0.008	0
22	12	0	0	0.048	0	0
28	19	0	0	0.076	0	0
4 June	1	0	0	0.004	0	0
11	4	2	0	0.016	0.008	0
18	14	0	0	0.056	0	0
27	8	2	1	0.032	0.008	0.004
2 July*	31	1	0	0.124	0.004	0
10	8	5	1	0.032	0.020	0.004
18	46	16	0	0.184	0.064	0
24	56	32	0	0.224	0.128	0
31	90	70	0	0.360	0.280	0
8 August	73	109	0	0.292	0.436	0
15	235	402	0	0.940	1.608	0
12 September	2	1	0	0.008	0.004	0

*Field cut 3 July

indirect hyperparasitoids. A. victrix also emerged from field-collected mummies. The remaining secondary species including five pteromalids, Asaphes lucens (Prov.), Coruna clavata Wlk., Pachycrepoideus vindemiae (Rond), Pachyneuron siphonophorae (Ash.) and Pachyneuron sp., one alloxystid Alloxysta megourae complex, three megaspilids Dendrocerus carpenteri (Curt), Dendrocerus sp."A" and Dendrocerus sp. and an encyrtid Aphidencyrtus aphidivorus (Mayr) emerged from field-collected mummies. With the exception of Alloxysta megourae complex and Aphidencyrtus aphidivorus reared once from Praon and Aphidius respectively, all of the species were reared from both Praon and Aphidius mummies.

4.2.4.1 Incidence of Parasitism by Secondary Parasitoid Species

The maximum incidence of parasitism by indirect secondary parasitoids in field-collected aphids was 0.5% (based on emergence) and occurred in 1982. In 1981 this figure was 0.02% and from 1983-85 19,333 aphids produced no indirect secondary parasitoids.

The incidence of parasitism by direct secondary parasitoids, based on emergence from field-collected mummies, varied widely and ranged up to 40.5% in 1982 (Table 21). There was insufficient data on peas to determine whether the incidence of secondary parasitoids differs between the two crops. There was no apparent seasonal trend in the incidence of parasitism by the secondary parasitoids except that the incidence was highest at the end of the season.

Asaphes lucens was the most abundant secondary parasitoid, based on emergence from field collected mummies (Table 21), and comprised 86.6%, 46.7%, 55.6%, 76.2% and 76.9% of the total secondary parasitoid emergence from 1981-85.

Table 21. Percentage of field-collected mummies of Acyrtosiphon pisum from which adults of each secondary parasitoid species emerged, 1981-1985. Number of collected mummies in parentheses.

Species of secondary parasitoids	1981 (121)	1982 (37)	1983 (248)	1984 (829)	1985 (735)
<u>Pteromalidae</u>					
<u>Asaphes lucens</u> (Prov.)	32.2	18.9	2.0	1.6	14.3
<u>Coruna clavata</u> Wlk.	2.5	0.0	0.0	0.0	0.0
<u>Pachycrepoideus vindemiae</u> (Rond.)	0.0	13.5	0.0	0.0	0.0
<u>Pachyneuron siphonophorae</u> (Ashm.)	1.7	0.0	0.8	0.0	0.5
<u>Pachyneuron</u> sp.	0.0	8.1	0.0	0.0	0.0
<u>Alloxystidae</u>					
<u>Alloxysta victrix</u> (Westw.)	0.0	0.0	0.8	0.0	0.4
<u>Alloxysta meqourae</u> Complex	0.0	0.0	0.0	0.0	0.1
<u>Megaspilidae</u>					
<u>Dendrocercus carpenteri</u> (Curt.)	0.8	0.0	0.0	0.0	0.0
<u>Dendrocercus</u> sp. "A"	0.0	0.0	0.0	0.0	3.3
<u>Dendrocercus</u> sp.	0.0	0.0	0.0	0.4	0.0
<u>Encyrtidae</u>					
<u>Aphidencyrtus aphidivorus</u> (Mayr)	0.0	0.0	0.0	0.1	0.0

The percentage of primary parasitoids killed by secondary parasitoids is higher than is indicated by adult emergence, because some mummies from which there was no emergence contained a dead secondary parasitoid. Some mummies examined in 1985 contained a dead primary parasitoid and had one or more drill holes believed to have been made by secondary parasitoids; the holes appeared identical to those made on pea aphid mummies that were exposed to females of Asaphes lucens in the laboratory. In 1985, of 214 unemerged mummies 17.3% had drill holes and 58% of these mummies had more than one. In 1985, the incidence of secondary parasitism based only on emergence was 18.6%, but was 27.1% when mummies with sting holes or unemerged secondary parasitoids were included.

5. DISCUSSION

Five primary parasitoids, including Praon occidentale, Praon peguorodum, Aphidius ervi, Aphidius pisivorus, and Aphidius smithi, all aphidiids, were found to parasitize Acyrtosiphon pisum in Manitoba. Three of the primary parasitoid species, P. occidentale, A. pisivorus and A. smithi were previously unrecorded as parasitizing A. pisum in Manitoba though all have been reared from pea aphids collected elsewhere in North America (Krombein et al. 1979). A. smithi was recorded only in 1984 and 1985 after releases started in Manitoba in 1983.

Three other aphidiids, Ephedrus californicus, Praon simulans and Monoctonus nervosus and two encyrtids, Aphelinus semiflavus and Aphelinus howardii, that parasitize A. pisum in North America (Mertins 1985) were not recorded in the present study. A. semiflavus was recorded in Manitoba by Batulla and Robinson (1984) but not as a parasitoid of A. pisum. The other four primary parasitoids may not occur in Manitoba, because the winter climate here is more severe than the climate in the ranges listed for these parasitoids by Krombein et al. (1979) and Gutierrez and van den Bosch (1970). Also, three of the species, E. californicus, P. simulans and M. nervosus are known to prefer other aphid species as hosts (Mackauer and Finlayson 1967; Sekhar 1960; Calvert and van den Bosch 1972). The species of Aphelinus are considered to be uncommon as pea aphid parasitoids in the field (Mackauer and Finlayson 1967; Mertins 1985).

