STUDIES OF THE TEMPORAL ABUNDANCE, SPATIAL DISTRIBUTION AND PARASITISM OF THE EUROPEAN CABBAGE MOTH, *MAMESTRA BRASSICAE* L. (LEPIDOPTERA: NOCTUIDAE) WITH SPECIAL REFERENCE TO THE LARVAL ENDOPARASITOID, *MICROPLITIS MEDIATOR* (HALIDAY) (HYMENOPTERA: BRACONIDAE).

A Thesis

Submitted to the Faculty of

Graduate Studies

The University of Manitoba

by

Nicole A. Lauro

In Partial Fulfilment of the

Requirements for the Degree

of

Master of Science

Department of Entomology

© October 2001

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BY

Nicole A. Lauro

A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of Manitoba in partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

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For the memory of James Loucks,
our beloved Jay.
1984-2001

ACKNOWLEDGMENTS

I greatly appreciate the support, advice and patience of my advisor, Dr. Neil Holliday. I would also like to express my appreciation to Dr. Ulli Kuhlmann for his support and guidance during my time in Switzerland. I would like to thank the members of my committee for helpful discussions; Dr. Ulli Kuhlmann, Dr. Peter Mason, Dr. Patricia Mackay and Dr. Rachael Scarth. I thank the following people for their help with field work in Switzerland: Emma Hunt for her exceptional and always enthusiastic technical aid in both years of my study and; to Jennifer Otani, Bettina Jahn, Silvia Micheletti, Stephanie Harris and Doris Herrmann for their cooperative assistance. I express my sincere appreciation to Roland Fasnacht, Walter Muhlemann and Thomas Kaenel for allowing samples to be taken from their organic fields; and to all those whose encouragement and advice has helped me along the way; S.A. Stockton, Dr. S.A. Marshall, Dr. U. Schaffner, H.D. White, L. Reimer and M. Alperyn. And of course, my family, for all of their love and support. The funding for this project has been provided by Agriculture and Agri-Food Canada through CABI Bioscience, and Agriculture Research and Development Initiative.

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ABSTRACT

Lauro, N.A., The University Of Manitoba, 2001. Studies of the temporal abundance, spatial distribution and parasitism of *Mamestra brassicae* L. (Lepidoptera: Noctuidae) with special reference to *Microplitis mediator* (Haliday) (Hymenoptera: Braconidae). Major Professor: N.J. Holliday.

The seasonal abundance, spatial distribution and parasitism of *M. brassicae* eggs and larvae were studied in organically managed field plots in the vegetable growing region of Bielersee, Switzerland in 1998 and 1999. Up to five field plots were sampled weekly from mid May to late September for egg masses and larvae of *M. brassicae*. All stages sampled were reared in the laboratory until either a parasitoid or a moth emerged.

Two annual generations of *M. brassicae* were found. All stages reached peak abundance in the second generation. In 1999, egg masses were oviposited randomly within field plots while eggs were highly aggregated. First instar larvae were also aggregated within field plots and shifted towards randomness as the larval stage increased in age. Six parasitoids were reared from *M. brassicae* egg masses and larvae in 1998 and 1999 including *Trichogramma buesi* Vogele (Hymenoptera: Trichogrammatidae), *Telenomus* sp. (Hymenoptera: Scelionidae). *Microplitis mediator* (Haliday) (Hymenoptera: Braconidae), *Exetastes atrator* (Retz) (Hymenoptera: Ichneumonidae), *Eurithia consobrina* (Meigen) (Diptera: Tachinidae) and one unidentified ectoparasitoid from

Eulophidae (Hymenoptera). The dominant parasitoid reared from *M. brassicae* larvae was *M. mediator*. Probabilities of parasitism differed among field plots and the number of larvae per plant influenced parasitism by *M. mediator*. In 1999, *M. mediator* was reared from three larvae of *Autographa gamma* L. (Lepidoptera: Noctuidae).

Microplitis mediator has been reported to attack early instar larvae of *M. brassicae* in Central Europe, however little is known about the rate of their acceptance and suitability as hosts. I examined the affect of the first three instars of *M. brassicae* on the frequency of attacks and ovipositions by *M. mediator* females and on the development of immature parasitoids under choice and no-choice offerings of host larvae. *Microplitis mediator* females attacked larvae of instar I, II and III equally. However the frequency of oviposition and survival of immature parasitoids was low in instar III larvae of *M. brassicae*. The results from this study suggest that instar I and to a lesser extent, instar II larvae of *M. brassicae* are highly suitable hosts for *M. mediator*.

Chapter 1: General Introduction

Biological control is a non-chemical approach to pest regulation. It is based on the principal that pest populations are naturally limited, in part, through predation, parasitism and disease (natural enemies) and, through some ecological disturbance, the population may at times surge to pest status (Murdoch et al., 1985; Van Driesche and Bellows, 1996). Many of the pest species targeted in biological control have been accidentally introduced into an area without their full complement of natural enemies; however pests that are indigenous to an area have also been targeted (Hokkanen and Pimentel, 1984; 1989). One approach to the control of an indigenous pest population is through the introduction of natural enemies that are associated with a similar host species from a different geographic region (Hokkanen and Pimentel, 1984; 1989; Waage and Mills, 1992; Wiedenmann and Smith, 1997).

The bertha armyworm, *Mamestra configurata* Walker is an indigenous pest of canola (*Brassica napus* L. and *B. rapa* L.) in Western Canada. Outbreaks of *M. configurata* occur sporadically and last for about 3 years; large populations of larvae cause millions of dollars in damage to the crop (Bracken, 1987). Although parasitoids are important regulators of *M. configurata* populations, they do not maintain host populations below economic levels during outbreaks (Turnock, 1988).

In 1971, *M. configurata* was targeted as a candidate for biological control in a joint project through Agriculture and Agri-Food Canada and CABi Bioscience Centre in Delemont, Switzerland (Turnock, 1984). Soon after the project's opening, the European cabbage moth, *Mamestra brassicae* L. (Lepidoptera: Noctuidae) was identified as a similar host species. *Mamestra brassicae* is a widespread pest of various *Brassica* sp. crops in central regions of Europe (Popova, 1993). The assemblage of parasitoids associated with *M. brassicae* consists of 47 species (see Turnock, 1984). As with *M. configurata*, only a few parasitoid species are abundant on *M. brassicae* (Wylie, 1977; Turnock, 1988). The parasitoids most commonly encountered in Central Europe include two egg parasitoids, *Trichogramma buesi* Vogele (Hymenoptera: Trichogrammatidae) (reported as *T. evanescens* Westwood by Turnock, 1984) and *Telenomus* sp. (Hymenoptera: Scelionidae) (Zeigler and Carl, 1996; Kuhlmann et al., 1997) and three larval parasitoids, *Exetastes atrator* (Forster)[1] (Hymenoptera: Ichneumonidae), *Microplitis mediator* (Haliday) (Hymenoptera: Braconidae) and *Eurithia consobrina* (Meigen) (Diptera: Tachinidae) (Turnock and Carl, 1995). All of these parasitoids are found in univoltine (northern) and bivoltine (southern) populations of *M. brassicae* and appear to synchronize their development with that of the host population being attacked (Turnock, 1984). In western Canada only *Banchus flavescens* Cresson (Hymenoptera: Ichneumonidae) and *Athrycia cincerea* (Coquillett) (Diptera: Tachinidae) are abundant on their host, *M. configurata*, at low host densities (Turnock, 1988). In 1976 it was proposed that

[1] *E. atrator* replaces *E. cinctipes* (Retzius) (CAB International, 1996)

M. mediator had the potential to occupy a niche not filled in the western Canadian parasitoid guild (Anon., 1976). However, despite several releases in Canada, the parasitoid has yet to establish (Mason et al., 2001).

Valuable insight into the difficulty of establishing *M. mediator* in Canada may be gained through examining how the parasitoid chooses its native host, *M. brassicae* in its country of origin. The following study is a first step in that direction. Specific objectives are:

1. to characterize the abundance and distribution of *M. brassicae* in organically produced *Brassica* sp. in Switzerland and to identify the naturally occurring parasitoids and their level of parasitism;
2. to make inferences about the effectiveness of *M. mediator* as a parasitoid of *M. brassicae* from spatial and temporal patterns and to identify alternative hosts for parasitism by *M. mediator* in the same habitat as *M. brassicae*; and
3. to compare the suitability of *M. brassicae* as a host with the host selection behaviour of *M. mediator.*

Chapter 2: Literature review

2.1 Predictions of Host Choice

Parasitoid females searching for hosts in the field follow a series of discrete host selection steps including host-habitat location, host location and host acceptance (Salt, 1941; Doutt, 1959). In addition to effective host selection, successful parasitoid reproduction also depends on host suitability (Vinson, 1976; Vinson and Iwantsch, 1980b) and host regulation (Vinson and Iwantsch, 1980a), both of which involve the fitness of an immature parasitoid developing within the host. At its most fundamental level, the successful development of an immature parasitoid to the adult stage is the criterion of host suitability and depends on the host's immune system, competition among parasitoids, toxins within the host and the host's nutritional quality (Vinson and Iwantsch, 1980b)

Foraging (= searching) behaviour in parasitoids has been studied to make predictions about the effectiveness of parasitoids in inflicting host mortality (Godfray, 1994). Optimal foraging theory is an ecologically and evolutionary approach to understanding animal foraging. First proposed by Emlen (1966) and MacArthur and Pianka (1966) it is based on the assumption that reproductive fitness is strongly linked with the selection of resources, and thus natural selection will favour those individuals that forage for those resources optimally. As applied to classical models of host acceptance, one prediction is that female parasitoids will make choices that lead to the acceptance of suitable hosts. Female choice is not so predictable though (review in Pyke, 1984). Although

host acceptance and suitability are often correlated in some species of parasitoid, host acceptance is not always an indicator of suitability and suitable hosts are not always accepted.

The intent of this review is to explore some of the factors associated with the selection of suitable hosts by parasitoids. The literature review will focus on studies that have examined hymenopterous endoparasitoids of herbivorous lepidopteran host larvae. The essence of host suitability, the main attributes of hosts associated with parasitism, and the availability of hosts for parasitism will be addressed. In addition I will discuss some methods used to measure parasitoid performance and briefly present studies that have examined the primary insects used in the thesis. Terms used to discuss host selection will be clarified.

2.1.1 Definitions

The development of hymenopterous parasitoids is holometabolous; defined by the development of the parasitoid from egg to larva to pupa to adult. Larval endoparasitoids grow and develop exclusively within a single larva (the host) and the host larva is eventually killed by the interaction; this process is referred to as parasitism. Most commonly, parasitoid adult females (from this point forward parasitoid adult female will be referred to as simply female parasitoid unless otherwise indicated) actively seek out hosts and oviposit one (solitary parasitoids) or multiple eggs (gregarious parasitoids) within a single host.

Depending on the species of parasitoid ovipositing, the host will be paralyzed (idiobiont parasitoids) or continue to feed and develop (koinobiont parasitoid). The terms generalist and specialist are used to define host range of parasitoids. The host range of a generalist parasitoid includes a large number of host species from a number of different families, whereas a specialist parasitoid is restricted to a few host species. Host preference is defined as the proportion of hosts attacked compared to the hosts available. Host acceptance is used in the strictest sense; it is the oviposition of a parasitoid egg by a female parasitoid within a host. A host attack is simply the insertion of the female parasitoid ovipositor through the cuticle of the host. Host suitability has been defined above. I use the definition from Hailemichael et al. (1994) to describe successful parasitization: as a two-step process in which the host is accepted and the host is suitable.

2.2 "A Suitable Host"

The detection of a foreign object within the host haemolymph often stimulates the host's immune system (Schmit and Ratcliffe, 1977). The immune response is commonly in the form of haemocytic encapsulation (see Ratcliffe, 1982 for other types of host immune response). When stimulated, haemocytes will become available in the host haemolymph and will migrate and adhere to the foreign object (Schmit and Ratcliffe, 1977). In some unsuitable hosts, haemocytes are capable of phagocytosis, however most form a capsule around the foreign object and wall it off from the body tissue of the host (Schmit and

Ratcliffe, 1977). Eventually the encapsulated immature parasitoid succumbs to asphyxiation. In dissected hosts, encapsulated parasitoids are discernable as a necrotic mass of melanized tissue.

In suitable hosts, different species of endoparasitoids use various strategies to overcome the physiological defences of the host (Tanaka, 1987; Bauer et al., 1998). Parasitism by the larval endoparasitoid *Cotesia glomerata* L. stimulates a haemocytic response in the host *Pieris brassicae* L., however encapsulation is avoided primarily due to the slow spreading rate of haemocytes to the parasitoid egg (Bauer et al., 1998). Suppression of encapsulation has also been associated with a coating of calyx fluids or virus on the parasitoid egg for some species and the injection of parasitoid venoms by other species at the time of oviposition (Kitano, 1986). Polydnavirus on the surface of parasitoid eggs can inhibit the haemocytes' adherence to foreign objects (Hayakawa and Yazaki, 1997; Strand et al. 1999) while in some host larvae, the virus masks the parasitoid egg entirely, which is evident by the absence of any immune response by the host (Beckage, 1998; reviews in Fleming, 1992). Other species of parasitoid have been shown to evade encapsulation altogether by ovipositing within specific host organs, such as the nerve ganglia, which are impenetrable by host haemocytes (Salt 1970).

2.3 Host Attributes and Parasitism

Successful parasitization is foremost dependent on the choices made by parasitoid females. By responding to the array of behavioural, chemical and visual attributes of the host, optimally foraging parasitoids are expected to reject unsuitable habitats and unsuitable hosts.

2.3.1 Behavioural Attributes

Host behaviour has usually been considered in the context of defensive strategy. Some host larvae bite, spit regurgitant or use evasive maneuvers to prevent contact with the attacking parasitoid (review in Gross, 1993). Host defensive behaviour may serve to limit the host range of parasitoids (Brodeur et al., 1996; 1998), inflict a cost in parasitoid searching time or increase the risk of injury or mortality to the parasitoid (Iwasa et al., 1984; Rajapakse et al., 1985; Lei and Camara, 1999; Potting et al., 1999). For instance, Potting et al. (1999) compared the level of acceptance of two species of moth, *Eldana saccharina* (Walker) and *Sesamia calamistis* Hampson by the larval endoparasitoid *Cotesia sesamiae* (Cameron). Although the aggressive behaviour of both species of moth poses a similar mortality risk to attacking parasitoids, only *S. calamistis* is suitable as a host for *C. sesamiae*. The results show that parasitoid females contact larvae from both species equally; however the level of host acceptance is markedly decreased for larvae of *E. saccharina*. These findings suggest that the unacceptability of an aggressive host is assessed through contact with the defending larvae.

2.3.2 Chemical Attributes

Oral secretions, contact and haemolymph kairmones, host frass and host diet are among the main chemical attributes of lepidopterous hosts that influence parasitoid choice (reviews in Vet and Dicke, 1992; Vet et al., 1995; Dicke, 1999). Some female parasitoids discriminate between chemical odours from plants damaged by herbivores and undamaged plants or starved herbivores, or between plants infested with suitable and unsuitable host larvae (McCall et al., 1993; Mattiacci and Dicke, 1995; Takabayashi et al., 1995; Sait et al., 1997; reviews in Vet et al., 1995; Dicke, 1999). Response to airborne odours is indicated because parasitoids are able to distinguish between various hosts and host stages without directly contacting the host. For instance, the parasitoid, *Cotesia kariyai* Watanabe, is more attracted to corn plants infested with early larval instars of *Pseudaletia separata* Walker than plants infested with late larval instars (Takabayashi et al., 1995). Although larvae of each instar, with the exception of instar I, are suitable for *C. kariyai*, the parasitoid's response is viewed as an optimal one since *P. separata* is host to several conspecific parasitoids, all of which attack early instars of the host. Under this competitive pressure, the allocation of search time and eggs to an unoccupied host stage is considered advantageous for the parasitoid (Takabayashi *et al.*, 1995). In contrast, the parasitoid *C. glomerata* does not distinguish between Brussel sprout plants (*Brassica oleracea* L. var. *gemmifera*, cv Titurel) infested with suitable and unsuitable larval instars of *Pieris brassicae* (Mattiacci and Dicke, 1995). However once the plant is contacted, *C. glomerata* females search for

longer periods on plants recently damaged by suitable instars. In this instance, the assessment of suitability is advantageous since it reduces the risk of coming into contact with late larval instars, which are exceptionally aggressive (Brodeur et al., 1996).

2.3.3 Visual Attributes

The colour, shape and size of potential hosts are among the key visual attributes used by parasitoids of eggs, aphids and fruit flies (review in Godfray, 1994). Few studies (Arthur, 1967; Eller et al., 1990; Hailemichael et al., 1994; Wackers and Lewis, 1994) have clearly addressed the role of visual cues for parasitoids attacking lepidopterous larvae. The deficiency is probably in part due to the difficulty of removing confounding variables, such as chemical and behavioural attributes of the host. By endeavoring to identify the best method for mass rearing *Microplitis croceipes* (Cresson), a parasitoid of several *Heliothis* species, Eller et al., (1990) were able to show that female parasitoids oviposit more readily into artificial oviposition substrates conforming to specific size, colour and colour concentration attributes.

