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

By

© Frank Oliver Matheson

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ABSTRACT

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Seasonal life history, abundance and biology of the parasitoids of the pea aphid, Acyrthosiphon 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, Dendrocerus carpenteri (Curtis), Dendrocerus sp. A, Dendrocerus 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, Acyrthosiphon 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, Acyrthosiphon 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, Pungerl (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, Pungerl (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 pequodorum, 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. pequodorum from Myzus persicae, Macrosiphum euphorbiae and Acyrthosiphon solani (Kaltenbach) but it may prefer species in the genus Acyrthosiphon (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 distributiion 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 ($\geq$14h).

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. pequorodum 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. pequodorum 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. pequodorum 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±2°F (26.6°C) and 36.6 days at 50±2°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,