This study found that the incidence of parasitism of the pea aphid in Manitoba increases through July and peaks in late July or early August but between years the peak incidence achieved may be affected by dramatic increases in aphid abundance. This was observed when in 1983, 9.55% of the reared and 4.6% of the dissected pea aphids from alfalfa were parasitized and corresponding values in 1984 were 8.81% and 8.5%, but for 1985, only 1.11% and 1.6%. The lower values in 1985 possibly reflect a delayed response by the parasitoids to the very high aphid densities sampled at the end of the 1985 season.

The mean incidence of parasitism each year from alfalfa was significantly higher than the corresponding values from peas. As the same parasitoid species occurred on the two crops, the higher values on alfalfa are attributed primarily to establishment and maintenance of populations of each primary parasitoid on the perennial crop; parasitoid females that emerge at the beginning of the season do not need to disperse to locate hosts. In contrast, the aphid population on peas, an annual crop, is exposed only to parasitoid females that disperse from the perennial crop; few alate aphids that migrate to pea plants each year are already parasitized, because the majority of the parasitized aphids die as fourth-instar larvae or young adults, before becoming capable of migration (Campbell and Mackauer 1975).

In 1985 among the reared aphids, there was over 50% mortality within a week of collection, before parasitoids matured, from infection by a fungus tentatively identified as Erynia neoaphidis Remaudiere and Hennebert (Milner 1981, 1982). Mortality from fungus

was also observed in the field, and mycelia were found in dissected aphids, but no infection by fungus was observed in other years.

A. ervi followed by P. pequodorum were responsible for most of the parasitism of pea aphids collected on alfalfa and peas. There was no consistent difference between the two crops in relative abundance of the various primary species. From the dissection data, among the larval instars parasitized, it appears the first instars are rarely attacked. The incidence of parasitism was always higher in third than in second instars and since pea aphids parasitized in the second instar do not mummify until the fourth instar (Campbell and Mackauer 1975) the magnitude of the difference between the parasitism in the second and third instars suggests that third instars are preferred or attacked more successfully than second instars. Since the incidence of parasitism in the fourth instars was similar to or greater than the third instars and some fourth instars mummify, an equal or greater number of aphids presumably are parasitized in this instar. The incidence of parasitism in dissected adults was similar to or lower than in dissected fourth instars, reflecting the fact (Campbell and Mackauer 1975) that some of the aphids parasitized in the third or fourth instar or as adults had mummified during the adult stage and were therefore not included in the adult samples collected.

A. ervi and P. pequodorum also comprised most of the primary parasitoid emergence from mummies collected during stem sampling. As in the reared aphids, A. ervi was the most abundant species each year and the two crops showed no obvious differences other than the

greater density of mummies on alfalfa which reflects higher levels of parasitism on this crop. When data from the two crops are pooled A. ervi predominated in 1983 and 1984 and P. pequodorum predominated in 1985. The failure of A. ervi to predominate in 1985 may be due to the presence of the entomophthoran fungus in the aphid population at the time when the abundance of A. ervi usually peaks. A. smithi was collected from a pea field at Glenlea in 1984 near a 1983 release site for this parasitoid which is evidence of the establishment of this species in Manitoba.

Mature larvae of the three Aphidius species invariably spun cocoons inside the mummies. In contrast, Praon larvae usually emerged from the mummies and made cocoons between the mummy and the plant; occasionally in the laboratory Praon larvae matured within aphids that were in the bottom of a cage, not on a firm substrate. Chow (1982) noted that elevated temperature during larval development of Praon also caused pupation within the mummy. No reliable criterion was found for separating mummies containing A. ervi, A. pisivorus or A. smithi, or for distinguishing cocoons of P. occidentale and P. pequodorum or the mummies in which these two parasitoids had developed.

Mortality of parasitoids within cocoons was noted throughout the study and the mortality rate among field-collected mummies held for emergence varied. In 1982 the emergence rate was 81.1% from mummies on stems that were cut and placed in a plastic bag. From stem sampling in 1983-85 the emergence rate from mummies formed on the stems was 54.7% from alfalfa and 55.5% from field peas. The lower

emergence rate from mummies collected during stem sampling may reflect damage to the mummies when the stems were tapped against the wire mesh to dislodge aphids. The emergence from mummies collected during 5-minute visual searches was 62.2% and 65.5% from alfalfa and field peas respectively. In 1984, 279 mummies collected from 1/2 m² quadrats were handled in the same manner as mummies from visual searches and had an emergence rate of 73.2% for collections made 2 August but fell to no emergence from 95 mummies collected 21 August. The low emergence from mummies collected in late August may be due to the fact that in the field mummies from which parasitoids emerged, weather off the plants (Hughes et al. 1981) and mummies containing dead parasitoids tend to accumulate toward the end of the season.

In addition to mortality caused by handling, some parasitoids in mummified aphids are probably killed by piercing by females of secondary species. In 1984 a high level of mortality of parasitoids within mummies occurred subsequent to several days when maximum daily temperatures reached 30°C and suggests that the effect of high temperatures on parasitoids within mummies should be examined. A temperature of 34°C is known to be lethal for Aphidius megourae Stary (Stary 1966).

Results obtained with the D-Vac confirmed P. pequodorum and A. ervi as the predominant primary parasitoids. However, P. pequodorum was relatively more abundant in D-Vac contacts than among parasitoids reared from field-collected aphids and mummies. This difference resulted from the fact that many D-Vac contacts were taken in May and June, before most aphids and mummies were collected, at a time when

adults of P. peguodorum were relatively more abundant. Data for both 1984 and 1985, when the largest number of D-Vac contacts were taken, show a progressive seasonal change in relative abundance of adults of the two species, with P. peguodorum predominant at first and A. ervi eventually becoming the more abundant species, particularly in 1985 due to a large peak in abundance in one field on 15 August. No seasonal trends were obvious in 1983 for which limited data are available or in 1982 when all collections were taken after mid-June, however A. ervi was the more abundant species each year. P. peguodorum adults predominated among the primary species collected with the D-Vac throughout the sampling period in 1981, in line with its higher recorded incidence of parasitism.