Within a species there is variation in larval size and nutritional quality (reviews in Salt, 1941; Vinson and Iwantsch, 1980b; Charnov et al., 1981). Evidence suggests that parasitoids may associate differences in host size with potential offspring fitness (Charnov et al., 1981; Hopper, 1986; Sait et al., 1997). The most compelling evidence for this is that some parasitoids adjust the sex ratio of

their offspring in response to the size of the host (Charnov et al., 1981; King, 1988; Hailemichael et al., 1994; Ueno, 1998; Kawaguchi and Tanaka, 1999; Lei and Camara, 1999; Oliveira et al., 1999). Some investigations of sex allocation show that parasitoid females are more commonly reared from larger instars (Hailemichael et al., 1994). Theory assumes that female parasitoids gain more fitness from being large than do male parasitoids (Charnov et al., 1981; King, 1988). For instance, female size is positively associated with the size and availability of eggs, and the longevity and searching efficiency of adults (Visser, 1994). Parasitoids are expected to preferentially allocate eggs when host size affects parasitoid progeny fitness (Charnov et al., 1981)

Investigations of host acceptance show that some parasitoids will indiscriminately attack hosts of various sizes (Tanaka et al., 1984; Hailemichael et al., 1994; Ngi-Song et al., 1995) or preferentially attack larger sized hosts (Oliveira et al., 1999). Clearly there is a limit to the size of host suitable for parasitism since not all attacks result in the production of viable offspring. Although seen as a greater nutritional resource for developing parasitoids, larger hosts are often less susceptible to parasitism because of the greater effectiveness of their behavioural (Rajapakse et al., 1985; Brodeur et al., 1996; Lei and Camara, 1999) and internal defences (Harvey et al., 1994; Brodeur et al., 1995; Bauer et al., 1998).

2.4 Experience with Host Attributes

The effect of experience on parasitism has received considerable attention in the literature (reviews in Lewis and Tumlinson 1988; Vet and Groenewold, 1990; Vet and Dicke, 1992; Dicke, 1999). In general, the act of oviposition or antennation of a host, host diet or host by-products, may enhance or discourage the response of parasitoids to repeated exposures with the same stimulus (Kester and Barbosa, 1992; Hailemichael et al., 1994; Parra et al., 1996; Baaren and Boivin, 1998). Both positive (Turlings et al., 1993; Vet et al., 1995) and negative experiences (Papaj et al., 1994; Potting et al., 1999) with host attributes play a role. A positive experience occurs when a stimulus is associated with successful oviposition (Vet et al., 1995). Parasitoids with positive experience with a host on undamaged (Guerrieri et al., 1997), or low host density plants (Geervliet et al., 1998) may increase the time spent searching for hosts in similar habitats in subsequent trials (Hemerik et al., 1993). In turn, negative experiences have been associated with unsuccessful parasitization resulting from either a lack of hosts (Papaj et al., 1994) or host defensive behaviours such as aggression (Lei and Camara, 1999; Potting et al., 1999). Although negative experiences have been shown to decrease search time in similar habitat to almost nothing (Papaj et al., 1994), the absence of suitable hosts on one plant is a poor indication of host absence on another plant, especially for parasitoids of patchily distributed hosts (Giessen et al., 1993; Papaj et al., 1994).

2.5 The Distribution of Hosts

It is not unusual for parasitoids to experience both positive and negative stimuli under field conditions. This is because the distribution of suitable hosts is likely to be variable over time and space. The most common distribution pattern for larval stages of lepidopterous hosts is aggregated. The pattern of oviposition by adult females within a habitat has an important effect on subsequent host larval distribution (Hoffmeister and Rohlfs, 2001). Agricultural crops provide a uniformly patterned habitat for searching adult females, but differences in host plant quality may exist. Differences in host plant quality have been shown to influence the frequency of oviposition by some lepidopteran species (Rausher, 1979a; 1979b; Renwick and Radke, 1983; 1988; Rojas, 1999b). For instance, adult females of *Mamestra brassicae* oviposit more frequently on cabbage plants previously damaged by chewing insects than on plants damaged by sucking insects or undamaged plants (Rojas, 1999b). Females of the pipevine swallowtail butterfly (Lepidoptera: Papillionidae) are more frequently deterred from ovipositing on herbivore infested plants (Rausher, 1979a). Aggregated distributions may also arise from random oviposition of clutches of eggs within a field that as a consequence of the clutch size, produces aggregations (Hoffmeister and Rohlfs, 2001).

2.6 Host Specialization

Strand and Obrycki (1996) predict that the range of host species accepted by a generalist parasitoid will be governed by the quality of all available host species in the habitat. For instance a parasitoid's host range is expected be narrow for

habitats with a high availability of a preferred host species and broad when the availability of the preferred host is low. Host phenology and feeding habits and the taxonomy of plants may also play key roles in shaping the range of hosts acceptable for parasitoids (Hoffmeister, 1992; Godfray, 1994). Hosts may be successfully parasitized under laboratory conditions, but may fall out of a parasitoid's realized range in the field if the host and parasitoid are poorly synchronized seasonally (Strand and Obrycki, 1996). Parasitoids may also accept a wide range of unrelated host species on plants that share similar architecture and chemistry but may reject the same species of host feeding on plants with different characteristics (Godfray, 1994).

The host range of parasitoids is partly influenced by the constancy of the habitat (Strand and Obrycki, 1996). Where parasitoids encounter temporal and spatial fluctuations in the distribution of host species, parasitoids are expected to exhibit multiple host selection strategies (Turlings et al., 1993; Baaren and Boivin, 1998; Geervliet et al., 1998). In generalist parasitoids, this is exhibited through changes in oviposition behaviour in response to changes in experience with host attributes (Cortesero et al., 1997; Geervliet et al., 1998; Rose et al., 1997). Specialist parasitoids in contrast show less reliance on experience. This is supported by laboratory studies in which specialist parasitoids exhibit fixed responses to specific host attributes. Specialist parasitoids are expected to arise when habitat and host availability are constant (Strand and Obrycki, 1996; Rose et al., 1997).

2.7 Measures of Parasitoid Performance

2.7.1 Parasitism

Host mortality due to parasitism has most commonly been measured through percent parasitism (Hassell and Waage, 1984). A common method of measuring parasitism is to take host samples and rear or dissect hosts and record the number of parasitoids emerging or found (Van Driesche, 1983). Parasitism is then measured as a percentage or a proportion; as the number of host larvae parasitized over the total number of host larvae collected. Problems often associated with percent parasitism are that no reference is made to the density of hosts from which parasitoids were sampled and this can create bias when percentages are based on small sample sizes (Van Driesche, 1983). Secondly, the susceptible host stage is rarely identified and this leads to misrepresentation of parasitism (Van Driesche, 1983). Greater accuracy comes from identifying the stages attacked and the stages from which the parasitoid emerges (Van Driesche et al., 1991). Finally parasitized larvae may develop at a different rate than unparasitized larvae. When parasitized larvae develop more slowly than unparasitized larvae, this may overestimate percent parasitism for samples taken sequentially over time (Van Driesche, 1983).

2.7.2 Host Suitability and Oviposition Behaviour

The selection of suitable hosts by parasitoids is of principal importance for parasitoid offspring survival. However there is growing evidence that oviposition

behaviour of parasitoids rarely conforms to the assumptions of optimal foraging theory since parasitoids oviposit more frequently than expected into marginal and unsuitable hosts (review in Pyke, 1984). Godfray (1994) notes that few studies have quantitatively compared host acceptance and preference with host suitability. Despite their importance, crude methods have been used to evaluate the preference, acceptability and suitability of various hosts and host instars for larval endoparasitoids. In such laboratory studies single or multiple hosts are presented to a mated parasitoid female(s) and often this is done without continuous observation of parasitoid behaviour in response to the host. After a certain time period has passed, hosts are removed to a rearing chamber and the number of parasitoids emerging is recorded. The results from such studies are a reflection of percent parasitism and do not offer any insight into the number of hosts actually attacked, the number of hosts accepted for oviposition or the number of hosts suitable.

In other laboratory studies, criteria to detect host selection are used. Two assumptions commonly used are: 1. that an egg is deposited when the ovipositor is inserted into a larva or; 2. an egg was deposited only if a parasitoid emerges. When parasitoids are able to assess host suitability through internal examination of the host or when the behavioural defences of the host are successful at preventing oviposition, host acceptance will be difficult to assess except through the dissection of attacked larvae. Although valuable insight is gained on host acceptance by using this method, the exclusive dissection of hosts does not

indicate anything about host suitability. In contrast, when attacked hosts are exclusively reared, assessment of suitability may be misleading since it is unclear whether a parasitoid egg was deposited and whether the parasitoid egg or parasitoid immature was encapsulated by the host since encapsulation is only rarely reported. A review of suitable methods is found in Godfray (1994).

2.7.3 The Selection of Parasitoids for Biological Control

The success of biological control is measured, in part, by the parasitoid's ability to establish in a new habitat and by its contribution to maintaining the target pest population below damaging levels (Waage, 1990; Roland, 1994). This requires, among other things, that a suitable host is available for the parasitoid and that the parasitoid accepts the pest as a host in the new habitat. Re-examination of the successes and failures of biological control has sparked the search for other methods by which to identify parasitoid candidates (Waage, 1990; Hokkanen and Pimentel 1984; 1989; Greathead, 1986; Gilstrap, 1997; Wiedenmann and Smith, 1997). Generally the potential of a parasitoid is evaluated according to the following criteria: the parasitoid exhibits a high searching efficiency; a narrow host range; a high reproductive rate and; an adaptability to novel habitats (Huffaker et al., 1971; Murdoch et al., 1985).

Though parasitoids meeting all the above requirements have been associated with successful pest control, other parasitoids with similar profiles have not. One problem is the criteria have been derived mainly from evaluation of studies with

pests in perennial habitats even though most of the parasitoid introductions have been against pests in temporary habitats (Gilstrap, 1997). Unlike perennial habitats, temporary habitats are destroyed annually. The goal of pest management in temporary habitats is to delay increases in pest abundance rather than to decrease an already abundant pest, as for perennial habitats (Wiedenmann and Smith, 1997). Thus, the successful control of a pest in temporary habitats requires a parasitoid that can survive when the availability of the pest is low.

Generalist parasitoids may be more effective at pest control in temporary habitats. This is because a generalist parasitoid is more likely to take refuge in alternative host species in more stable surrounding habitats when the target pest species and its habitat are unavailable (Murdoch et al., 1985; Wiedenmann and Smith, 1997). However, specialist parasitoids are more commonly used in biological control in temporary habitats. This is because specialist parasitoids are considered to be more synchronized with their host, more physiologically adapted to the host and less harmful to non-target hosts (Sands, 1997). This is supported in that most of the successful parasitoid introductions have been specialists (see Greathead 1986). However, more detailed field studies on host range show that species previously thought to be host specific have a broader host range (Sands 1997). Generally the selection of parasitoids that are associated with hosts in temporary habitats in their country of origin may

increase the chance that the parasitoid will be successful in other temporary habitats.

2.8 The Study Organisms

2.8.1 *Mamestra brassicae* L.

The European cabbage moth, *Mamestra brassicae* (Lepidoptera: Noctuidae) is a Palaearctic species of wide geographic distribution (Turnock, 1984). The moth is most commonly considered as a pest of cultivated crops from the family Brassicaceae, but is recorded from more than 70 plant species in 22 families (Popova, 1993).

Moths emerge from overwintered pupae and within three to six days after emergence, mated females fly to host plants for egg laying (Rojas, 1999a). Several factors influence the flight response of *M. brassicae* to host plants. These include the age, mating status and egg load of female moths (Rojas, 1999a), response to damaged host plants (Rojas, 1999b) and visual plant characteristics, such as the plant size and colour (Rojas and Wyatt, 1999). Laboratory reared adults produce up to 1000 eggs each in a lifetime (in Johansen, 1997). After hatching, first instar larvae feed gregariously on plant tissue and within two days, larvae disperse to surrounding leaves and plants (Johansen, 1997). Larvae continue to disperse until they enter the soil to pupate (Johansen, 1997). There is no biorhythm to the feeding activity of first instar larvae (Bornert et al., 1975). The feeding activity of *M. brassicae* larvae shifts

towards nocturnal feeding as the age of the larva increases (Bornert et al., 1975). In the northerly range of its distribution, *M. brassicae* is univoltine or partially bivoltine (Johansen, 1997).

Up to 47 parasitoid species have been recorded from *M. brassicae* populations over the range of its geographic distribution. Turnock (1984) lists 23 species of parasitoids occurring in western European and Russian populations. Of the nine parasitoid species found in western Europe, only four are reported to be common: the egg parasitoid *Trichogramma buesi* Vogele (reported as *T. evanescens* Westwood by Turnock, 1984) and the larval parasitoids, *Exetastes atrator* Forster, *Eurithia consobrina* Meigen and *Microplitis mediator* (Haliday).

2.8.2 *Microplitis mediator* (Haliday)

Microplitis mediator is a solitary larval endoparasitoid of *M. brassicae*. It is a widespread and common parasitoid in northern and western regions of Europe (Nixon, 1970). The host range of *M. mediator* consists of almost 40 species of lepidopterous larvae over two families, Noctuidae and Geometridae (Nixon, 1970; Shenefelt, 1973).

In Central Europe, *M. mediator* is detected in *M. brassicae* larvae from June until early October and it is suggested that the parasitoid is multivoltine (Carl and Sommer, 1975). Previous studies show that parasitoid females attack the first three larval instars of *M. brassicae* and deposit a single egg within each host;

although self- superparasitism of larvae is common in the laboratory, only one immature parasitoid survives (Anon., 1979). The development of the immature parasitoid stages within the host is short for *M. brassicae*: at 22°C, egg and larval development takes a total of 11-12 days (Carl and Sommer, 1975) which is slightly greater than that reported for *Leucania separata* (Lepidoptera: Noctuidae) (Tanaka et al., 1984) but less than that reported for *M. configurata* (Arthur and Mason, 1986). In *M. configurata* there are three larval instars of *M. mediator* (Arthur and Mason, 1986) whereas in *L. separata* only two larval instars are reported (Tanaka et al., 1984). The third instar parasitoid emerges from the fifth or sixth abdominal segment in *M. configurata* larvae and cocoons are immediately spun (Arthur and Mason, 1986). Cocoon development to adult emergence takes 7 to 8 days at 22°C in *M. brassicae* hosts (Carl and Sommer, 1975) and parasitoid adults live for approximately three weeks under laboratory conditions (Anon., 1979). Tanaka et al. (1984) found no differences in male and female development time within the larvae, however in second and third instars of *L. separata* larvae, male adults emerged from cocoons earlier than females.

Preliminary studies suggest that for *M. mediator* the first instar of *M. brassicae* is the most preferred host stage followed by second instars; although *M. mediator* females attack third instars of *M. brassicae*, no parasitoids have yet been reported to develop within the host (Anon., 1979; Carl et al., 1995). In *M. configurata*, *M. mediator* attacks larvae in the first three instars (Arthur and Mason, 1986) and attacks on third instar larvae result in greater than 50 %

parasitoid cocoon emergence (Pivnick, 1993). *Microplitis mediator* attacks larvae of the first four instars of *L. separata* (Tanaka et al., 1984). The number of parasitoid cocoons resulting from attacks on first to early third instar larvae is high with ranges between 75 to 93% however the number of parasitoid cocoons resulting from attacks on late third to fourth instars is markedly decreased (Tanaka et al., 1984).

Chapter 3: Seasonal abundance, parasitism and distribution of *Mamestra brassicae* L. in organic vegetable field plots in Switzerland.

Abstract

In 1998 and 1999 egg masses and larvae of *Mamestra brassicae* were collected weekly from late May until late September to study the host and parasitoid seasonal abundance and to assess rates of parasitism in the region of Bielersee, Switzerland. In 1999, additional information was gathered to study the spatial distribution of *M. brassicae* and the larval parasitoid *Microplitis mediator* (Haliday). Additionally in 1999, other lepidopterous hosts in the larval stage were collected in the same field plots as *M. brassicae* and reared in the laboratory to examine the range of hosts used by *M. mediator*. All samples were reared in the laboratory until a parasitoid emerged or the adult moth emerged.

Two generations per year of *M. brassicae* were observed. Egg and larval abundance was characterized as low in the first generation and higher in the second generation. Egg masses were distributed randomly in field plots, however the number of eggs per mass resulted in an aggregated distribution of eggs and first instars. Random distributions were more common as larval instar increased. The egg parasitoids *Trichogramma buesi* Vogele and *Telenomus* sp., were present in both generations of the host, with the exception of the first host generation in 1998. Four larval parasitoids were reared: *M. mediator*, *Exetastes atrator* (Forster), *Eurithia consobrina* (Meigen) and one ectoparasitoid from Eulophidae. *Microplitis mediator* was the dominant larval parasitoid in both years

of this study. Probability of parasitism varied among field plots and was inversely related to the number of larvae per plant. *Microplitis mediator* was reared from three larvae of *Autographa gamma* L.. The low incidence of parasitism suggests that *M. mediator* has a narrow host range within fields containing *M. brassicae.*

3.1 Introduction

Mamestra configurata Walker is an economically important pest of canola in western Canada (Bracken, 1987). Although parasitoids are important regulators of *M. configurata*, they do not maintain host populations below economic levels during outbreaks of the pest (Wylie and Bucher, 1977; Turnock, 1988). *Microplitis mediator* (Haliday) is an important larval parasitoid of the European cabbage moth, *Mamestra brassicae* L. in Europe (Turnock, 1984). The parasitoid may be a useful addition to the western Canadian parasitoid guild (Carl et al., 1986). The purpose of the following study was to characterize some of the key interactions of *M. mediator* with its native host, in its native host habitat by examining the temporal abundance and spatial distribution of *M. brassicae*, the temporal abundance of parasitoids associated with *M. brassicae* and the host range of *M. mediator* within the host habitat of *M. brassicae* in Central Switzerland.