A population build-up of the two parasitoids during July and August may not depend solely upon the pea aphid, but possibly on other host species on other adjacent crops, as well. For example, P. peguodorum was reared from Macrosiphum euphorbiae collected in August, 1985 in a flax field 0.5 kilometer from a sampled pea field at Ste. Agathe and both parasitoid species have other host species as well (Krombein et al. 1979).

Adults of P. peguodorum and A. ervi were collected as early as 16 May and as late as 12 September. In the laboratory, the generation time for each of these species when propagated at 20°C was approximately 14 days, and adults lived approximately 10 days. Therefore, depending on weather conditions, five to ten generations of each species could develop each year. Mature parasitoid larvae in diapause were found in cocoons beneath Praon mummies and inside

Aphidius mummies reared from aphids collected as early as 26 July in 1982 and 1983, and in association with Praon mummies reared from aphids collected on 22 July 1981. The diapause, however, may have been induced by handling conditions in the laboratory, as diapausing P. pequodorum were often observed in laboratory cultures of this species after the plants on which the parasitized aphids had been feeding were cut and the mummies had formed on cut leaves. In the field, diapausing parasitoid larvae were found beneath Praon mummies collected in August, 1984 and August, 1985 and inside Aphidius mummies collected in August 1983 and September, 1985. This finding suggests that both Praon and Aphidius species, probably P. pequodorum and A. ervi, overwinter in Manitoba. If so, the diapausing parasitoids presumably spend the winter attached to dessicated leaves among debris on the ground.

Eight of the twelve secondary parasitoid species reared from pea aphids or pea aphid mummies were identified to the species level. Due to revisions now underway in the Pteromalidae, Alloxystidae and Megaspilidae (C.M. Yoshimoto pers. comm.), the other four secondary species were identified only to the genus or complex level. Seven of the eight identified secondary parasitoid species were already known to hyperparasitize A. pisum (Mertins 1985); the eighth, a pteromalid, Pachycrepoideus vindemiae (Rondani) had previously been recorded as a parasitoid mainly of dipterous pupae (Krombein et al. 1979) and occasionally of hymenopterous larvae in cocoons (Thompson 1958). Both Alloxysta victrix (Westwood) and Phaenoglyphis ambrosiae (Ashm.) emerged from mummies that formed in the laboratory from

field-collected aphids during the preliminary study confirming that both alloxystids are indirect hyperparasitoids. A. victrix also emerged from field-collected mummies, as did Aphidencyrtus aphidivorus (Mayr), which is reported to be an indirect hyperparasitoid (Mertins 1985); presumably, both species had attacked parasitized pea aphids that subsequently mummified in the field before being collected. Three specimens of A. aphidivorus emerged from the same mummy; this is the first report that this species is gregarious, however it is known to oviposit several eggs in one host (Griswold 1929). The remaining secondary species emerged only from field-collected mummies and, in view of information about their biologies (Mertins 1985), are considered to be direct hyperparasitoids. All the species, except Alloxysta megourae complex and Aphidencyrtus aphidivorus reared only once from Praon and Aphidius respectively, were reared from both Praon and Aphidius mummies.

Asaphes vulgaris Walker, reported by some investigators to hyperparasitize pea aphid in North America (Mertins 1985), was not recorded in the present study. Specimens from North America in the Canadian National Collection of Insects labelled as A. vulgaris were recently re-examined, and all were found to be Asaphes lucens (Prov.) (C.M. Yoshimoto, pers. comm.). On this basis, the record of A. vulgaris from Manitoba by Batulla and Robinson (1984) may refer to A. lucens, for their specimens were identified before the CNC specimens were re-examined.

The present list, from 2691 mummies, is the most extensive of secondary parasitoids of pea aphid from one locality in North America. Mertins (1985) listed four species from >434 mummies from his research in Iowa; Hutchison and Hogg (1985), and Thiboldeaux *et al.* (1987), each recorded four species from 747 and 941 mummies respectively from Wisconsin; and Matejko and Sullivan (1984), four species in New Jersey from 4803 mummies.

The incidence of parasitism by indirect secondary parasitoids in field-collected aphids can be considered negligible as only 2 specimens each of Alloxysta victrix and Phaenoglyphis ambrosiae were reared from 9490 aphids in 1981-82 and during 1983-85 19333 aphids produced no indirect secondary parasitoids.

The incidence of parasitism by direct secondary parasitoids, based on emergence from field-collected mummies, varied widely and ranged up to 40.5% in 1982. The inter-year variability in the incidence of hyperparasitism may result in part from changes in secondary parasitoid abundance caused by between-year differences in the abundance of alternate hosts for the secondary parasitoids. Most of the secondary parasitoids recorded in this study also parasitize other primary parasitoids from other aphid species, Pachyneuron siphonophorae, Asaphes lucens, Aphidencyrthus aphidivorous and Alloxysta sp. (Gilstrap *et al.* 1984).

The higher incidence of parasitism by the secondary parasitoids at the end of the season probably reflects the fact that mummies collected late in the season will produce mostly secondary parasitoids, because primary parasitoids have already emerged; in the

laboratory at 20°C the emergence of primary parasitoids from field-collected mummies ended after 9 days as compared to 20 days for the secondary parasitoids. A. lucens was the most abundant secondary parasitoid, based on emergence from field-collected mummies.

The percentage of primary parasitoids killed by secondary parasitoids is probably higher than is indicated by adult emergence. Some mummies from which there was no emergence contained a dead secondary parasitoid that could not be identified and others contained a dead primary parasitoid and had one or more drill holes believed to have been made by secondary parasitoids. Since one attack by A. lucens paralyzes a primary parasitoid (Sullivan 1972), multiple attacks probably kill it and make it unsuitable for the secondary parasitoid species (Walker 1967). Therefore, the impact of secondary parasitism of pea aphid will be underestimated if only emerged parasitoids are counted.

6. CONCLUSION

In Manitoba, five primary and eight secondary parasitoid species were reared from the pea aphid, Acyrtosiphon pisum (Harris), or from pea aphid mummies. Four other secondary parasitoid species, identified only to genus or to complex were also recorded. All the primary parasitoids were aphidiids and were known to parasitize the pea aphid in North America, but only two were previously known to do so in Manitoba. These two species, Aphidius ervi Haliday, which was introduced to North America in 1959, and an indigenous species Praon piquodorum Viereck, made up over 90% of the primary parasitoids reared from pea aphid in each of 5 years. Praon occidentale Baker and Aphidius pisivorus Smith, which are both indigenous, and Aphidius smithi Sharma and Subba Rao, a species introduced to Manitoba in 1983, comprised the remainder of the primary parasitoid complex. The incidence of parasitism by primary parasitoids was higher in alfalfa than field peas and the parasitism was similar in both dissected and reared series of aphids in both crops. The maximum incidence of parasitism by the primary parasitoids was found in alfalfa and based on dissections was $13.37 \pm 3.63\%$ in August, 1984 and based on rearings this peak was $14.27 \pm 2.34\%$. Females of each species parasitized pea aphids from May to September, and mature larvae overwintered inside or adjacent to mummies.

One secondary parasitoid species, Pachycrepoideus vindemiae, was not previously known to hyperparasitize pea aphid in North America. Two of the secondary species, Alloxysta victrix and Phaenoglyphis ambrosiae were indirect; both of these alloxystids were reared from field-collected aphids as well as from field-collected mummies. Another indirect parasitoid, an encyrtid, Aphidencyrtus aphidivorus (Mayr) was reared once from a field-collected mummy and found to be gregarious as 3 adults emerged. Four pteromalids, Asaphes lucens (Provancher), Coruna clavata Walker, Pachyneuron siphonopharae (Ashmead) and Pachycrepoideus vindemiae (Rondani), as well as a megaspilid, Dendrocerus carpenteri (Curt), were reared only from field-collected mummies and are considered to be direct secondary parasitoids. Most of the secondary parasitoids, except Alloxysta megourae complex and Aphidencyrtus aphidivorus reared only once from Praon and Aphidius respectively were associated with both primary genera. A. lucens comprised from 46.7% to 86.6% of the total secondary emergence from field-collected mummies from 1981-85. The incidence of parasitism by secondary parasitoids varied widely but was as high as 40.5%, based on emergence, in 1982. The incidence of secondary parasitism, based only on emergence, may be underestimated as additional mortality caused by stinging by secondary parasitoids may occur in the field.

This study shows the most effective method for determining the relative abundance of pea aphid parasitoids is by a timed visual search for mummies in alfalfa fields during July and August. If this method of monitoring the parasitoid population is pursued, however, a

further study should be made into the mortality of parasitoids within mummies.

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Appendix 1 (cont'd).

	Ste. Agathe (peas)							
	June	July				August		
	28	5-6	12	19-21	26	2	8	16
N	100	100	100	100	100	100	****	
MEAN	0.02	1.64	6.13	8.91	6.24	9.21		
VAR.	0.02	10.15	79.29	88.85	102.33	97.22		
S.D.	0.14	3.19	8.90	9.43	10.12	9.86		
S.E.	0.01	0.32	0.89	0.94	1.01	0.99		
MAX.	1.00	18.00	64.00	42.00	80.00	65.00		
MIN.	0.00	0.00	0.00	0.00	0.00	0.00		
		Morris (peas)						
N	**	100	100	***100	100	100	100	****
MEAN		1.57	11.43	0.76	2.02	0.06	0.17	
VAR.		11.11	110.07	6.91	38.79	0.10	0.34	
S.D.		3.33	10.49	2.63	6.23	0.31	0.59	
S.E.		0.33	1.05	0.26	0.62	0.03	0.06	
MAX.		26.00	45.00	22.00	40.00	2.00	3.00	
MIN.		0.00	0.00	0.00	0.00	0.00	0.00	
		Glenlea (peas)						
N	**	100	100	100	100	100	100	****
MEAN		4.91	9.34	10.49	7.87	8.79	1.64	
VAR.		49.11	143.24	178.37	132.24	77.99	7.24	
S.D.		7.01	11.97	13.36	11.50	8.83	2.69	
S.E.		0.70	1.20	1.34	1.15	0.88	0.27	
MAX.		39.00	75.00	50.00	63.00	41.00	20.00	
MIN.		0.00	0.00	0.00	0.00	0.00	0.00	

**field recently planted - no samples taken

***field sprayed prior to sampling - no samples taken

****senescence complete - no samples taken

Appendix 1 (cont'd).

1984

Ste. Agathe (alfalfa)								
July					August			
	4	10	17	24	1	8	14	
N	*	*	100	100	100	100	100	
MEAN			0.09	1.88	2.67	0.42	0.11	
VAR.			0.08	5.40	10.34	0.81	0.22	
S.D.			0.29	2.32	3.22	0.90	0.47	
S.E.			0.03	0.23	0.32	0.09	0.05	
MAX.			1.00	13.00	13.00	4.00	4.00	
MIN.			0.00	0.00	0.00	0.00	0.00	
St. Adolphe (alfalfa)								
N	*	*	100	100	100	*	*	
MEAN			0.37	2.03	4.46			
VAR.			0.56	5.28	21.00			
S.D.			0.75	2.30	4.58			
S.E.			0.07	0.23	0.46			
MAX.			3.00	14.00	24.00			
MIN.			0.00	0.00	0.00			
Glenlea (alfalfa)								
N	100	100	100	*	100	100	100	
MEAN	0.74	3.63	1.22		2.68	0.79	0.08	
VAR.	1.59	14.34	2.46		9.71	1.50	0.13	
S.D.	1.26	3.79	1.57		3.12	1.23	0.37	
S.E.	0.13	0.38	0.16		0.31	0.12	0.04	
MAX.	7.00	22.00	8.00		15.00	6.00	2.00	
MIN.	0.00	0.00	0.00		0.00	0.00	0.00	

*field recently cut - no samples taken.

Appendix 1 (cont'd).