3.2 Materials and Methods

3.2.1 Field Plot Description. The study was carried out in field plots in the vegetable growing region of Bielersee, near to Galmiz in Switzerland. Figure 3.2.1 is a schematic representation of a field plot. A field plot was an area often contained within a larger field with borders adjoining road, woodland, or other crops however some field plots were contained by only woodland, road or grassy margins. Samples were taken from commercially managed, organic field plots each of various size and planted with at least one of the following crop varieties

of *Brassica oleracea* L.: broccoli, cauliflower, red or white cabbage or brussel sprouts (Table 3.2.1). Often the plants contained within the field plot were a mixture of crop varieties from *B. oleracea* in different beds. Beds were arranged lengthwise within the field plot and spaced 60 cm apart. Each bed consisted of four rows of plants spaced 30 cm apart. Within each row, plants were spaced 30 cm apart. At no time during the sampling season were synthetic chemical pesticides applied to the plants.

3.2.2 Sampling *M. brassicae*: 1998. In 1998, adult male pheromone traps (Biotrap- Hoechst Schering AgrEvo GmbH Germany) were used to monitor the flight period of *M. brassicae*. Four traps were initially set up on 15 May at the edge and centre of two field plots and checked weekly for adult males.

A randomized systematic sampling programme for immature *M. brassicae* stages was used for field plots managed under continuous (one harvest per season) or discontinuous (more than one harvest per season) production. Samples were taken at weekly intervals. The sample selection procedure was designed to minimize the probability of sampling the same plant twice throughout the season. Field plots were divided into three regions (Figure 3.2.1). Regions 1 and 3 always consisted of two beds. Region 2 was in the middle of the field plot and consisted of two beds unless the field plot had five beds in which case, region 2 consisted of one bed. In field plots with more than six beds there were unsampled beds between the sampled regions. Each week, a random number

of steps, not exceeding 10, were taken along the space between the two beds of each region. At the stopping point, one plant was randomly selected from the eight level with the sampler. Randomization was achieved by selecting a number from 1-8 prior to arriving at the stopping point. The plant was checked for egg masses and larvae of *M. brassicae* by carefully examining the upper and lower side of each leaf of the plant. After the first randomly selected stopping point, samplers stopped at five step intervals and selected and sampled plants at each stop as described. Within each region, 33 plants were sampled in this manner. One additional plant was sampled to total 100 plants sampled per field plot. Sampling took place between 0800 and 1800 hours.

The egg masses and larvae sampled from the field plot were pooled for the 100 plants and transferred to the laboratory at CABI Bioscience, Delemont for sorting. The numbers of *M. brassicae* egg masses, eggs per mass and larvae of each instar were recorded for each field plot and date. Head capsule measurements were used to separate larval instars of *M. brassicae.* The widest section of the head capsule was measured for each instar at a magnification of 2 x calibrated to 15 units : 1 mm.

Collected eggs were subsequently reared, using the method of Corrigan and Laing (1991), in glass vials at room temperature and 16:8h L: D light conditions. On the date of sampling and every two days after, each glass vial was carefully

examined for emerging egg parasitoids. Adult parasitoids were identified to species. Voucher specimens were deposited at CABI Bioscience, Delemont.

Collected larvae were kept in 9 cm diameter Petri dishes with a maximum of five individuals of the same stadium in each Petri dish. Dishes were maintained at room temperature and 16:8h L:D. Larvae were fed organic cabbage from the gardens of CABI Bioscience. On the date of sampling and every two days after, Petri dishes were examined for larval parasitoids. If no parasitoid was detected, the Petri dish was cleaned with a 1% bleach solution and fresh cabbage was supplied. If a parasitoid cocoon was detected, it was carefully removed from the petri dish and placed individually in a glass vial containing moistened vermiculite for rearing at room temperature and 16:8h L:D. Observations of a larva ceased when either a parasitoid cocoon was formed or the adult host stage was reached. The species of larval parasitoid was determined at CABI Bioscience using keys of Herting (1960) and Nixon (1970). Voucher specimens were deposited at CABI Bioscience, Delemont.

For all emerging egg and larval parasitoids, records were kept on the stage at which the cocoon formed and the field plot and date in which the host was collected. These data were used to calculate the percent parasitism: the number of parasitized individuals over the number of susceptible individuals. Susceptible individuals included only the stages where parasitism was evident.

3.2.3 Sampling *M. brassicae* 1999. In 1999, only immature *M. brassicae* were sampled and methods were identical to those described for the 1998 field season, with the following exceptions. Field plots with an even number of beds were subdivided into three regions, each with two beds and from these, 33 plants were sampled. An additional plant was sampled to total 100 plants sampled per field plot per week. Field plots with an odd number of beds were also subdivided into three regions; two bordering regions each consisting of two beds and 40 plants sampled in each; one central region consisting of one bed only and 20 plants sampled. To sample the entire length of each region, random numbers between 5 and 15 were selected to determine the initial plant to be sampled and the distance between subsequent plants was calculated by dividing the total number of plants in a row less 10 plants, by the number of plants to be sampled in that region (for instance, a region within a field plot with an even number of beds would be divisible by 33).

Unlike in 1998, in 1999 samples from each individual plant were kept separate, so both host and parasitoid data could be related precisely to location of the source plant in the field plot. The rearing procedures for parasitoids were similar to those in 1998.

3.2.4 Host Range. On each sampling date in 1999, other herbivorous lepidopteran larvae found on plants being sampled for *M. brassicae*, were collected. Larvae were separated according to species. Larvae of the same

species and from the same sampling date were reared on organically grown cabbage in 15.5 cm height x 10.5 cm diameter cylinders with mesh covers. All larvae were checked every two days for parasitoids common to *M. brassicae*.

3.2.5 Statistical Analysis. The variance to mean ratio ($s^2/\bar{x}$) (Southwood, 1978) was used to characterize the distribution of eggs, egg masses and each larval instar of *M. brassicae* over the course of the 1999 season. Distributions were defined as uniform ($s^2/\bar{x} < 1$), random ($s^2/\bar{x} = 1$) or aggregated ($s^2/\bar{x} > 1$) (Southwood, 1978). The degree of departure of $s^2/\bar{x}$ from the Poisson series (randomness) was tested by comparing the index of dispersion (I_D) where $I_D = s^2 (n - 1)/ \bar{x}$ and n = number of samples in one field plot on one sampling date with the χ^2 distribution with n-1 degrees of freedom where $p = 1 - [\chi^2 (I_D, n-1)]$ (Southwood, 1978).

Binomial logistic regressions (Hosmer and Lemeshow, 1989) were used to analyze probability of parasitism of *M. brassicae* by *Microplitis mediator*. Terms for the model were selected using a step-up procedure with an alpha level of $p \leq 0.15$ to add terms.

All statistical analyses were performed using SYSTAT (Systat, 1999).

3.3 Results

3.3.1 Sampling 1998.

Attempts to monitor the flight period of *M. brassicae* adults in 1998 proved unsuccessful. No males of *M. brassicae* were caught in the pheromone traps.

The mean number of *M. brassicae* eggs and egg masses per plant is shown in Figure 3.3.1 a. Two distinct periods of egg abundance were seen; each characterized by a rise in abundance to a peak and followed by a decline in abundance. *Mamestra brassicae* eggs and egg masses were found in low abundance in the first period from 04 June to 24 June and in the second period were more abundant for a longer duration, from 08 July to 02 September. On 05 August, the mean number of eggs per plant peaked at 4.76 ± 1.5. During the first period, eggs were commonly found on the underside of leaves in single layered masses averaging 16.3 ± 1.7 (n = 12) eggs per mass (Table 3.3.1). Egg masses were found on both the upper and underside of leaves in the second period in single layered masses averaging 21.4 ± 1.1 eggs per mass (n = 219) (Table 3.3.1)

The mean number of *M. brassicae* larvae per plant is shown in Figure 3.3.1 b & c. Head capsule measurements of larvae indicate a total of six instars for *M. brassicae* (Table 3.3.2). Similar to the egg stage of *M. brassicae*, two distinct periods of larval abundance were seen. The first period was characterized by a relatively low mean abundance of larvae and a shorter duration in field plots than

the second period. Field plot observations note that instars I to III were more commonly found on the underside of leaves next to small, irregularly shaped feeding holes and less commonly on the upper side of the leaf or near the bracts of the plant. Larval instars IV-VI were more commonly found near the bracts of plants and during the heading phase of the plant, tunneled into the vegetative head. Larvae were generally inactive during the day when sampling was done.

Parasitoids. Six primary parasitoid species were reared from *M. brassicae* egg masses and larvae (Table 3.3.3). Figure 3.3.2 shows the mean percent of *M. brassicae* eggs parasitized by two egg parasitoids, *Trichogramma buesi* Vogele and *Telenomus* sp. for each sampling date. Egg parasitoids were reared exclusively from egg masses sampled in the second period. *Trichogramma buesi* was reared with the highest frequency from host eggs and occurred at the most locations sampled (Table 3.3.4).

Four parasitoid species of *M. brassicae* larvae were reared (Table 3.3.3). *Microplitis mediator* was the only parasitoid reared in both periods, on each date when susceptible larvae were present (Figure 3.3.3), and in all locations sampled (Table 3.3.4). The range of mean percent parasitism by *M. mediator* was similar in both periods of susceptible host larvae (Figure 3.3.3). *Exetastes atrator* was the second most abundant parasitoid and was reared from susceptible larvae in the second period only (Table 3.3.4). Five individuals of *Eurithia consobrina* and

two individuals of a species of Eulophidae were reared from susceptible larvae in the second period only.

3.3.2 Sampling 1999.

In 1999, the seasonal pattern of abundance of eggs and egg masses was similar to that described in 1998 (Figure 3.3.4a). Mean numbers per plant were greater in 1999 than in 1998 and the mean number of eggs per plant peaked at 6.65 ± 0.9 on 11 August. Unlike 1998, in 1999 eggs were commonly found on both sides of the leaf in single layered masses averaging 13.4 ± 2.8 (n = 9) in the first period and increasing in size to 25.3 ± 1.3 (n = 200) in the second period (Table 3.3.5)

The mean number of larvae for each instar is shown in Figure 3.3.4 b & c. As in 1998, six larval instars of *M. brassicae* were recorded (Table 3.3.2). The seasonal pattern of larval abundance was similar to that described for 1998. The mean number of larvae per plant was lower in 1999 than in 1998. Field plot observations noting larval arrangement on plants were similar to observations made in 1998.

Parasitoids. Four primary parasitoids were reared from *M. brassicae* egg masses and larvae (Table 3.3.3). Figure 3.3.5 shows the mean percent of *M. brassicae* eggs parasitized by two egg parasitoids, *T. buesi* and *T.* sp. for each sampling date. The seasonal pattern in the mean percent parasitism by egg

parasitoids differed from those seen in 1998; in 1999 *T. buesi* and *T.* sp. were reared from both periods of host eggs. No egg parasitoids were reared from egg masses found in two of the field plots sampled (Table 3.3.6).

Two parasitoid species of *M. brassicae* larvae were reared (Table 3.3.3) in both periods of susceptible larvae and in each location sampled (Table 3.3.6). As in 1998, *M. mediator* was the most common parasitoid species. The range of mean percent parasitism by *M. mediator* was greater in the first period of susceptible larvae. Percent parasitism for 21 July and 28 July were calculated for samples containing few individual host larvae. Unlike 1998, the larval parasitoid *E. atrator* was sampled in both periods of susceptible larvae and in each location sampled (Table 3.3.6). The percentage of susceptible larvae parasitized by *E. atrator* was greater in field plots sampled in the first period of *M. brassicae*.

3.3.3 Host Distribution

The distribution of *M. brassicae* eggs, egg masses and larvae (instars I-VI) on a per plant level was calculated for each sampling date and each field plot using the variance to mean ratio ($s^2/\bar{x}$) for the 1999 sampling season only (Table 3.3.7). Values for the $s^2/\bar{x}$ of egg masses were not significantly different from 1.0, whereas values for individual eggs were significantly greater than 1.0. Values of $s^2/\bar{x}$ gradually shifted back to 1.0 as the larval stage matured.

3.3.4 Parasitism Rate and Host Density

The 1999 parasitism data for *M. mediator* were used for binomial logistic regression analysis. Each larval instar susceptible to parasitism was tested separately by selecting plants infested with host larvae of only one instar. Step-up logistic analysis shows that a model with the terms 'field plot' and 'number of larvae per plant' is significant (L.R.χ^2 = 84.7; d.f. = 5; $p < 0.005$). Estimates of terms from the complete model, and significance of individual models, one for each instar, are listed in Table 3.3.8. The value of the logit presented in Table 3.3.8 represents the degree of parasitism for the term tested; the logit value is positively associated with parasitism. It should be noted that estimates are highly influenced by the number of data points available for analysis.

Probability of parasitism for each instar was affected by the field plot (Table 3.3.8). Negative relationships and hence, lower probabilities of parasitism, were estimated for field plots B and D with the exception of instar IV in field plot B and instar II in field plot D. Positive relationships were estimated for field plots A, C and E. Highest probabilities of parasitism for instars I through IV were estimated in field plots E, D, A and A respectively.

Probability of parasitism for each instar was affected by the number of larvae per plant (Table 3.3.8). Estimates were similarly negative for each instar analyzed. A graphical representation of estimated and observed parasitism is presented for each larval instar of *M. brassicae* for selected field plots (Figures 3.3.7-3.3.10).

The following equations were used for graphical representation of probability of parasitism by *M. mediator*:

Equation (1): Pooled logit (L_p)

$$(L_p) = constant + (X)*b$$

Equation (2): Logit for individual field plot (L_f)

$$(L_f) = L_P + estimate\ of\ field\ plot$$

Equation (3): Probability of parasitism for individual field plots (P_f)

$$(P_f) = exp(L_f) / [1 + exp(L_f)]$$

Where X is the number of larvae per plant and b is the logit parameter for the term 'larvae per plant'. Although 'larvae per plant' logit parameters were similarly negative for each instar modeled, the observed mean number of larvae per plant tends to decrease as larval instar increases (Table 3.3.8).

3.3.5 Host Range.

Other larvae sampled in field plots in 1999 included *Plutella xylostella* L. (Lepidoptera: Yponomeutidae), *Pieris brassicae* L. (Lepidoptera: Pieridae), *P. rapae* L. (Lepidoptera: Pieridae) and *Autographa gamma* L. (Lepidoptera: Noctuidae) (Table 3.3.9). The species collected with the highest frequency was *Plutella xylostella*, which was sampled in both periods of *M. brassicae*. *Microplitis mediator* was successfully reared from three individuals of *A. gamma* in the second period of *M. brassicae* larvae.

3.4 Discussion

3.4.1 Seasonal Abundance

In both 1998 and 1999, we were able to follow the development of the egg and larval stages of *M. brassicae*. Two developmental periods were observed: the first commencing in late May and persisting until late July and the second commencing in late July and persisting until the end of the sampling season in late September. This seasonal pattern indicates a life history consisting of two annual generations of *M. brassicae*. Univoltine populations have been reported from the northerly part of the range (Johansen, 1997), whereas, in the southerly portion, up to three generations per year have been recorded (in Turnock 1984). My findings in Switzerland concur with past records of a bivoltine population occupying the central range of Europe. A low level of abundance of all stages characterizes the first generation, whereas a relatively high level of abundance characterizes the second generation. Differences between generations within one season have been well documented for European populations of *M. brassicae* (Anon., 1977; Turnock and Carl, 1995).

For *M. brassicae* the rate of food consumption increases as the age of the larva increases. This is reflected in the economic threshold. The economic threshold for *M. brassicae* is 1-3 early instar larvae (instars I-III) per plant and 0.1-0.4 late instar larvae (instars IV-VI) per plant (Anon., 1998). In 1998, early instar larvae remained below the economic threshold (Figure 3.4.1) in both generations and in 1999 surpassed the lower limit on only one sampling date at the peak of the

second generation (Figure 3.4.2). In both 1998 (Figure 3.4.3) and 1999 (Figure 3.4.4) late instar larvae surpassed the lower limit of their economic threshold in mid-August and continued to increase above the upper limit until the end of the sampling season in late September. Studies have shown that the period between the heading stage and the harvesting stage of broccoli, cabbage and cauliflower is the most sensitive to feeding damage, whereas, feeding from transplanting to heading is less likely to affect yield (Stewart et al., 1990). For *M. brassicae* the larval instars that feed on the vegetative head were present in high abundance during the most sensitive stage of the plant.

3.4.2 Parasitism

In Western Europe, nine parasitoid species have been recorded from *M. brassicae* populations (Turnock, 1984). Of the nine species, only five are considered important mortality factors of *M. brassicae* (Turnock, 1984; Turnock and Carl, 1995; Ziegler and Carl, 1996). In the present study, six parasitoid species were recorded from the egg and larval stages of *M. brassicae*, and these include the five key parasitoid species reported by Turnock (1984) (Table 3.3.3). The sixth parasitoid species recorded, from the family Eulophidae, is a new record of a larval ectoparasitoid species for Switzerland (P. Mason, personal communication). The eulophid species was collected from only one location in 1998 from two *M. brassicae* larvae in the fourth and fifth instar respectively. Three parasitoid species from Eulophidae have been recorded in northern populations of *M. brassicae* in Krasnodar, Kharkov and Sakhalin (Turnock,

1984). The absence of the eulophid species in our study in 1999 suggests a rare association with *M. brassicae* in Switzerland.