		1985							
		Ste. Agathe (alfalfa)							
		June	July				August		
		18	3	9	16	24-25	30	7	15
N	40	*	*	100	100	100	100	30	*
MEAN	0.00			0.09	0.33	2.80	29.00		
VAR.	0.00			0.16	0.69	13.62	469.79		
S.D.	0.00			0.40	0.83	3.69	21.67		
S.E.	0.00			0.04	0.08	0.37	3.96		
MAX.	0.00			3.00	5.00	14.00	92.00		
MIN.	0.00			0.00	0.00	0.00	2.00		
		St. Adolphe (alfalfa)							
N	40	*	*	100	100	*	*****		
MEAN	0.05			2.44	24.68				
VAR.	0.05			14.43	674.79				
S.D.	0.22			3.80	25.98				
S.E.	0.03			0.38	2.60				
MAX.	1.00			27.00	130.00				
MIN.	0.00			0.00	0.00				
		Glenlea (alfalfa)							
N	40	*	100	100	100	100	50	20	
MEAN	0.05		0.38	2.65	6.51	16.23	31.76	33.60	
VAR.	0.05		0.70	16.59	37.89	288.64	627.98	81.31	
S.D.	0.22		0.84	4.07	6.16	16.99	25.06	9.02	
S.E.	0.03		0.08	0.41	0.62	1.70	3.54	2.02	
MAX.	1.00		4.00	23.00	30.00	80.00	117.00	51.00	
MIN.	0.00		0.00	0.00	0.00	0.00	3.00	17.00	

*field recently cut - no samples taken

*****field cultivated - no samples taken

Appendix 1 (cont'd).

		Rosenort (peas)							
		June	July				August		
		18	3	9	16	24-25	30	7	15
N	**		100	100	100	100	100	***100	0
MEAN			0.43	0.27	1.05	2.53	6.64	0.20	
VAR.			4.61	1.37	10.01	35.81	177.73	0.67	
S.D.			2.15	1.17	3.16	5.98	13.33	0.82	
S.E.			0.21	0.12	0.32	0.60	1.33	0.08	
MAX.			19.00	8.00	21.00	42.00	83.00	7.00	
MIN.			0.00	0.00	0.00	0.00	0.00	0.00	
		Ste. Agathe (peas)							
N	**		100	100	100	100	100	50	20
MEAN			6.23	13.22	7.00	2.75	6.52	24.56	57.50
VAR.			76.44	355.10	67.58	20.59	75.42	300.29	1338.05
S.D.			8.74	18.84	8.22	4.54	8.68	17.33	36.58
S.E.			0.87	1.88	0.82	0.45	0.87	2.45	8.18
MAX.			44.00	93.00	39.00	23.00	45.00	74.00	158.00
MIN.			0.00	0.00	0.00	0.00	0.00	1.00	12.00
		Glenlea (peas)							
N	**		100	100	100	100	100	100	50
MEAN			0.66	1.58	2.65	4.91	15.38	24.57	18.94
VAR.			3.26	8.97	60.47	101.52	585.27	763.06	156.30
S.D.			1.80	3.00	7.78	10.08	24.19	27.62	12.50
S.E.			0.18	0.30	0.78	1.01	2.42	2.76	1.77
MAX.			10.00	14.00	50.00	72.00	127.00	167.00	75.00
MIN.			0.00	0.00	0.00	0.00	0.00	0.00	2.00

**field recently planted - no samples taken

***field sprayed with insecticide prior to sampling

****senescence complete - no samples taken

Appendix 2. Incidence of parasitism for three alfalfa fields and three pea fields each year, 1983-1985. Each field location column gives the number of parasitized aphids over the number of aphids reared or dissected. The number of parasitized reared aphids also includes those parasitoids that died or entered diapause during rearing.

ALFALFA REARED												
Date	No. of aphids	Ste. Agathe	St. Adolphe	Glenlea	N	Mean %	Var.	S.D.	S.E.	Max.	Min.	
1983	28 June	30	5/8	1/22	*	2	33.50	1682.0	41.01	29.00	62.50	4.50
	5 July	84	2/19	2/43	2/22	3	8.10	9.16	3.03	1.75	10.50	4.70
	12	193	*	*	12/193	1	6.20					
	21	246	3/61	3/33	4/152	3	5.53	10.86	3.03	1.90	9.10	0.00
	26	302	26/100	3/77	7/125	3	11.83	151.24	12.30	7.10	26.00	3.90
	2 August	337	8/46	3/59	25/232	3	11.10	37.89	6.16	3.55	17.40	5.10
	8	54	1/2	0/1	12/51	3	24.50	625.75	25.01	14.44	50.0	0.00
	TOTAL	1246	45/236	12/235	62/775	3	10.73	54.60	7.39	4.27	19.10	5.10
			Ste. Agathe	St. Adolphe	Glenlea							
1984	4 July	39	*	*	1/39	1	2.50					
	10	214	*	*	0/214	1	0.00					
	17	95	1/3	3/24	0/68	3	15.27	282.96	16.82	9.71	33.30	0.00
	24	265	4/141	16/124	*	2	7.85	51.00	7.14	5.05	12.90	2.80
	1 August	441	25/144	32/204	9/93	3	14.27	16.36	4.05	2.34	17.40	9.70
	8	63	2/22	*	4/41	2	9.45	0.25	0.49	0.35	9.80	9.10
	14	7	2/6	*	0/1	2	16.65	554.44	23.55	16.65	33.30	0.00
	TOTAL	1124	34/316	51/352	14/456	3	9.47	33.82	5.82	3.36	14.50	3.10
			Ste. Agathe	St. Adolphe	Glenlea							
1985	9 July	27	*	*	0/27	1	0.00					
	16	211	0/2	3/88	2/121	3	1.70	2.89	1.70	0.98	3.40	0.00
	24	1771	1/28	6/1404	9/339	3	2.20	2.91	1.71	0.98	3.60	0.30
	30	849	1/113	*	14/736	2	1.40	0.50	0.71	0.50	1.90	0.90
	*** 7 August	926	0/270	**	9/656	2	0.70	0.98	0.99	0.70	1.40	0.00
	*** 15	277	*	**	0/277	1	0.00					
	TOTAL	4061	2/413	9/1492	34/2156	3	0.90	0.37	0.61	0.35	1.60	0.50

*field recently cut - no samples taken

**field cultivated - no samples taken

***high mortality among reared aphids due to entomophthoran fungi

Appendix 2 (cont'd).

ALFALFA DISSECTED												
Date	No. of aphids	Ste. Agathe	St. Adolphe	Glenlea	N	Mean %	Var.	S.D.	S.E.	Max.	Min.	
1983	28 June	12	0/6	0/6	*	2	0.00					
	5 July	118	2/63	2/27	0/28	3	3.53	13.77	3.71	2.14	7.40	0.00
	12	348	*	*	19/348	1	5.50					
	21	230	0/25	0/17	9/188	3	1.60	7.68	2.77	1.60	4.80	0.00
	26	251	6/67	2/77	0/107	3	3.87	21.45	4.63	2.67	9.00	0.00
	2 August	327	4/17	0/49	4/261	3	8.33	173.08	13.16	7.60	23.50	0.00
	8	58	3/6	0/0	11/52	3	23.73	629.81	25.10	14.49	50.00	0.00
	TOTAL	1344	15/184	4/176	43/984	3	4.97	8.94	2.99	1.73	8.20	2.30
			Ste. Agathe	St. Adolphe	Glenlea							
1984	4 July	45	*	*	1/45	1	2.20					
	10	140	*	*	0/140	1	0.00					
	17	70	0/2	1/14	0/54	3	2.37	16.80	4.10	2.37	7.10	0.00
	24	219	0/111	5/108	*	2	2.30	10.58	3.25	2.30	4.60	0.00
	1 August	762	34/183	45/298	18/281	3	13.37	39.46	6.28	3.63	18.60	6.40
	8	59	3/21	*	4/38	2	12.40	7.22	2.69	1.90	14.30	10.50
	14	7	0/4	*	0/3	2	0.00					
	TOTAL	1302	37/321	51/420	23/561	3	9.23	19.85	4.46	2.57	12.10	4.10
			Ste. Agathe	St. Adolphe	Glenlea							
1985	9 July	17	*	*	1/17	1	5.90					
	16	320	0/5	0/128	1/187	3	0.17	0.08	0.29	0.17	0.50	0.00
	24	1156	1/10	2/843	4/303	3	3.83	28.82	5.37	3.10	10.00	0.20
	30	1086	0/142	*	35/944	2	1.85	6.85	2.62	1.85	3.70	0.00
	7 August	1163	2/277	**	17/886	2	1.30	0.72	0.85	0.60	1.90	0.70
	15	342	*	**	1/342	1	0.30					
	TOTAL	4084	3/434	2/971	59/2679	3	1.03	1.08	1.04	0.60	2.20	0.20

*field recently cut - no samples taken

**field cultivated - no samples taken

Appendix 2 (cont'd).

		PEAS - REARED										
Date	No. of aphids	Ste. Agathe	Morris	Glenlea	N	Mean %	Var.	S.D.	S.E.	Max.	Min.	
1983	28 June	0	0/0	-	-	1	0.00					
	5 July	401	0/94	0/62	2/245	3	0.27	0.21	0.46	0.27	0.80	0.00
	12	1139	0/267	0/477	2/395	3	0.17	0.08	0.29	0.17	0.50	0.00
	21	642	1/264	0/39****	2/339	3	0.33	0.09	0.31	0.18	0.60	0.00
	26	569	4/203	0/100	0/266	3	0.67	1.33	1.15	0.67	2.00	0.00
	2 August	715	9/338	0/3	8/374	3	1.60	2.01	1.42	0.82	2.70	0.00
	8	80	-	0/8	6/72	2	4.15	34.45	5.87	4.15	8.30	0.00
	TOTAL	3546	14/1166	0/689	20/1691	3	0.80	0.48	0.69	0.40	1.20	0.00
			Ste. Agathe ¹	Ste. Agathe ²	Glenlea							
1984	4 July	841	0/321	1/488	0/32	3	0.07	0.01	0.12	0.07	0.20	0.00
	10	704	1/265	2/401	0/38	3	0.30	0.07	0.26	0.15	0.50	0.00
	17	458	4/251	0/178	0/29	3	0.53	0.85	0.92	0.53	1.60	0.00
	24	325	2/137	2/43	1/145	3	2.30	4.48	2.12	1.22	4.70	0.70
	1 August	707	6/394	2/93	7/220	3	2.30	0.73	0.85	0.49	3.20	1.50
	8	614	1/255	1/204	3/155	3	0.93	0.70	0.84	0.48	1.90	0.40
	14	323	2/146	3/61	2/116	3	2.67	3.76	1.94	1.12	4.90	1.40
	TOTAL	3972	16/1769	11/1468	13/735	3	1.13	0.34	0.59	0.34	1.80	0.70
			Ste. Agathe	Rosenort	Glenlea							
1985	3 July	190	0/168	0/0	0/22	3	0.00					
	9	614	0/509	0/19	0/86	3	0.00					
	16	438	0/320	0/53	0/65	3	0.00					
	24	499	0/140	0/137	0/222	3	0.00					
	30	1567	1/291	0/326	1/950	3	0.13	0.02	0.15	0.09	0.30	0.00
***	7 August	1387	0/650	0/7****	3/730	3	0.13	0.05	0.23	0.13	0.40	0.00
***	15	649	0/380	-	0/269	2	0.00					
	TOTAL	5344	1/2458	0/542	4/2344	3	0.08	0.01	0.11	0.06	0.20	0.00

****field sprayed with insecticide prior to sampling

Appendix 2 (cont'd).