Two egg parasitoids, *T. buesi* and *T.* sp. were recorded in both years of our study. In 1998 *T. buesi* was a dominant parasitoid in the second generation of *M. brassicae* whereas in 1999, *Telenomus* sp. was more dominant. Percent parasitism was always less than 60% except when eggs were rare in field plots (Figures 3.3.3 and 3.3.5). In 1998, egg parasitoids were not recorded from the first generation of *M. brassicae*. Why egg parasitism was entirely undetected is unclear. It is possible that conditions in the field plots during this time period were not favourable for parasitism by either species of parasitoid. Hassan (1993) suggests that the effectiveness of *Trichogramma* spp. depends largely on favourable environmental conditions; for instance, temperatures below 18°C negatively affect parasitism rates (Hassan and Rost, 1985). However even under these conditions, at least some egg parasitism is evident in field studies (Rost and Hassan, 1983; Hassan and Rost, 1985). Another possibility is that the quality of *M. brassicae* eggs was not favourable for parasitism. *Telenomus* sp. is less able to pierce older eggs of *M. brassicae* with her ovipositor, however *T. buesi* will readily accept older eggs (Anon, 1996). Thus it is conceivable that the absence of egg parasitism in the first generation of *M. brassicae* in 1998 is a combined effect of poor environmental conditions for parasitism by *T. buesi* and poor quality of eggs for parasitism by *T.* sp., and that these two factors may not be mutually exclusive ie. environmental conditions affect the quality of *M.*

brassicae egg masses. A follow up study of these two parasitoid species under various environmental conditions would be valuable for determining their affect on the probability of egg parasitism.

Parasitism of *M. brassicae* larvae was found in both generations of high and low abundance in both years of this study. The predominant parasitoid was *M. mediator*. Percent parasitism by *M. mediator* remained fairly constant regardless of differences in larval abundance with the exception of two sampling dates at the end of the first generation in 1999. These 100% parasitism were based on small sample sizes and could indicate one of two possibilities. The first is that adult parasitoids were active in the field during this time, which suggests a highly efficient search profile for hosts. The second possibility is that these few larvae were parasitized at an earlier date which suggests there is developmental differences between parasitized and unparasitized larvae as seen by Tanaka et al. (1984) in the host *Leucania separata*. This would account for the 100% parasitism of *M. brassicae* larvae since only parasitized individuals remained in the field. This is supported by the fact that these few larvae were primarily in the third and fourth instars; which are the two instars where *M. mediator* emerges from to spin cocoons. It would be useful to study the effect of parasitism by *M. mediator* on the development of *M. brassicae* larvae.

3.4.3 Spatial Distribution

The indices of dispersion for the 1999 field season show that adult female *M. brassicae* deposit egg masses randomly within field plots. The random spatial pattern is not unexpected since agricultural habitats provide a uniform resource for fecund *M. brassicae* females (Smith, 1996). There is some evidence that *M. brassicae* adult females are strongly attracted to injured cabbage plants especially to those injured by chewing insects (Rojas, 1999b). However, in the present study, oviposition coincided with early growth stages of the plant and it is possible that there was little previous insect injury. In the absence of damaged plants, *M. brassicae* adult females continue to respond positively to *Brassica* crops (Rojas, 1999b). In contrast to egg masses, eggs were highly aggregated within field plots. The aggregated distribution of eggs is a consequence of each egg mass containing multiple eggs.

The distribution of first instar larvae was also highly aggregated, however to a lesser degree than eggs. Johansen (1997) examined the rate of dispersal of *M. brassicae* larvae on *Brassica oleracea* var. *capitata* (L.) and found that within one to two days after emergence from an egg mass, 64.5% of first instar larvae had moved off the original plant to neighbouring plants. The highly dispersive nature of first instar larvae may, in part, account for the lower level of aggregation found. *Mamestra brassicae* larvae continue to disperse throughout the larval stage (Johansen, 1997) and tend to decrease in abundance (Figures 3.3.1 and 3.3.4); this may explain the trend towards randomness as larval instar increases.

Results from the binomial logistic regression indicate that the parasitoid *M. mediator* responds to *M. brassicae* larvae on two different spatial scales: on a field plot scale and a plant by plant scale. Estimates of parasitism were variable among field plots and highest estimates appear to be positively coupled with the abundance of larvae in field plots (Table 3.3.8). If this is so, it suggests that *M. mediator* is initially attracted to fields of relatively high host abundance.

Within each field plot, the probability of parasitism for plants infested with the same larval instar was negatively associated with larval density (Figures 3.3.7-3.3.10). The negative response of *M. mediator* to natural densities of hosts is of interest. Waage (1983) suggests that inverse density dependence may arise from increased handling time of hosts that lowers the maximum attack rate by parasitoids. Another possibility involves the density of searching parasitoids within fields. If parasitoids are attracted to patches of high host abundance, as suggested by our estimates of parasitism on a field plot scale, then there may be a tendency for aggregations of parasitoids to increase within these host patches. Parasitoid encounters with other adults (mutual interference) or with previously parasitized larvae may increase the frequency of parasitoid dispersal away from host patches (Hassell and Waage, 1984).

The estimation of parasitism poses several problems. To get a clear indication of what choices were available to *M. mediator* females at the time of oviposition,

plants infested with only one instar were selected. This method of selection was based on two studies: one which shows that *M. brassicae* adult females are attracted to plants damaged by chewing insects for oviposition (Rojas, 1999b) and the second which shows that larvae are dispersive (Johansen, 1997). If recruitment of larvae through subsequent ovipositions occurs, this would add to the original density of larvae that were available for parasitism on the plant and would thus underestimate parasitism. Though aggregations of eggs are initially restricted to the leaf where the egg mass was oviposited, within the same day of larvae emerging, aggregations may extend to the entire plant and to neighbouring plants (Johansen, 1997). The dispersive behaviour of larvae will either underestimate or overestimate parasitism on the plant depending on whether larvae are dispersing to or from the plant respectively. This is especially so if there are differences between the dispersal of parasitized versus unparasitized larvae.

By selecting plants with the same instar however, it is possible that parasitism was overestimated at low host densities. This is if the development of parasitized larvae differs from unparasitized larvae as suggested by my examination of seasonal parasitism by *M. mediator* in 1999. If parasitism prolongs the development of larvae, than it is likely that the unparasitized cohort would have developed to the next instar. These larval cohorts would thus be excluded from the analysis since more than one instar would be present on the plant.

It seems that difficulties in estimating parasitism arise from not being able to clearly define the boundaries of the host patch at the time of parasitization. Though the inverse density dependence is clearly a real effect of this study, whether the mechanisms for the response are a result of parasitoid behaviour or host behaviour are largely unknown and results should be interpreted with caution. Future study should focus on the density of adult parasitoids within fields, the characterization of the host patch and the dispersive behaviour of parasitized *M. brassicae* larvae, to evaluate the response of *M. mediator* to host density.

3.4.4 Host Range

Microplitis mediator has been reared from over 40 lepidopterous host larvae spanning two families: Noctuidae and Geometridae (Shenefelt, 1973). From May until late September of 1999, only four other lepidopterous larval species were collected (Table 3.3.9) and of these, only two species, *A. gamma* and *P. xylostella* have previously been recorded as hosts for *M. mediator* (Shenefelt, 1973; Peters, 1992; Forster et al. 1992). In this study, *M. mediator* was successfully reared from only three individuals of one species, *A. gamma.* *Microplitis mediator* is recorded as the dominant parasitoid of *A. gamma* in central and northern parts of Europe (Sengonca and Peters, 1991; Peters, 1992). The parasitoid has been reported to contribute up to 65% of total parasitism of *A. gamma* (Peters, 1992). However, similar to this study, the number of *A. gamma* hosts available for parasitism is exceptionally low. Peters

(1992) reported percentages as low as 3.1% of total host species composition in *Brassica* crops. *Autographa gamma* is a migrant to central parts of Europe from Africa with flight periods occurring between July and September (Whittle, 1986). This largely coincides with the second, more abundant generation of *M. brassicae* larvae. Strand and Obrycki (1996) predict that the host range of a parasitoid is influenced by the availability and suitability of other host species within a habitat. Thus it is not clear from our study whether the use of *A. gamma* as a host by *M. mediator* would increase under low host abundance of *M. brassicae* or alternatively, under high host abundance of *A. gamma*. The results from this study suggest that the host range of *M. mediator* is narrow within *Brassica* crops infested with *M. brassicae* in Switzerland.

Figure 3.2.1 A schematic representation of one field plot used for sampling *Mamestra brassicae* egg masses and larvae from 1998-1999 in the vegetable growing region of Bielersee, near to Galmiz, Switzerland.

Road or Woodland
Other Vegetable Crops
Region 1
Region 2
Region 3
Road or Woodland
Row 1
Row 2
Row 3
Row 4
Row 5
Row 6
Row 7
Row 8
30 cm
60 cm
30 cm
Bed
Bed
Region 2

Table 3.2.1 Description of field plots sampled weekly in 1998 and 1999 including labels, plants sampled and number of plants sampled each week during the sampling interval.

Year	Field Plot Label	Sampling Interval[4]	Plant Sampled	Total No. of Samples Taken
1998[1][3]	A	June 04-July 08[5]	Cauliflower, Broccoli	500
	B	June 04-July 29	Cauliflower, Broccoli	900
	C	July 08-September 02	Brussel Sprouts, White Cabbage	800
	D	August 05-September 21[6]	Cauliflower	600
	E	August 05-September 21[6]	Cauliflower, Broccoli	600
1999[2]	A	May 26-July 21	Broccoli, Cauliflower, Green Cabbage	900
	B	May 26-July 21	Cauliflower	900
	C	July 15-September 08	Cauliflower	900
	D	August 03-September 21	White Cabbage	800
	E	July 28-September 15	Cauliflower	800

Note: [1] In 1998, the size of the largest field plot was 10 m x 50 m and the size of the smallest field plot was 7.2 m x 37 m. [2] In 1999, the size of the largest field plot was 8.7 m x 200 m and the size of the smallest field plot was 7.2 m x 87 m. [3] Preliminary samples were taken in one field plot on 15 May and again on 22 May 1998. [4]The date of the first sample followed two to three weeks from crop transplantation and the last date coincided with crop harvest. [5]Samples were not taken during the week of 10 June. [6]Samples were not taken during the weeks of 09 September and 16 September.

Figure 3.3.1 Seasonal abundance of *Mamestra brassicae* a) eggs and egg masses and larval instars b) one to three and c) four to six in five field plots sampled in the region of Bielersee, near to Galmiz, Switzerland in 1998.

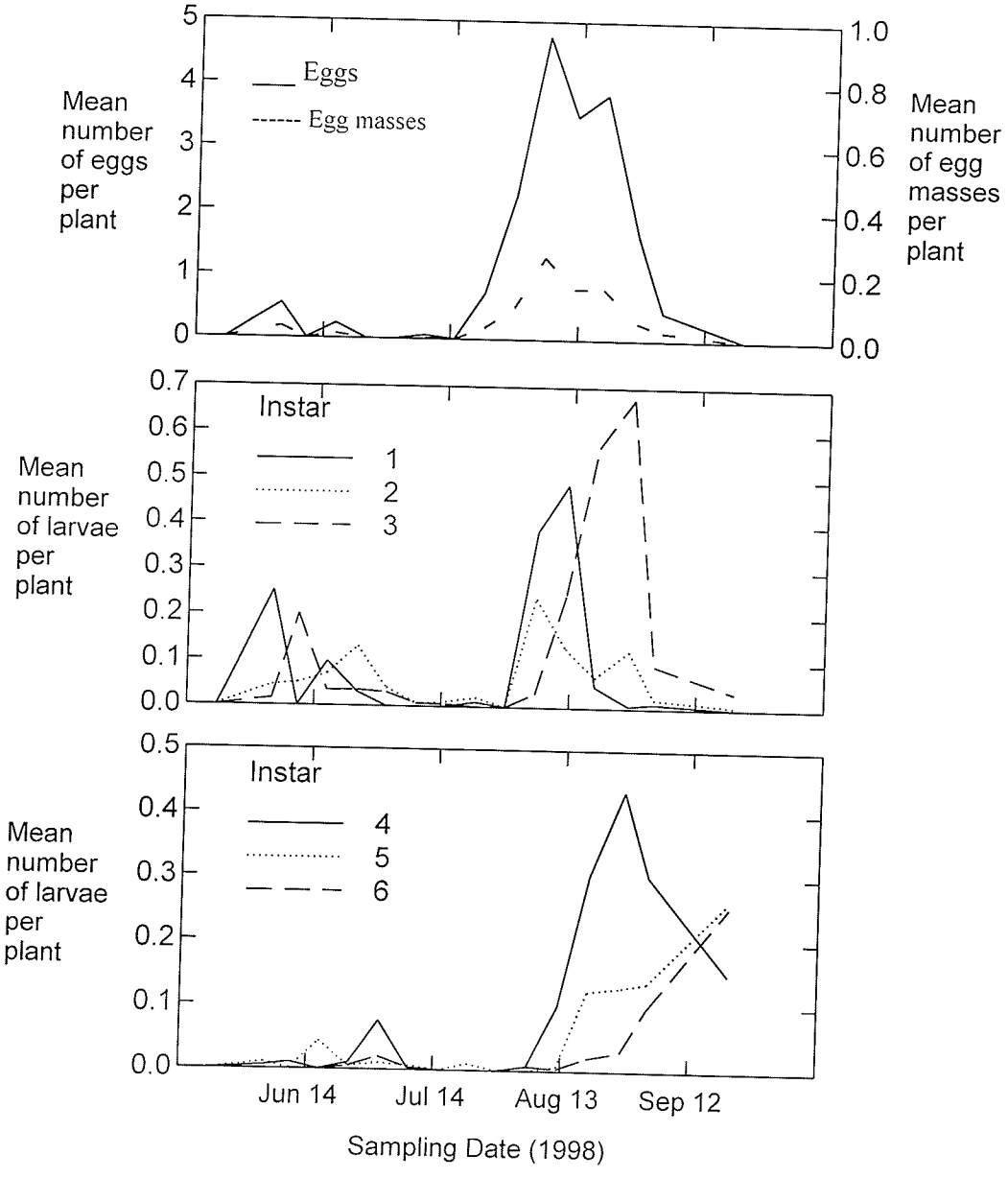

Mean number of eggs per plant
Eggs
Egg masses
Mean number of egg masses per plant
Mean number of larvae per plant
Instar
1
2
3
Mean number of larvae per plant
Instar
4
5
6
Jun 14
Jul 14
Aug 13
Sep 12
Sampling Date (1998)

Table 3.3.1 Average number of eggs ± SEM oviposited per egg mass by *Mamestra brassicae* in field plots sampled weekly in two oviposition periods in 1998.

Oviposition period	Sampling date	Number of egg masses collected	Average number of eggs per mass ± SEM
I	June 4	7	15.3 ± 2.6
	June 17	4	17.5 ± 2.7
	July 08	1	18 ± 0.0
II	July 22	7	20.6 ± 5.9
	July 29	20	23.0 ± 4.0
	August 5	77	18.5 ± 2.0
	August 12	48	21.8 ± 2.1
	August 19	48	24.0 ± 2.2
	August 27	11	29.5 ± 5.4
	September 2	8	16.4 ± 5.2

Table 3.3.2 The number of larval instars of *Mamestra brassicae* for larvae collected in vegetable field plots in Bielersee, Switzerland between May and September of 1998 and 1999 and the mean head capsule width (mm) ± S.E.M. for each instar (n = 100 larvae for each instar).

Instar	Mean head capsule width (mm)
1	0.33± 0.00
2	0.53 ± 0.00
3	0.86 ± 0.01
4	1.24 ± 0.01
5	2.09 ± 0.01
6	3.32 ± 0.02

Table 3.3.3 Parasitoid species composition reared from eggs (E) and larvae (L: instars I-VI) of *Mamestra brassicae* sampled from field plots near Galmiz, Switzerland in 1998 and 1999 (√ = presence, × = absence).

Parasitoid Species	Susceptible Host Stage	Year Sampled	
		1998	1999
Hymenoptera			
Braconidae			
Microplitis mediator (Haliday)	L:I-IV	√	√
Ichneumonidae			
Exetastes atrator (Forster)	L:I-V	√	√
Trichogrammatidae			
Trichogramma buesi Vogele	E	√	√
Scelionidae			
Telenomus sp.	E	√	√
Eulophidae			
Eulophid species	L:IV-V	√	×
Diptera			
Tachinidae			
Eurithia consobrina (Meigen)	L:I-VI	√	×

Figure 3.3.2 Mean weekly parasitism (%) of *Mamestra brassicae* eggs by two egg parasitoids, *Trichogramma buesi* and *Telenomus* sp. in five field plots sampled in 1998.

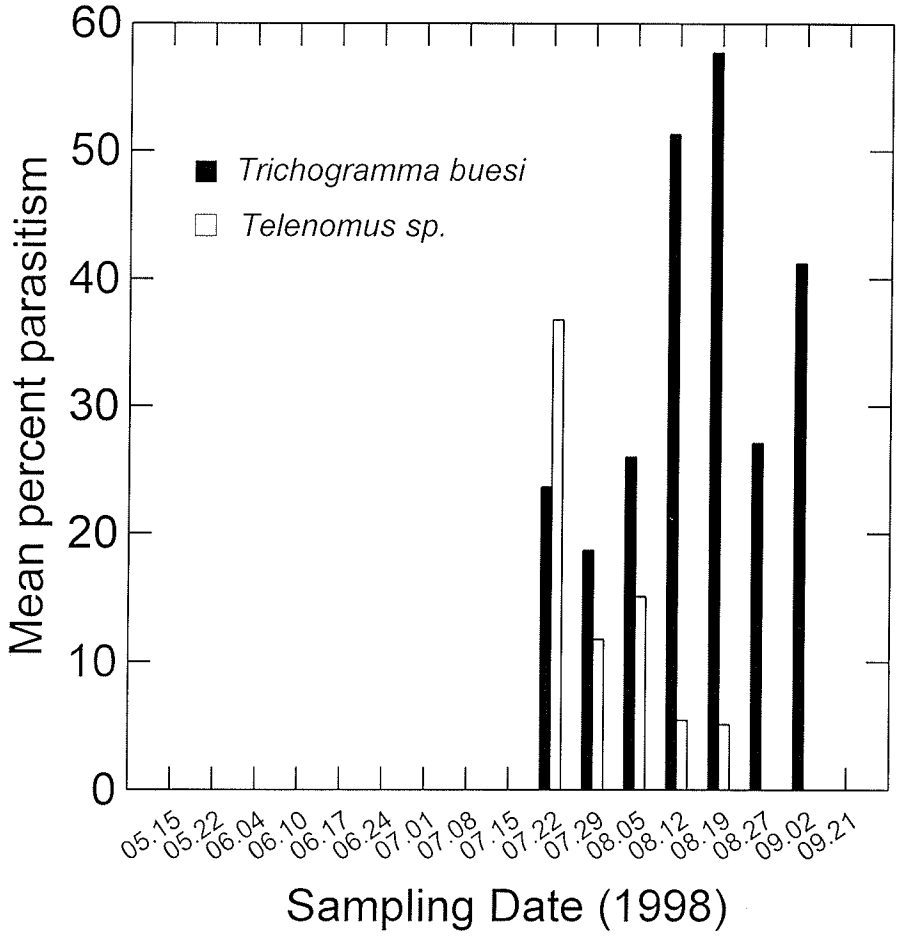

60
50
40
30
20
10
0
Mean percent parasitism
Trichogramma buesi
Telenomus sp.
05.15
05.22
06.04
06.10
06.17
06.24
07.01
07.08
07.15
07.22
07.29
08.05
08.12
08.19
08.27
09.02
09.21
Sampling Date (1998)

Table 3.3.4 Percent parasitism of susceptible stages of *Mamestra brassicae* in each of five field plots sampled in 1998.

Field plot sampled	Percent of susceptible host stages parasitized (number of susceptible host stages)			
	Trichogramma buesi	*Telenomus sp.*	*Microplitis mediator*	*Exetastes atrator*
A	0% (91)	0% (91)	20% (85)	0% (102)
B	23% (151)	17% (151)	16% (141)	0% (144)
C	41% (2527)	16% (2527)	32% (44)	2% (53)
D	42% (971)	0% (971)	22% (708)	3% (829)
E	32% (1118)	0% (1118)	33% (444)	2% (475)

Figure 3.3.3 Mean weekly parasitism of *Mamestra brassicae* larvae (instars I-IV) by *Microplitis mediator* in five field plots sampled in 1998. Numbers above bars represent percent parasitism of larval instars I-IV by *M. mediator*.

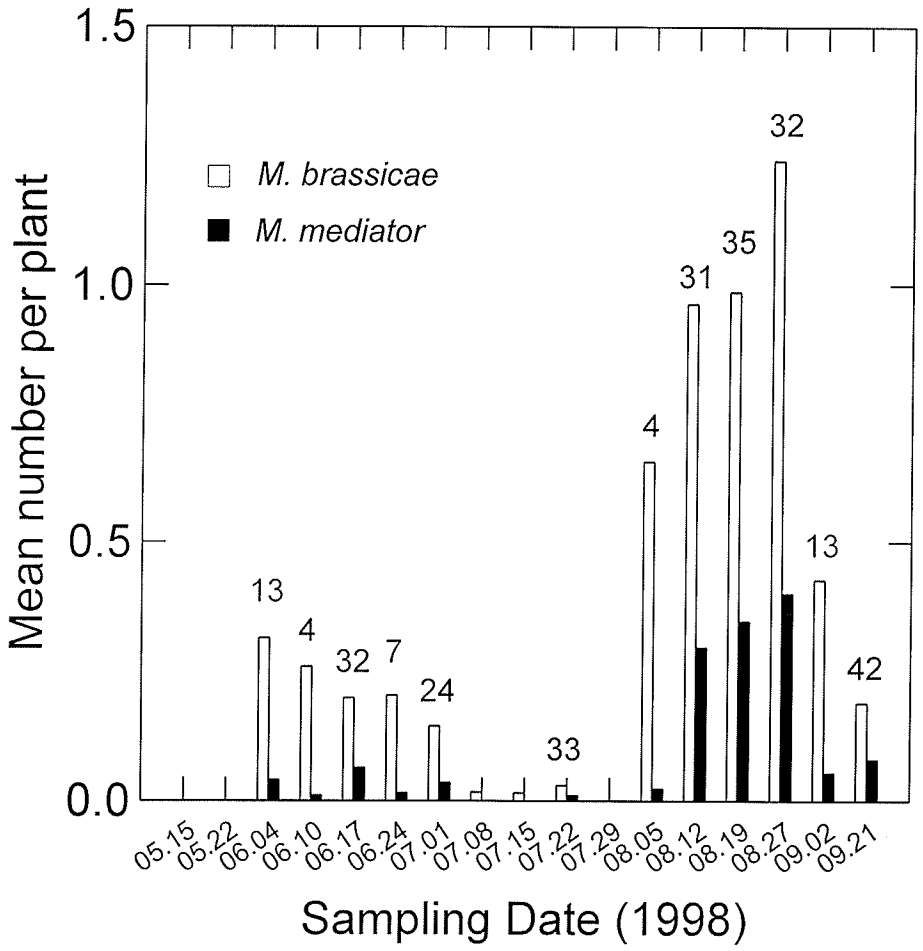

1.5
1.0
0.5
0.0
Mean number per plant
M. brassicae
M. mediator
13
4
32
7
24
33
4
31
35
32
13
42
05.15
05.22
06.04
06.10
06.17
06.24
07.01
07.08
07.15
07.22
07.29
08.05
08.12
08.19
08.27
09.02
09.21
Sampling Date (1998)

Figure 3.3.4 Seasonal abundance of *Mamestra brassicae* a) eggs and egg masses and larval instars b) one to three and c) four to six in five field plots sampled in the region of Bielersee, near to Galmiz, Switzerland in 1999.

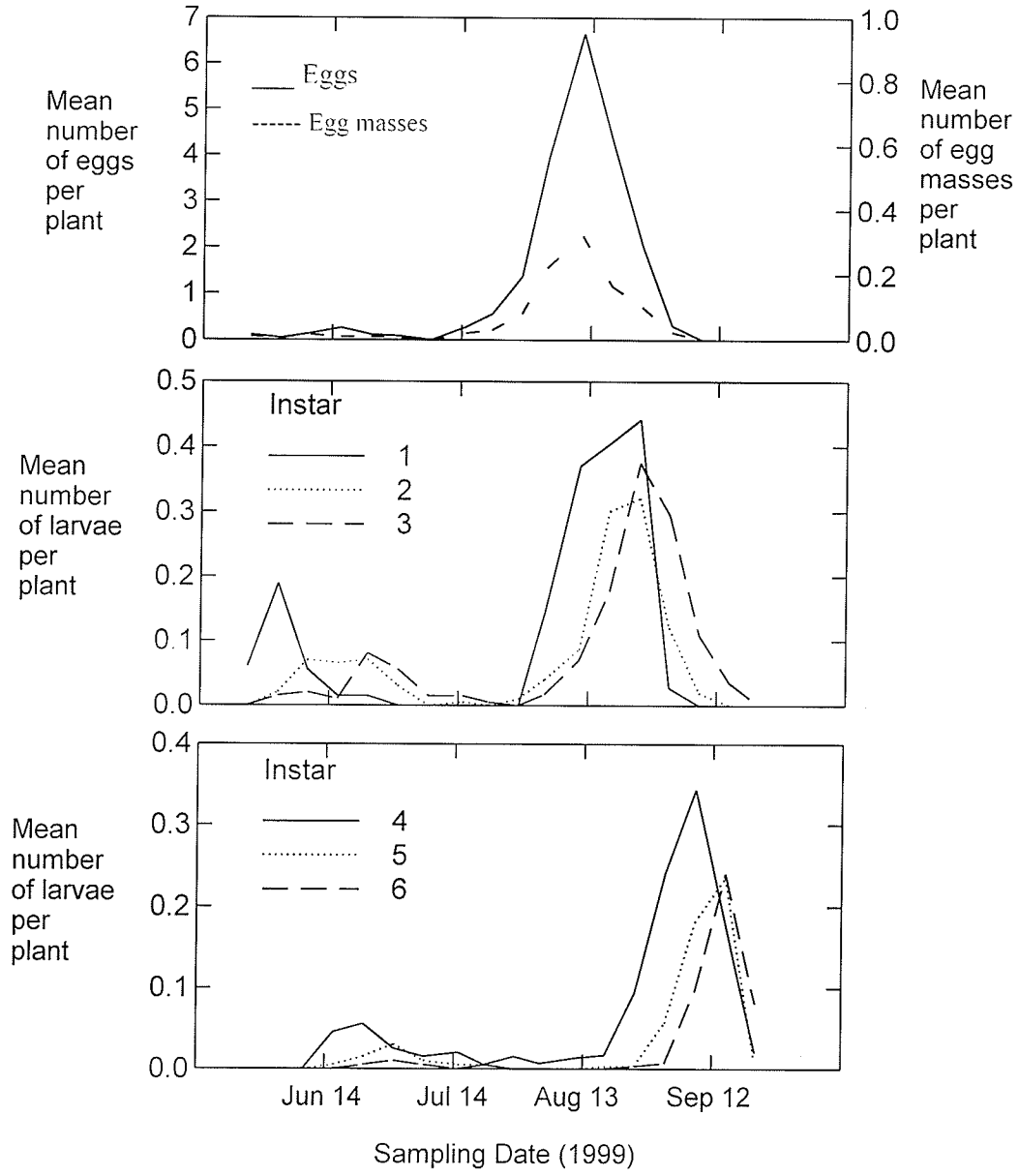

Mean number of eggs per plant
Eggs
Egg masses
Mean number of egg masses per plant
Instar
1
2
3
Mean number of larvae per plant
Instar
4
5
6
Mean number of larvae per plant
Jun 14
Jul 14
Aug 13
Sep 12
Sampling Date (1999)

Table 3.3.5 Average number of eggs ± S.E.M. oviposited per egg mass by *Mamestra brassicae* in field plots sampled weekly in two oviposition periods in 1999.

Oviposition period	Sampling date	Number of egg masses collected	Average number of eggs per mass ± SEM
I	May 26	2	11.0 ± 1.0
	June 2	1	8.0 ± 0.0
	June 9	2	8.5 ± 1.5
	June 16	1	35.0 ± 0.0
	June 23	2	11.5 ± 0.5
	June 30	1	16.0 ± 0.0
II	July 15	4	13.8 ± 3.1
	July 21	4	27.8 ± 11.3
	July 28	14	19.5 ± 4.4
	August 3	52	20.5 ± 2.0
	August 11	62	28.5 ± 2.9
	August 18	37	30.4 ± 3.1
	August 25	23	25.0 ± 3.1
	September 1	4	22.5 ± 4.0

Figure 3.3.5 Mean weekly parasitism (%) of *Mamestra brassicae* eggs by two egg parasitoids, *Trichogramma buesi* and *Telenomus* sp. in five field plots sampled in 1999.

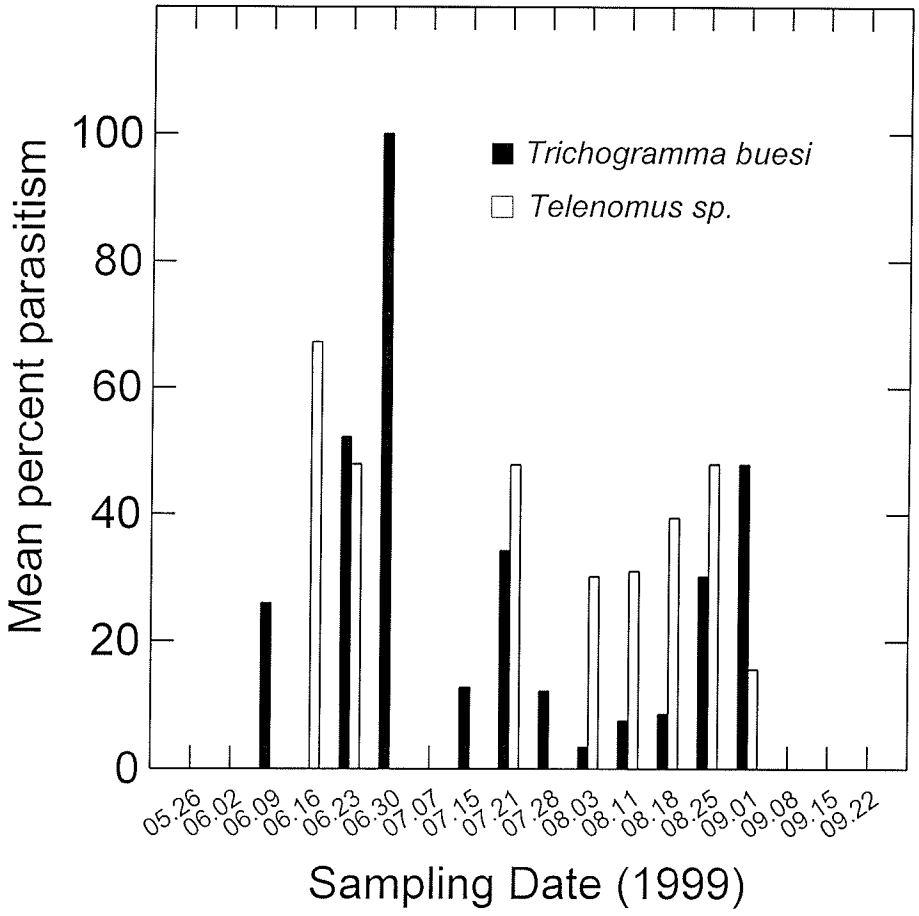

Mean percent parasitism
100
80
60
40
20
0
Trichogramma buesi
Telenomus sp.
05.26
06.02
06.09
06.16
06.23
06.30
07.07
07.15
07.21
07.28
08.03
08.11
08.18
08.25
09.01
09.08
09.15
09.22
Sampling Date (1999)

Table 3.3.6 Percent parasitism of susceptible *Mamestra brassicae* stages in each of five field plots sampled in 1999.

Field plot sampled	Percent of susceptible host stages parasitized (number of susceptible host stages)			
	Trichogramma buesi	*Telenomus sp.*	*Microplitis mediator*	*Exetastes atrator*
A	29% (121)	30% (121)	31% (107)	5% (115)
B	0% (27)	0% (27)	17% (83)	13% (91)
C	12% (1238)	15% (1238)	28% (457)	1% (476)
D	0% (529)	0% (529)	17% (148)	2% (169)
E	11% (3711)	43% (3711)	32% (628)	1% (709)

Figure 3.3.6 Mean weekly parasitism of *Mamestra brassicae* larvae (instars I-IV) by *Microplitis mediator* in five field plots sampled in 1999. Numbers above bars represent percent parasitism of larval instars I-IV by *M. mediator*.

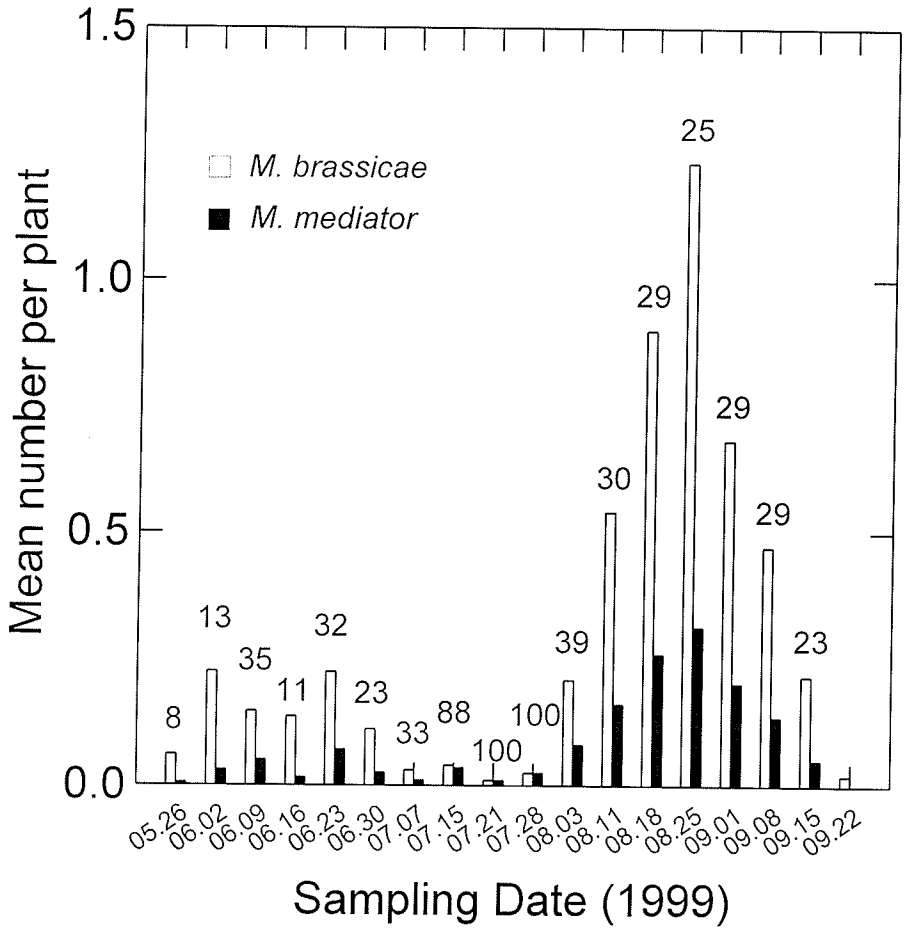

1.5
1.0
0.5
0.0
Mean number per plant
M. brassicae
M. mediator
8
13
35
11
32
23
33
88
100
100
39
30
29
25
29
29
23
05.26
06.02
06.09
06.16
06.23
06.30
07.07
07.15
07.21
07.28
08.03
08.11
08.18
08.25
09.01
09.08
09.15
09.22
Sampling Date (1999)

Table 3.3.7. Mean numbers ± S.E.M. and variance to mean ratios ($s^2/\bar{x}$) of *Mamestra brassicae* eggs, egg masses, and larvae (instars I-VI) per plant for samples taken weekly in five field plots (A-E) in 1999.