PEAS - DISSECTED												
Date	No. of aphids	Ste. Agathe	Morris	Glenlea	N	Mean %	Var.	S.D.	S.E.	Max.	Min.	
1983	28 June	2	0/2	-	-	1	0.00					
	5 July	308	0/68	0/67	0/173	3	0.00					
	12	1244	1/313	1/470	0/461	3	0.17	0.02	0.15	0.09	0.30	0.00
	21	1064	2/487	0/14****	1/563	3	0.20	0.04	0.20	0.12	0.40	0.00
	26	854	3/365	0/106	1/383	3	0.37	0.16	0.40	0.23	0.80	0.00
	2 August	809	6/410	0/8	5/391	3	0.93	0.66	0.81	0.47	1.50	0.00
	8	67	-	0/8	2/59	2	1.70	5.78	2.40	1.70	3.40	0.00
	TOTAL	4348	12/1645	1/673	9/2030	3	0.43	0.06	0.25	0.15	0.70	0.20
			Ste. Agathe ¹	Ste. Agathe ²	Glenlea							
1984	4 July	849	0/484	0/355	0/10	3	0.00					
	10	1050	0/307	0/670	0/73	3	0.00					
	17	541	0/254	0/268	0/19	3	0.00					
	24	261	1/139	1/23	0/99	3	1.70	5.59	2.36	1.37	4.40	0.00
	1 August	603	2/343	0/89	2/171	3	0.60	0.36	0.60	0.35	1.20	0.00
	8	553	15/291	7/151	1/111	3	3.57	5.42	2.33	1.34	5.20	0.90
	14	289	6/127	4/114	4/48	3	5.50	6.24	2.50	1.44	8.30	3.50
	TOTAL	4146	24/1945	12/1670	7/531	3	1.07	0.10	0.32	0.19	1.30	0.70
			Ste. Agathe	Rosenort	Glenlea							
1985	3 July	481	0/410	0/36	0/35	3	0.00					
	9	856	1/801	0/6	1/49	3	0.70	1.27	1.13	0.65	2.00	0.00
	16	572	0/329	0/36	0/207	3	0.00					
	24	539	0/142	0/162	0/235	3	0.00					
	30	1288	2/324	0/325	1/639	3	0.27	0.09	0.31	0.18	0.60	0.00
	7 August	2005	2/461	0/9****	9/1535	3	0.33	0.09	0.31	0.18	0.60	0.00
	15	1367	23/916	-	3/451	2	1.60	1.62	1.27	0.90	2.50	0.70
	TOTAL	7108	28/3383	0/574	14/3151	3	0.40	0.16	0.40	0.23	0.80	0.00

Appendix 3. Mean number of mummies per stem collected during stem sampling from three alfalfa fields and three pea fields each year, 1983-1985. Each field location column gives the number of mummies collected over the number of stems sampled.

ALFALFA												
Year	Date	No. of stems	No. of mummies			N	Mean	Var.	S.D.	S.E.	Max.	Min.
			Ste. Agathe	St. Adolphe	Glenlea							
1983	28 June	200	1/100	2/100	*	2	0.02	0.00	0.01	0.01	0.02	0.01
	5&6 July	300	1/100	4/100	0/100	3	0.02	0.00	0.02	0.01	0.04	0.00
	12	100	*	*	0/100	1	0.00	0.00				
	19&21	300	0/100	1/100	10/100	3	0.04	0.00	0.06	0.03	0.10	0.00
	26	300	0/100	3/100	5/100	3	0.03	0.00	0.03	0.01	0.05	0.00
	2 August	300	6/100	4/100	8/100	3	0.06	0.00	0.02	0.01	0.08	0.04
	8	300	1/100	0/100	3/100	3	0.01	0.00	0.02	0.01	0.03	0.00
	16	200	0/100	*	3/100	2	0.02	0.00	0.02	0.02	0.03	0.00
	TOTAL	2000	9/700	14/600	29/700	3	0.03	0.00	0.01	0.01	0.04	0.01
1984	4 July	100	*	*	4/100	1	0.04					
	10	100	*	*	3/100	1	0.03					
	17	300	0/100	0/100	0/100	3	0.00					
	24	200	4/100	10/100	*	2	0.07	0.00	0.04	0.03	0.10	0.04
	1 August	300	15/100	15/100	15/100	3	0.15	0.00	0.00	0.00	0.15	0.15
	8	200	2/100	*	32/100	2	0.17	0.05	0.21	0.15	0.32	0.02
	14	200	1/100	*	24/100	2	0.13	0.03	0.16	0.12	0.24	0.01
	TOTAL	1400	22/500	25/300	78/600	3	0.09	0.00	0.04	0.02	0.13	0.04
	1985	9 July	100	*	*	2/100	1	0.02				
16		300	0/100	1/100	2/100	3	0.01	0.00	0.01	0.01	0.02	0.00
24		300	0/100	3/100	3/100	3	0.02	0.00	0.02	0.01	0.03	0.00
30		200	0/100	*	11/100	2	0.06	0.01	0.08	0.06	0.11	0.00
7 August		80	17/30	**	20/50	2	0.49	0.01	0.12	0.09	0.57	0.40
15		20	*	**	9/20	1	0.45					
TOTAL		1000	17/330	4/200	47/470	3	0.06	0.00	0.04	0.02	0.10	0.02

*field recently cut - no samples taken

**field cultivated - no samples taken

Appendix 3 (cont'd).

Year	Date	No. of stems	PEAS			N	Mean	Var.	S.D.	S.E.	Max.	Min.
			Ste. Agathe	Morris	Glenlea							
1983	28 June	100	1/100	-	-	1	0.01					
	5&6 July	300	0/100	0/100	0/100	3	0.00					
	12	300	0/100	1/100	1/100	3	0.01	0.00	0.01	0.00	0.01	0.00
	19&21	300	6/100	0/100***	0/100	3	0.02	0.00	0.03	0.02	0.06	0.00
	26	300	5/100	0/100	0/100	3	0.02	0.00	0.03	0.02	0.05	0.00
	2 August	300	0/100	0/100	0/100	3	0.00					
	8	200	-	0/100	0/100	2	0.00					
TOTAL		1800	12/600	1/600	1/600	3	0.01	0.00	0.01	0.01	0.02	0.00
			Ste. Agathe ¹	Ste. Agathe ²	Glenlea							
1984	4 July	300	0/100	0/100	0/100	3	0.00					
	10	300	0/100	1/100	0/100	3	0.00	0.00	0.01	0.00	0.01	0.00
	17	300	0/100	0/100	0/100	3	0.00					
	24	300	2/100	4/100	2/100	3	0.03	0.00	0.01	0.01	0.04	0.02
	1 August	300	4/100	0/100	0/100	3	0.01	0.00	0.02	0.01	0.04	0.00
	8	300	8/100	2/100	6/100	3	0.05	0.00	0.03	0.02	0.08	0.02
	14	300	5/100	2/100	4/100	3	0.04	0.00	0.02	0.01	0.05	0.02
TOTAL		2100	19/700	9/700	12/700	3	0.02	0.00	0.01	0.01	0.03	0.01
			Ste. Agathe	Rosenort	Glenlea							
1985	3 July	300	0/100	0/100	0/100	3	0.00					
	9	300	0/100	0/100	0/100	3	0.00					
	16	300	0/100	0/100	0/100	3	0.00					
	24&25	300	0/100	0/100	0/100	3	0.00					
	30	300	1/100	1/100	1/100	3	0.01	0.00	0.00	0.00	0.01	0.01
	7 August	250	0/50	0/100***	3/100	3	0.01	0.00	0.02	0.01	0.03	0.00
	15	70	3/20	-	0/50	2	0.08	0.01	0.11	0.08	0.15	0.00
TOTAL		1820	4/570	1/600	4/650	3	0.01	0.00	0.00	0.00	0.01	0.00