Field Plot A

Date of Sample	Eggs per plant		Egg masses per plant	
	$\bar{x}$ ± sem	$s^2/\bar{x}$	$\bar{x}$ ± sem	$s^2/\bar{x}$
May 26	0.22 ± 0.16	10.9***	0.02 ± 0.01	0.9
June 02	0.08 ± 0.08	8.0***	0.01 ± 0.01	1.0
June 09	0.17 ± 0.12	8.7***	0.02 ± 0.01	0.9
June16	0.35 ± 0.35	35.0***	0.01 ± 0.01	0.9
June 23	0.23 ± 0.16	11.4***	0.02 ± 0.01	0.9
June 30	0.16 ± 0.16	16.0***	0.01 ± 0.01	0.9
July 07	.	.	.	.
July 15	0.27 ± 0.21	16.5***	0.02 ± 0.01	0.9
July 21	0.76 ± 0.33	51.7***	0.03 ± 0.02	1.7***

***$P < 0.005$.

Table 3.3.7. continued.

Field Plot B

Date of Sample	Eggs per plant		Egg masses per plant	
	$\bar{x} \pm$ sem	$s^2/\bar{x}$	$\bar{x} \pm$ sem	$s^2/\bar{x}$
May 26	.	.	.	.
June 2	.	.	.	.
June 9	0.10±0.10	10.0***	0.01±0.01	1.0
June16	0.17±0.17	16.9***	0.01±0.01	1.0
June 23	.	.	.	.
June 30	.	.	.	.
July 7	.	.	.	.

***$P < 0.005$.

Table 3.3.7. continued.

Field Plot C

Date of Sample	Eggs per plant		Egg masses per plant	
	$\bar{x}$ ± sem	$s^2/\bar{x}$	$\bar{x}$ ± sem	$s^2/\bar{x}$
July 15	0.28±0.21	15.0***	0.02±0.01	0.9
July 21	0.35±0.25	18.5***	0.03±0.02	1.7***
July 28	2.05±0.85	34.9***	0.12±0.04	1.2
Aug. 3	3.46±0.86	21.5***	0.23±0.05	0.9
Aug. 11	4.46±1.41	44.3***	0.16±0.04	1.1
Aug. 18	1.18±0.71	42.8***	0.03±0.02	0.9
Aug. 25	0.60±0.46	34.5***	0.03±0.02	1.7***
Sept. 1	.	.	.	.
Sept 8	.	.	.	.

***P < 0.005.

Table 3.3.7. continued.

Field Plot D

Date of Sample	Eggs per plant		Egg masses per plant	
	$\bar{x} \pm$ sem	$s^2/\bar{x}$	$\bar{x} \pm$ sem	$s^2/\bar{x}$
Aug. 3	1.10±0.48	20.5***	0.06±0.02	0.9
Aug. 11	2.39±0.91	35.0***	0.10±0.03	1.1
Aug. 18	1.49±0.69	31.7***	0.05±0.02	0.9
Aug. 25	0.34±0.25	18.3***	0.02±0.01	0.9
Sept. 1	.	.	.	.
Sept 8	.	.	.	.
Sept.15	.	.	.	.
Sept. 22	.	.	.	.

***$P < 0.005$.

Table 3.3.7. continued.

Field Plot E

Date of Sample	Eggs per plant		Egg masses per plant	
	$\bar{x}$ ± sem	$s^2/\bar{x}$	$\bar{x}$ ± sem	$s^2/\bar{x}$
July 28	0.68±0.37	19.9***	0.04±0.02	0.9
Aug 03	7.22±1.37	26.0***	0.38±0.06	1.1
Aug 11	13.11±2.04	31.6***	0.70±0.10	1.3**
Aug 18	10.08±1.79	31.9***	0.41±0.06	0.9
Aug 25	5.12±1.20	28.2***	0.25±0.05	1.1
Sept 1	0.90±0.46	23.9***	0.07±0.04	1.8***
Sept 8	.	.	.	.
Sept 15	.	.	.	.

**P < 0.01, ***P < 0.005.

Table 3.3.7. continued.

Field Plot A

Date of Sample	Larvae per plant, Instar I		Instar II		Instar III		Instar IV		Instar V		Instar VI	
	$\bar{x}$ ± sem	$s^2/\bar{x}$	$\bar{x}$ ± sem	$s^2/\bar{x}$	$\bar{x}$ ± sem	$s^2/\bar{x}$	$\bar{x}$ ± sem	$s^2/\bar{x}$	$\bar{x}$ ± sem	$s^2/\bar{x}$	$\bar{x}$ ± sem	$s^2/\bar{x}$
May 26	0.12±0.06	3.1***	.	.	.	.	.	.	.	.	.	
June 02	0.21±0.18	15.6***	0.03±0.02	0.9	0.03±0.02	0.9	.	.	.	.	.	
June 09	0.07±0.54	4.1***	0.11±0.04	1.6***	0.02±0.01	0.9	.	.	.	.	.	
June16	0.01±0.01	1.0	0.06±0.04	2.9***	.	.	0.03±0.02	0.9	0.01±0.01	1.0	.	
June 23	0.02±0.01	0.9	0.07±0.04	2.7***	0.06±0.04	1.9***	.	.	.	.	.	
June 30	.	.	0.04±0.03	1.5**	0.05±0.03	1.8***	0.04±0.02	0.9	0.03±0.02	0.9	0.01±0.01	1.0
July 07	.	.	.	.	0.02±0.01	0.9	0.02±0.01	0.9	0.01±0.01	1.0	.	
July 15	.	.	.	.	0.02±0.01	0.9	0.04±0.03	1.5**	0.01±0.01	1.0	.	
July 21	.	.	.	.	.	.	0.01±0.01	1.0	0.01±0.01	1.0	0.01±0.01	1.0

**P < 0.01, ***P < 0.005.

Table 3.3.7. continued.

Field Plot B

Date of Sample	Larvae per plant Instar I $\bar{x} \pm$ sem	 $s^2/\bar{x}$	 II $\bar{x} \pm$ sem	 $s^2/\bar{x}$	 III $\bar{x} \pm$ sem	 $s^2/\bar{x}$	 IV $\bar{x} \pm$ sem	 $s^2/\bar{x}$	 V $\bar{x} \pm$ sem	 $s^2/\bar{x}$	 VI $\bar{x} \pm$ sem	 $s^2/\bar{x}$
May 26	.	.	.	.	.	.	.	.	.	.		
June 02	0.17±0.11	6.9***	0.01±0.01	1.0	.	.	.	.	.	.		
June 09	0.04±0.03	2.5***	0.03±0.02	0.9	0.02±0.01	0.9	.	.	.	.		
June16	0.02±0.01	0.9	0.07±0.04	1.8***	0.02±0.01	0.9	0.06±0.02	0.9	.	.		
June 23	0.01±0.01	1.0	0.07±0.04	1.8***	0.10±0.03	0.9	0.11±0.03	0.9	0.03±0.02	0.9	0.01±0.01	1.0
June 30	.	.	0.02±0.02	0.9	0.06±0.03	1.6***	0.01±0.01	1.0	0.03±0.02	0.9	0.01±0.01	1.0
July 07	.	.	.	.	0.01±0.01	1.0	0.01±0.01	1.0	0.01±0.01	1.0	0.01±0.01	1.0

***P < 0.005.

Table 3.3.7. continued.

Field Plot C

Date of Sample	Larvae per plant — Instar I $\bar{x}$ ± sem	I $s^2/\bar{x}$	II $\bar{x}$ ± sem	II $s^2/\bar{x}$	III $\bar{x}$ ± sem	III $s^2/\bar{x}$	IV $\bar{x}$ ± sem	IV $s^2/\bar{x}$	V $\bar{x}$ ± sem	V $s^2/\bar{x}$	VI $\bar{x}$ ± sem	VI $s^2/\bar{x}$
July 15	.	.	0.01±0.01	1.0	0.01±0.01	1.0	.	.	.	.	.	.
July 21	.	.	.	.	0.01±0.01	1.0	.	.	.	.	.	.
July 28	.	.	0.01±0.01	1.0	.	.	0.03±0.02	1.7***	.	.	.	.
Aug. 3	0.22±0.11	5.7***	0.04±0.03	2.5***	0.03±0.02	0.9	.	.	.	.	.	.
Aug. 11	0.48±0.23	11.3***	0.15±0.04	1.3*	0.10±0.04	1.5***	0.02±0.01	0.9	.	.	.	.
Aug. 18	0.48±0.28	16.9***	0.54±0.10	1.8***	0.36±0.07	1.3**	0.03±0.02	0.9	.	.	.	.
Aug. 25	0.34±0.11	3.3***	0.30±0.07	1.7***	0.62±0.12	2.3***	0.13±0.05	1.8***	0.01±0.01	1.0	.	.
Sept. 1	.	.	0.04±0.02	0.9	0.21±0.06	1.9***	0.32±0.07	1.5***	0.08±0.03	0.9	0.01±0.01	1.0
Sept 8	.	.	.	.	0.03±0.02	0.9	0.13±0.05	1.1	0.15±0.05	1.1	0.30±0.07	1.1

*P < 0.05, **P < 0.01, ***P < 0.005.

Table 3.3.7. continued

Field Plot D

Larvae per plant

	Instar											
	I		II		III		IV		V		VI	
Date of Sample	$\bar{x} \pm$ sem	$s^2/\bar{x}$	$\bar{x} \pm$ sem	$s^2/\bar{x}$	$\bar{x} \pm$ sem	$s^2/\bar{x}$	$\bar{x} \pm$ sem	$s^2/\bar{x}$	$\bar{x} \pm$ sem	$s^2/\bar{x}$	$\bar{x} \pm$ sem	$s^2/\bar{x}$
Aug. 3	0.11±0.08	5.5***	0.03±0.02	1.7***	0.02±0.01	0.9	0.02±0.01	0.9	.	.	.	.
Aug. 11	0.12±0.05	1.9***	0.06±0.03	1.3*	0.04±0.02	0.9	.	.	.	.	.	.
Aug. 18	0.06±0.04	1.9***	0.05±0.02	0.9	0.02±0.01	0.9	0.01±0.01	1.0	0.01±0.01	1.0	.	.
Aug. 25	0.21±0.10	4.3***	0.12±0.05	1.7***	0.06±0.04	1.9***	0.08±0.05	2.7***	.	.	0.01±0.01	1.0
Sept. 1	.	.	0.04±0.02	0.9	0.07±0.03	0.9	0.11±0.04	1.3***	0.05±0.02	0.9	0.01±0.01	1.0
Sept 8	.	.	0.03±0.02	0.9	0.01±0.01	1.0	0.12±0.03	0.9	0.05±0.02	0.9	0.02±0.01	0.9
Sept.15	.	.	.	.	0.02±0.01	0.9	0.05±0.02	0.9	0.09±0.03	1.1	0.08±0.03	0.9
Sept. 22	.	.	.	.	.	.	0.02±0.01	0.9	0.01±0.01	1.0	0.08±0.03	0.9

*** $P < 0.005$.

Table 3.3.7. continued.

Field Plot E

Larvae per plant

	Instar											
	I		II		III		IV		V		VI	
Date of Sample	$\bar{x} \pm$ sem	$s^2/\bar{x}$	$\bar{x} \pm$ sem	$s^2/\bar{x}$	$\bar{x} \pm$ sem	$s^2/\bar{x}$	$\bar{x} \pm$ sem	$s^2/\bar{x}$	$\bar{x} \pm$ sem	$s^2/\bar{x}$	$\bar{x} \pm$ sem	$s^2/\bar{x}$
July 28	.	.	0.01±0.01	1.0	.		.		.	.	.	.
Aug 03	0.10±0.04	1.5^{***}	0.05±0.03	1.4^{**}	.		.		.	.	.	.
Aug 11	0.51±0.15	4.3^{***}	0.05±0.03	1.4^{**}	0.07±0.03	0.9	0.02±0.01	0.9	.	.	.	.
Aug 18	0.67±0.17	4.2^{***}	0.31±0.08	2.2^{***}	0.15±0.05	1.4^{**}	0.01±0.01	1.0	.	.	.	.
Aug 25	0.77±0.23	6.6^{***}	0.54±0.12	2.5^{***}	0.44±0.07	1.2	0.07±0.03	0.9	.	.	.	.
Sept 1	0.08±0.04	2.4^{***}	0.28±0.10	3.4^{***}	0.60±0.09	1.4^{**}	0.29±0.07	1.6^{***}	0.04±0.02	0.9	.	.
Sept 8	.	.	0.02±0.01	0.9	0.25±0.07	2.1^{***}	0.69±0.11	1.8^{***}	0.33±0.06	1.0	0.05±0.02	0.9
Sept 15	.	.	.	.	0.05±0.03	2.2^{***}	0.31±0.06	1.3^{*}	0.38±0.09	2.4^{***}	0.40±0.07	1.4^{**}

$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.005$.

Table 3.3.8 Estimates of parasitism for terms fitted by binomial logistic regression, modeling probability of parasitism by *Microplitis mediator* for plants infested with the same instar of *Mamestra brassicae*, including estimated percent parasitism (%), the mean number of larvae per plant (± S.E.M) and the total number of *M. brassicae* larvae sampled in field plots.

Terms tested	Instar of *M. brassicae* larvae															
	I				II				III				IV			
	Estimates of parasitism		Mean number of larvae/plant ±S.E.M	Total number of larvae	Estimates of parasitism		Mean number of larvae/plant ±S.E.M	Total number of larvae	Estimates of parasitism		Mean number of larvae/plant ±S.E.M	Total number of larvae	Estimates of parasitism		Mean number of larvae/plant ±S.E.M	Total number of larvae
	Logit parameter	%[a]			Logit parameter	%[a]			Logit parameter	%[a]			Logit parameter	%[a]		
Constant	-1.684	12%	-	-	-0.214	36%	-	-	-0.326	29%	-	-	-1.489	13%	-	-
Field A	1.025	27%	3.3 ± 1.3	43	0.228	42%	1.6 ± 0.2	31	1.353	62%	1.3 ± 0.1	20	1.936	51%	1.1 ± 0.1	14
B	-0.100	11%	2.7 ± 0.9	24	-2.104	6%	1.3 ± 0.2	20	-0.270	24%	1.1± 0.1	21	1.475	40%	1.0± 0.0	19
C	1.682	41%	3.3 ± 0.7	152	0.106	39%	1.6 ± 0.1	109	0.860	50%	1.6 ± 0.1	136	1.224	34%	1.1± 0.1	61
D	-4.442	0%	1.9 ± 0.4	50	1.120	63%	1.2 ± 0.1	33	-3.206	2%	1.1± 0.1	41	-6.219	0%	1.1± 0.1	41
E	1.835	45%	2.6 ± 0.3	213	0.650	52%	1.9 ± 0.2	126	1.263	60%	1.5 ± 0.1	156	1.584	43%	1.5 ± 0.1	139
Larvae per plant	-0.345	-	2.7 ± 0.3	-	-0.357	-	1.6 ± 0.7	-	-0.550	-	1.4 ± 0.5	-	-0.391	-	1.1± 0.5	-
Significance of model	L.R.χ^2 = 60.9; d.f. = 5; p < 0.005				L.R.χ^2 = 14.0; d.f. = 5; p = 0.015				L.R.χ^2 = 19.3; d.f. = 5; p = 0.002				L.R.χ^2 = 13.4; d.f. = 5; p = 0.02			

[a] predicted estimate for one larva per plant

Figure 3.3.7 Comparison of estimated and observed (± S.E.M.) probability of parasitism by *Microplitis mediator* for plants infested with only first instar larvae of *Mamestra brassicae* for field plot E sampled in 1999. Logit [p]= a + bx; where a = constant + logit parameter for field plot; b = is the logit parameter for the number of larvae of the same instar per plant and; x = the number of larvae per plant.

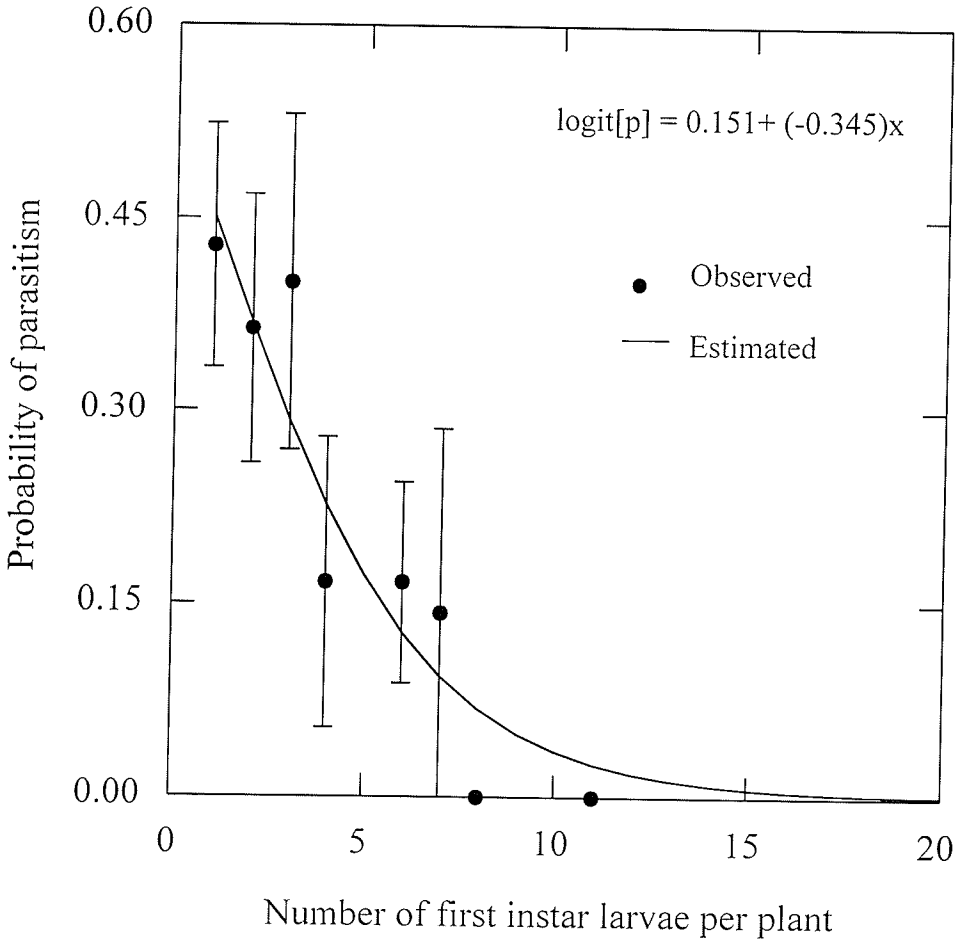

0.60
0.45
0.30
0.15
0.00
Probability of parasitism
logit[p] = 0.151+ (-0.345)x
Observed
Estimated
0
5
10
15
20
Number of first instar larvae per plant

Figure 3.3.8 Comparison of estimated and observed (± S.E.M.) probability of parasitism by *Microplitis mediator* for plants infested with only second instar larvae of *Mamestra brassicae* for C field plot sampled in 1999. Logit [p]= a + bx; where a = constant + logit parameter for field plot; b = is the logit parameter for the number of larvae of the same instar per plant and; x = the number of larvae per plant.

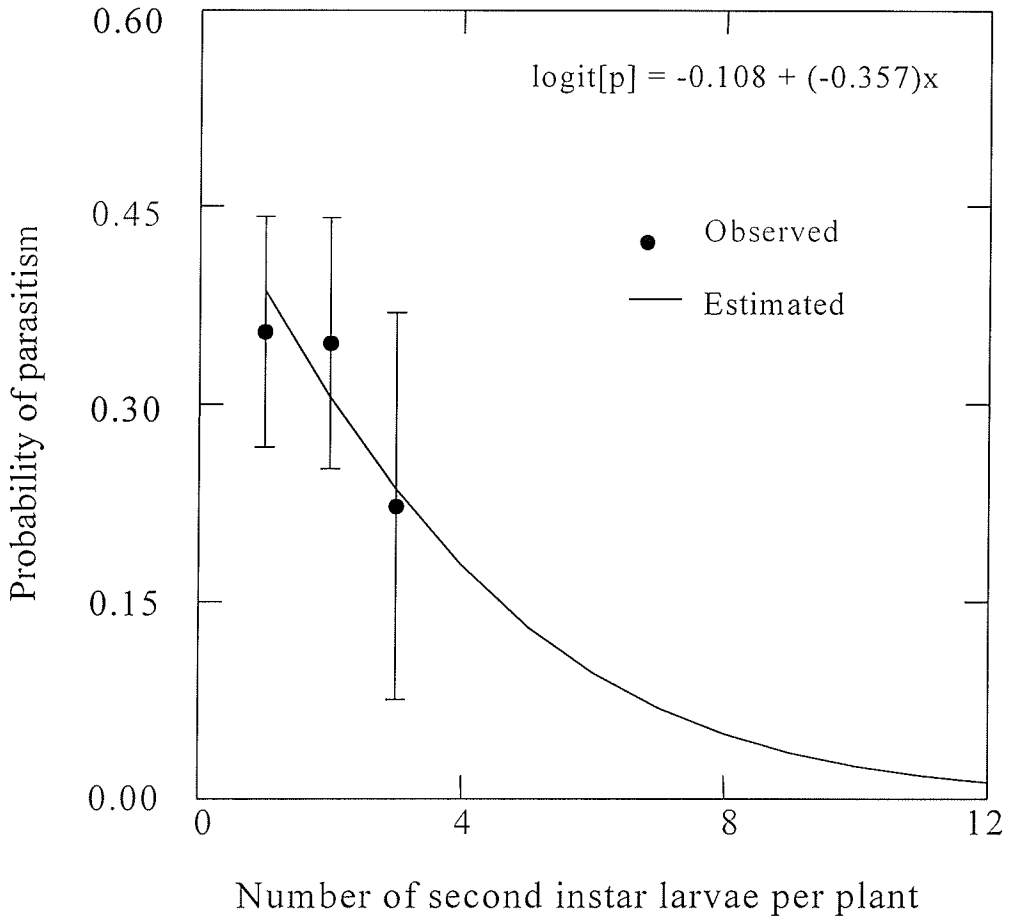

0.60
0.45
0.30
0.15
0.00
Probability of parasitism
logit[p] = -0.108 + (-0.357)x
Observed
Estimated
0
4
8
12
Number of second instar larvae per plant

Figure 3.3.9 Comparison of estimated and observed (± S.E.M.) probability of parasitism by *Microplitis mediator* for plants infested with only third instar larvae of *Mamestra brassicae* for field plot C sampled in 1999. Logit [p]= a + bx; where a = constant + logit parameter for field plot; b = is the logit parameter for the number of larvae of the same instar per plant and; x = the number of larvae per plant.

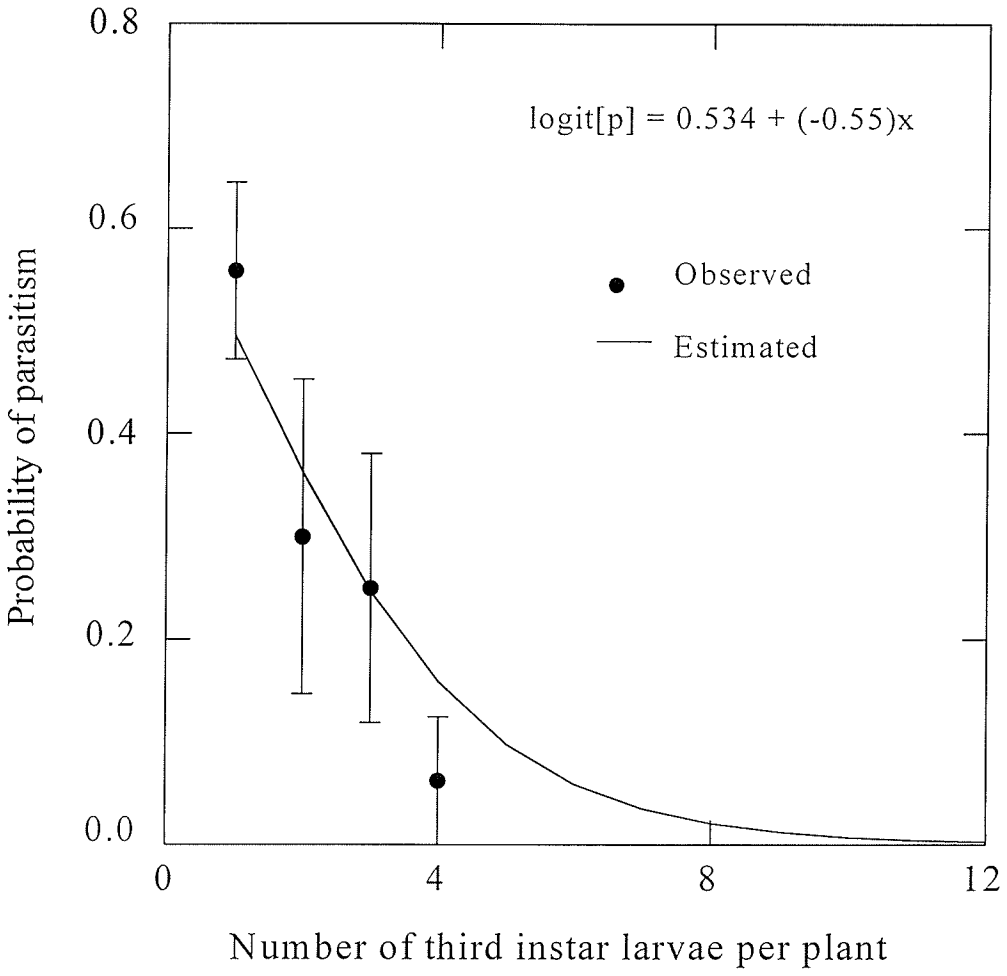

0.8
0.6
0.4
0.2
0.0
Probability of parasitism
logit[p] = 0.534 + (-0.55)x
Observed
Estimated
0
4
8
12
Number of third instar larvae per plant

Figure 3.3.10 Comparison of estimated and observed (± S.E.M.) probability of parasitism by *Microplitis mediator* for plants infested with only fourth instar larvae of *Mamestra brassicae* for field plot E sampled in 1999. Logit [p]= a + bx; where a = constant + logit parameter for field plot; b = is the logit parameter for the number of larvae of the same instar per plant and; x = the number of larvae per plant.

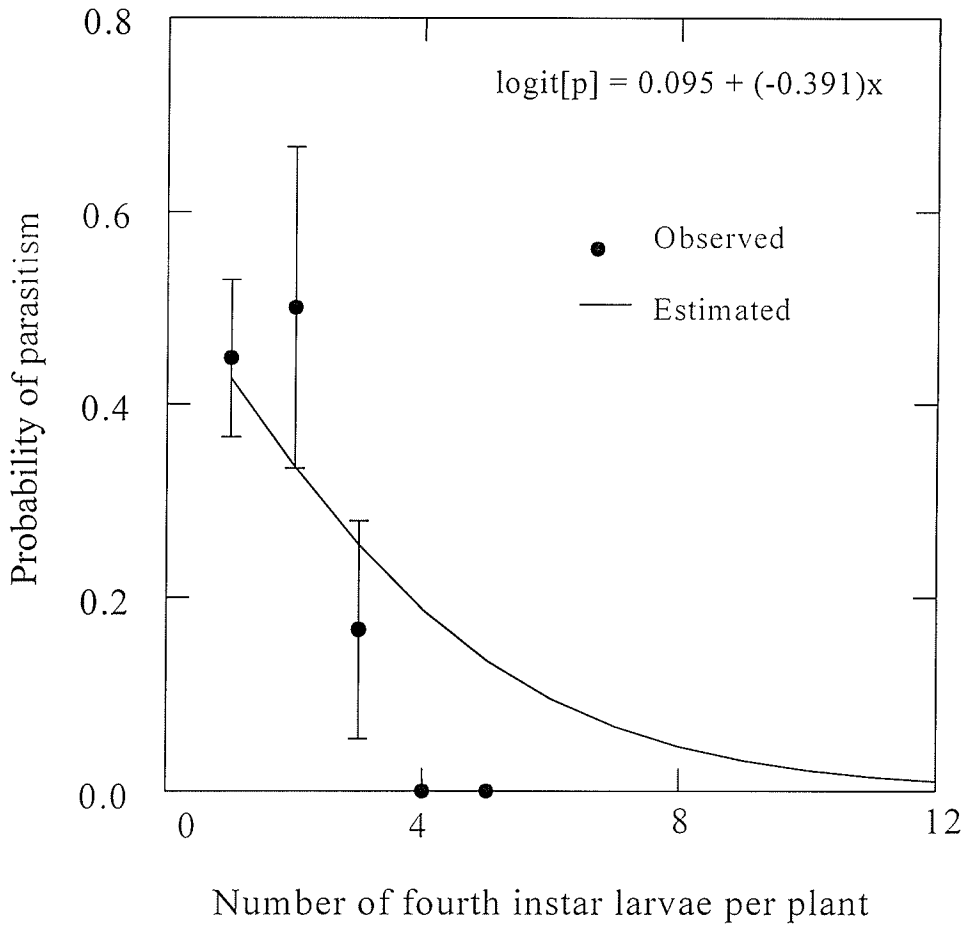

0.8
0.6
0.4
0.2
0.0
Probability of parasitism
logit[p] = 0.095 + (-0.391)x
Observed
Estimated
0
4
8
12
Number of fourth instar larvae per plant

Table 3.3.9 The total number of other lepidopteran larvae collected from plants in the same field plots as *Mamestra brassicae* in 1999 and the total number of these larvae from which *Microplitis mediator* adults were reared from.

Potential Host	Number of larvae collected	Number of *M. mediator*
Plutella xylostella	229	0
Pieris rapae	161	0
Pieris brassicae	38	0
Autographa gamma	23	3

Figure 3.4.1 Seasonal abundance of early larval instars (I-III) of *Mamestra brassicae* for 1998 showing the upper and lower limits of the economic threshold.

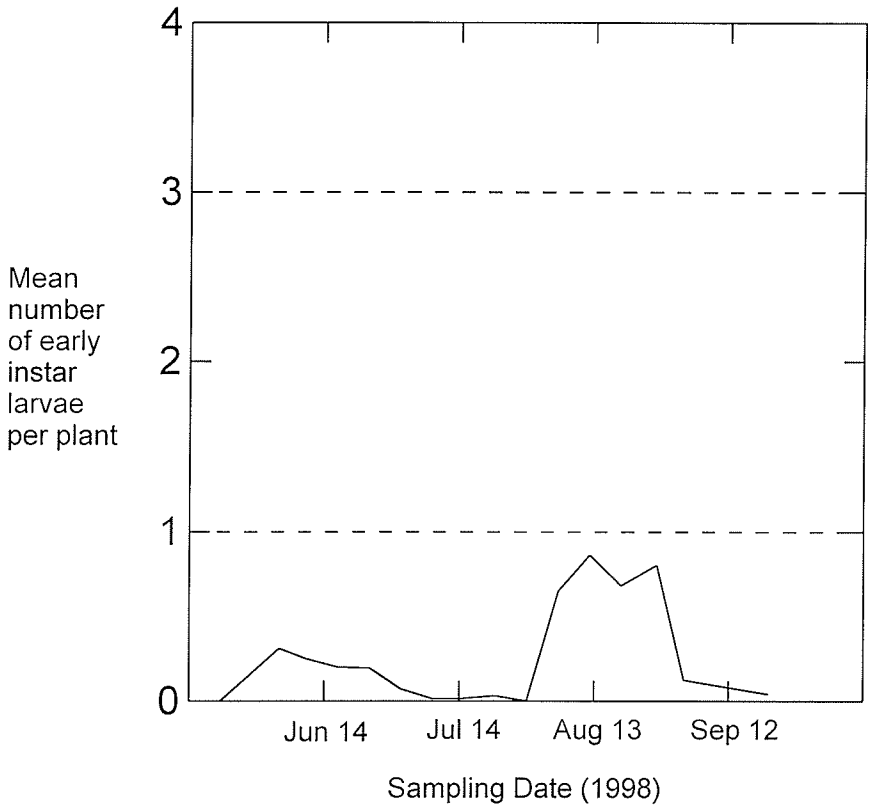

4
3
2
1
0
Mean number of early instar larvae per plant
Jun 14
Jul 14
Aug 13
Sep 12
Sampling Date (1998)

Figure 3.4.2 Seasonal abundance of early larval instars (I-III) of *Mamestra brassicae* for 1999 showing the upper and lower limits of the economic threshold.