***field sprayed with insecticide prior to sampling

Appendix 4. Mean number of mummies collected per minute of visual search from weekly visual searches in three alfalfa fields and three pea fields each year, 1983-1985. Each field location column gives the number of mummies collected over the number of minutes spent searching.

ALFALFA												
Year	Date	No. of minutes	Ste. Agathe	St. Adolphe	Glenlea	N	Mean	Var.	S.D.	S.E.	Max.	Min.
1983	28 June	20	0/10	0/10	-	2	0.00					
	5&6 July	30	1/10	2/10	0/10	3	0.10	0.01	0.10	0.06	0.20	0.00
	12	10	-	-	6/10	1	0.60					
	19&21	30	4/10	1/10	71/10	3	2.53	15.66	3.96	2.28	7.10	0.10
	26	30	2/10	3/10	22/10	3	0.90	1.27	1.13	0.65	2.20	0.20
	2 August	30	13/10	5/10	16/10	3	1.13	0.32	0.57	0.33	1.60	0.50
	8	20	0/10	-	12/10	2	0.60	0.72	0.85	0.60	1.20	0.00
	16	0	-	-	-							
TOTAL		170	20/60	11/50	127/60	3	0.89	1.14	1.07	0.62	2.12	0.22
1984			Ste. Agathe	St. Adolphe	Glenlea							
	4 July	10	-	-	6/10	1	0.60					
	10	10	-	-	9/10	1	0.90					
	17	10	-	-	3/10	1	0.30					
	24	20	16/10	18/10	-	2	1.70	0.02	0.14	0.10	1.80	1.60
	1 August	30	35/10	82/10	35/10	3	5.07	7.36	2.71	1.57	8.20	3.50
	8	30	36/10	45/10	20/10	3	3.37	1.60	1.27	0.73	4.50	2.00
	14	20	12/10	-	41/10	2	2.65	4.21	2.05	1.45	4.10	1.20
TOTAL		130	99/40	145/30	114/60	3	3.07	2.41	1.55	0.90	4.83	1.90
1985			Ste. Agathe	St. Adolphe	Glenlea							
	9 July	10	-	-	32/10	1	3.20					
	16	30	0/10	8/10	23/10	3	1.03	1.36	1.17	0.67	2.30	0.00
	24&25	30	0/10	61/10	29/10	3	3.00	9.31	3.05	1.76	6.10	0.00
	30	30	0/10	58/10	86/10	3	4.80	19.24	4.39	2.53	8.60	0.00
	7 August	20	77/10	-	66/10	2	7.15	0.61	0.78	0.55	7.70	6.60
	15	10	-	-	50/10	1	5.00					
TOTAL		130	77/40	127/30	286/60	3	3.64	2.27	1.51	0.87	4.77	1.93

Appendix 4 (cont'd).

Year	Date	No. of minutes	PEAS			N	Mean	Var.	S.D.	S.E.	Max.	Min.
			Ste. Agathe	Morris	Glenlea							
1983	28 June	10	0/10	-	-	1	0.00					
	5&6 July	30	0/10	0/10	2/10	3	0.07	0.01	0.12	0.07	0.20	0.00
	12	20	0/10	-	0/10	2	0.00					
	19&21	30	7/10	0/10***	4/10	3	0.37	0.12	0.35	0.20	0.70	0.00
	26	30	5/10	0/10	2/10	3	0.23	0.06	0.25	0.15	0.50	0.00
	2 August	30	0/10	0/10	4/10	3	0.13	0.05	0.23	0.13	0.40	0.00
	8	10	-	0/10	-	1	0.00					
	TOTAL	160	12/60	0/50	12/50	3	0.15	0.02	0.13	0.07	0.24	0.00
			Ste. Agathe ¹	Ste. Agathe ²	Glenlea							
1984	4 July	30	1/10	1/10	0/10	3	0.07	0.00	0.06	0.03	0.10	0.00
	10	30	0/10	8/10	0/10	3	0.27	0.21	0.46	0.27	0.80	0.00
	17	20	0/10	0/10	-	2	0.00					
	24	30	5/10	4/10	2/10	3	0.37	0.02	0.15	0.09	0.50	0.20
	1 August	20	1/10	0/10	-	2	0.10	0.00	0.00	0.00	0.10	0.10
	8	30	1/10	0/10	3/10	3	0.13	0.02	0.15	0.09	0.30	0.00
	14	20	1/10	0/10	-	2	0.05	0.01	0.07	0.05	0.10	0.00
	TOTAL	180	9/70	13/70	5/40	3	0.15	0.00	0.03	0.02	0.19	0.13
			Ste. Agathe	Rosenort	Glenlea							
1985	3 July	0	-	-	-							
	9	0	-	-	-							
	16	10	0/10	-	-	1	0.00					
	24&25	30	0/10	0/10	0/10	3	0.00					
	30	30	0/10	0/10	0/10	3	0.00					
	7 August	30	3/10	0/10***	0/10	3	0.10	0.03	0.17	0.10	0.30	0.00
	15	20	11/10	-	0/10	2	0.55	0.61	0.78	0.55	0.10	0.00
	TOTAL	120	14/50	0/30	0/40	3	0.09	0.03	0.16	0.09	0.28	0.00