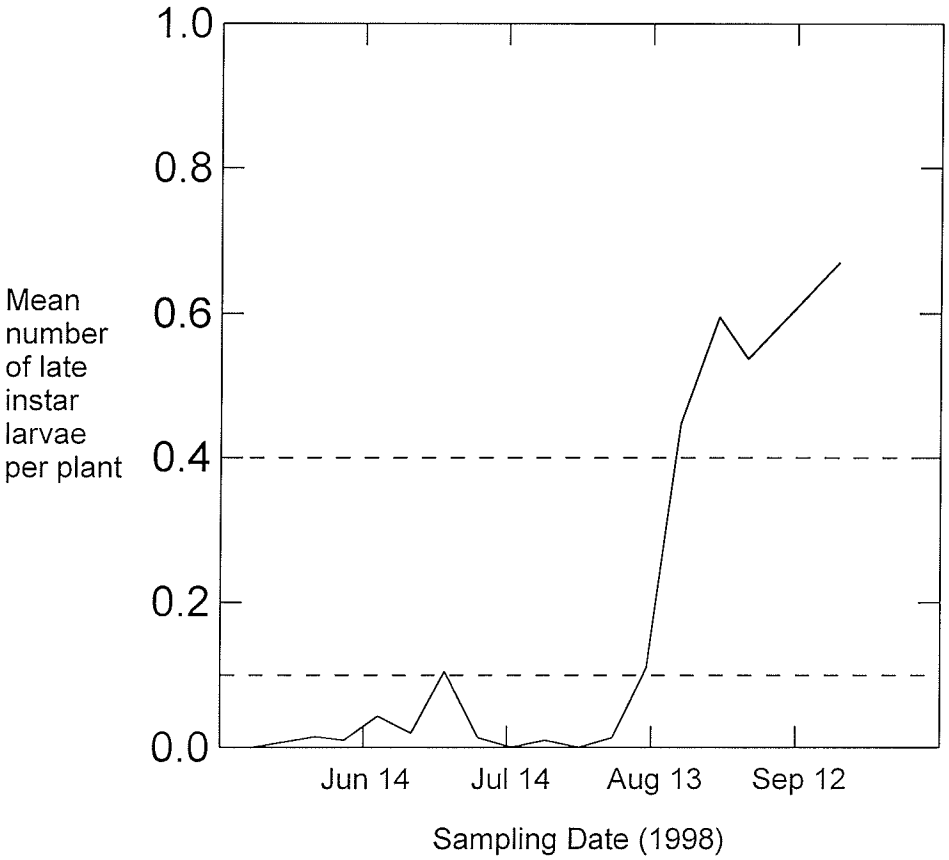

1.0
0.8
0.6
0.4
0.2
0.0
Mean number of late instar larvae per plant
Jun 14
Jul 14
Aug 13
Sep 12
Sampling Date (1998)

Figure 3.4.3 Seasonal abundance of late larval instars (IV-VI) of *Mamestra brassicae* for 1998 showing the upper and lower limits of the economic threshold.

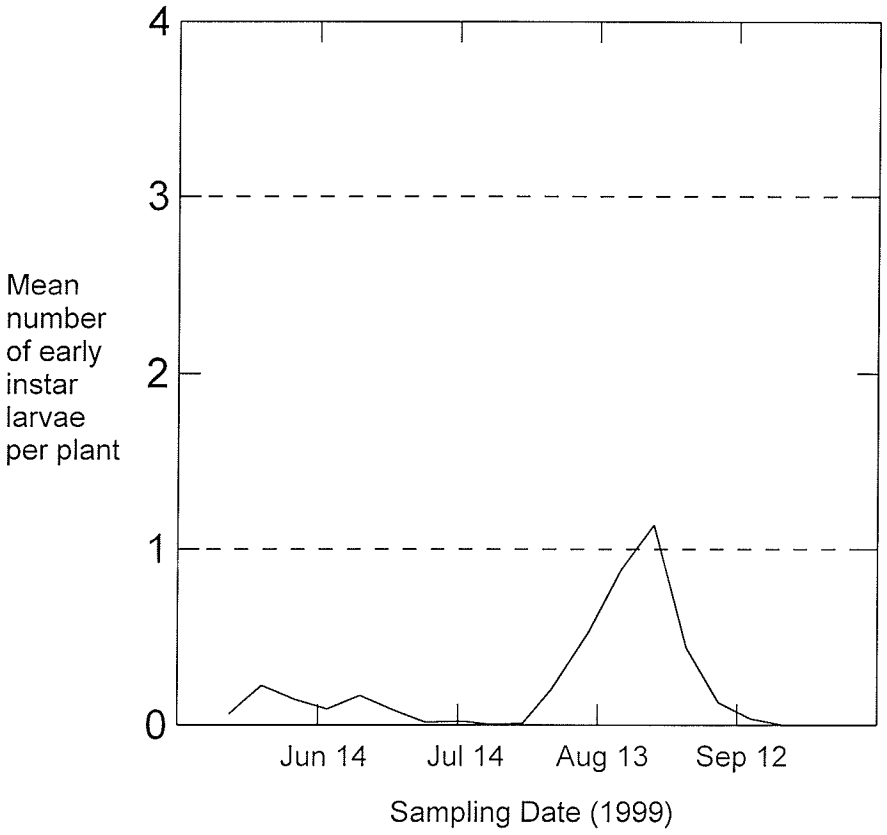
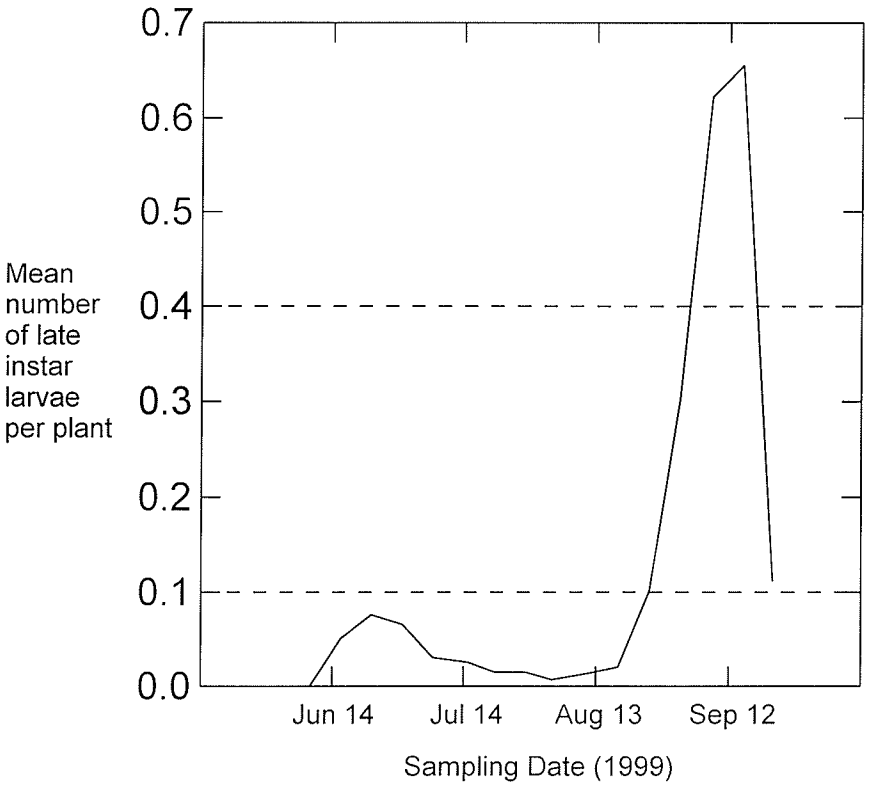

4
3
2
1
0
Mean number of early instar larvae per plant
Jun 14
Jul 14
Aug 13
Sep 12
Sampling Date (1999)

Figure 3.4.4 Seasonal abundance of early larval instars (IV-VI) of *Mamestra brassicae* for 1999 showing the upper and lower limits of the economic threshold.


0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Mean number of late instar larvae per plant
Jun 14
Jul 14
Aug 13
Sep 12
Sampling Date (1999)

Chapter 4: Host choice by a solitary larval endoparasitoid, *Microplitis mediator* (Haliday) (Hymenoptera: Braconidae): host acceptance and host suitability.

Abstract

In 1999, a laboratory study was performed to determine the larval instar of *Mamestra brassicae* L. preferred for egg laying by female *Microplitis mediator*, and the larval instar of *M. brassicae* that was most favourable for survival and development of the parasitoid. These studies were carried out in two forms: no-choice tests, in which female parasitoids were presented with *M. brassicae* larvae one at a time, and choice tests, in which female parasitoids were simultaneously presented with one individual of each of the first three larval instars of *M. brassicae*.

Female parasitoids attacked a high number of hosts in both choice and no-choice tests and showed no preference among instars. Experience with instars decreased the time female parasitoids took to attack hosts in no-choice tests and increased the frequency of attacks on instar I hosts. Dissections of larvae in choice tests showed that not all attacks on hosts resulted in oviposition. Highest egg to attack ratios occurred for instar I and to a lesser extent, instar II. Only 49% of attacks on instar III larvae resulted in oviposition by *M. mediator*. Rearing of larvae in no-choice tests showed that not all attacks on hosts resulted in successful parasitoid development. As with the analysis of oviposition, highest levels of emergence occurred with attacks on instar I and to a lesser extent,

instar II. Only 19% of all attacks on instar III larvae resulted in successful parasitoid emergence.

The results from this study suggest that instar I and to a lesser extent, instar II larvae of *M. brassicae* are highly suitable hosts for *M. mediator*. The host selection behaviour of *M. mediator* is discussed in the context of optimal foraging theory. Implications for biological control using *M. mediator* are presented.

4.1 Introduction

Interactions of hymenopterous parasitoids and their host commonly involve five steps: habitat location, host location, host acceptance, host suitability (Salt, 1941; Doutt, 1959; Vinson and Iwantsch, 1980b), and host regulation (Vinson, 1976; Vinson and Iwantsch, 1980a). Host selection comprises the first three categories and is the result of choices made by searching female parasitoids. Host suitability and host regulation involve the fitness of an immature parasitoid developing within the host. At its most fundamental level, the successful development of an immature parasitoid to the adult stage is the criterion of host suitability and depends on the host's immune system, competition among parasitoids, toxins within the host and the host's nutritional quality (Vinson and Iwantsch, 1980b).

Classical models incorporating optimality theory of host selection predict that searching female parasitoids will accept suitable hosts by rejecting unsuitable habitats and non-hosts (MacArthur and Pianka, 1966; Iwasa, et al. 1984; Miller and Strickler, 1984; Courtney et al., 1989). This prediction is grounded on the principal that host suitability greatly influences reproductive fitness and that female parasitoids develop host selection strategies that maximize reproductive fitness. Although there is evidence to support this prediction (Tillman and Powell, 1989; Brodeur and Vet, 1995; Brodeur et al., 1996; 1998), the cumulation of studies has shown that as suitable hosts are not always accepted by female parasitoids (Shepard et al., 1983; Brodeur et al., 1996), acceptance is

not always closely correlated with host suitability (Temerak, 1983; Caballero et al., 1993; Hailemichael et al., 1994; Wiedenmann and Smith, 1993; Ngi-Song et al., 1995; Brodeur and Vet, 1995; Oliveira et al., 1999).

Microplitis mediator (Haliday) is a solitary larval endoparasitoid reported to attack at least 40 species of lepidopterous hosts in two families: Noctuidae and Geometridae (Nixon, 1970; Shenefelt, 1973). In Central Europe, *M. mediator* is a dominant parasitoid of early instar larvae of the European cabbage moth, *Mamestra brassicae* L. (Lepidoptera: Noctuidae) (Turnock, 1984). Because of its success on *M. brassicae* and potential to utilize a wide range of hosts, *M. mediator* was considered for the biological control of the novel host *Mamestra configurata* Walker (Lepidoptera: Noctuidae) in Canada (Carl and Sommer, 1975; Turnock, 1984; Mason et al., 2001). Though females can successfully parasitize early instars of *M. configurata* larvae (Arthur and Mason, 1986; Pivnick, 1993), despite several releases of *M. mediator* in Canada (Mason and Youngs, 1994; Mason, 1999) the parasitoid has yet to establish on *M. configurata* (Mason et al., 2001). There is little information to explain why *M. mediator* did not establish.

To date there have been no quantitative studies comparing the host selection behaviour of *M. mediator* with the suitability of early instar larvae of either *M. brassicae* or *M. configurata*. Examination of how adult females choose their native host, *M. brassicae*, may assist in establishing biological control of *M.*

configurata by *M. mediator*. Therefore the following laboratory experiments were done to investigate host attacks and acceptance of *M. mediator* on first to third instar larvae of *M. brassicae* and the suitability of these instars for parasitoid development.

4.2 Materials and Methods

4.2.1 Rearing of Hosts. Larvae of *M. brassicae* were collected from broccoli, cauliflower and cabbage fields in the Bielersee region of Switzerland in 1998 and 1999. In the laboratory, larvae were reared in 40 x 30 x 20 cm brown plastic cat litter boxes that had the tops covered by screen (mesh size 0.2 mm). The boxes contained sterilized soil (approximately 4 cm in depth) and organically grown cabbage leaves. Rearing boxes were maintained at room temperature (24 $\pm$1°C) under artificial light conditions of 16:8h L:D. Cabbage leaves were changed three times weekly and soil was cleaned once weekly. Pupae were removed from soil and groups of 20 of the same sex were placed in plastic cylinders (15.5 cm height x 10.5 cm diameter) on top of 6 cm of moistened sifted peat. The peat was sprayed with water daily. Under these conditions, adults emerged from pupae within 22-24 days. Adults were maintained in the same plastic cylinders used for pupae, but for adults, cylinders were lined and sealed with dry paper towels and equipped with a dental wick saturated with a 1:1:5 honey-sucrose-water solution. The parts of paper towels on which egg masses were laid were cut out and placed on moist filter paper. Egg masses were incubated at 24°C and eggs hatched in 4-5 days.

Eggs and larvae were reared continuously until sufficient numbers of larvae were available for the experiments. Head capsule measurements of larvae were used to separate instars, and within instars larvae were selected according to the following age criteria: instar I, 2-4 days; instar II, 7-8 days; instar III, 10-12 days (numbers represent days since hatching from eggs). Instar IV was not selected as preliminary exposures showed that larvae of this instar were too aggressive with *M. mediator* adult females.

4.2.2 Rearing of Parasitoids. *Microplitis mediator* cultures were started from field collected instars I-IV of *M. brassicae* from the Bielersee region of Switzerland in 1998. Adult parasitoids that emerged in the laboratory were placed in 10 cm height x 12 cm diameter transparent cylinders that had the tops covered by screen (mesh size 0.2 mm) for mating. No more than 20 adults, 10 of each sex, were placed in each cylinder. At the bottom of each cylinder were two holes, each 1 cm in diameter, through which dental wicks were inserted. One wick provided a 1:4 honey-water solution and the other provided distilled water. Under light conditions, mated adult female parasitoids were offered laboratory reared larval instar II of *M. brassicae* for parasitization in a 8000 cm^3 container structured of four sides of wood, a facing side of plexiglass and a rear side of woven plastic. Host larvae were reared in groups of 10 on leaves of organically grown white cabbage in 9 x 2 cm Petri dishes at room temperature ($24 \pm 1^{\circ}C$) under artificial light (16:8h L:D). Petri dishes were checked every second day for parasitoid cocoons and cabbage leaves were changed at the

same time. Parasitoid cocoons were carefully removed from Petri dishes with a moistened paintbrush and placed in glass vials containing moistened vermiculite. From the time of parasitization until parasitoid adults emerged was 20-25 days.

4.2.3 Attacks by Parasitoids. The number of host larvae attacked by *M. mediator* was investigated in a no-choice and a choice experiment. An attack was defined as the observed insertion of the parasitoid's ovipositor into the host. In the no-choice experiment, one mated, initially naive female was exposed in a 9 x 2 cm Petri dish to a single host larva (instar I, II or III) for a maximum of 10 minutes (Figure 4.2.1). Each female parasitoid was exposed sequentially to three host larvae, one of each instar. The order of presentation was random. Each sequence of three presentations was termed an experience. In total a female parasitoid had four experiences; thus there were a total of 12 host larvae presented, four of each instar. During each presentation, if the female parasitoid attacked a host larva, or if the maximum time of 10 minutes was met, the presentation was immediately terminated and the host larva was removed to a separate 9 x 2 cm Petri dish for rearing under the standard rearing conditions described above. Observations of an attack and time of attack was recorded. Between presentations the female parasitoid was removed to a 9 x 2 cm Petri dish for one minute of grooming and resting. The experiment was replicated 10 times, each with a different female parasitoid.

For the choice experiment, the experimental arena was the same as for the no-choice experiment but three host larvae (instars I, II and III) were simultaneously presented to a female parasitoid (Figure 4.2.2). A single presentation lasted 30 minutes during which the female parasitoid could repeatedly attack the larvae. Four sequential presentations of three larvae, each separated by a rest period of 10 minutes, constituted a trial. Each presentation equalled one experience. In the choice trials, each observation of an attack was recorded together with the instar attacked. In total, the experiment was replicated 25 times, each with a different female parasitoid.

4.2.4 Oviposition by Parasitoids. The number of attacked host larvae with one or more parasitoid eggs was determined in the choice experiment only. In the three days following each replicate, all attacked host larvae were dissected and examined for parasitoid eggs or encapsulated eggs.

4.2.5 Host Suitability. The number of attacked host larvae suitable for the development of a parasitoid cocoon was examined in the no-choice experiment only. After removal from the experimental arena, host larvae were reared individually as described above until either a parasitoid cocoon emerged or instar V of the host was reached. Instar V larvae were dissected and examined for the presence of any parasitoid development. Parasitoid cocoons were reared individually as described above until an adult parasitoid emerged. The sex of the emerging adult parasitoid was recorded.

4.2.6 Statistical Analysis. Analysis of both experiments was performed by constructing contingency tables and fitting hierarchical log-linear models (Bishop et al. 1975). In each analysis, a 4 (experience) x 3 (instar) x 2 (response variable) contingency table was set up with a total of 24 cells. The log-likelihood ratio chi-squared statistic (L.R.χ^2 = 2Σ[observed no.] x log[observed no. ÷ expected no.]) (Bishop *et. al.,* 1975) was used to investigate the significance of influences on the response variable for the three way interaction (two factor, one response interaction) and for the two way interactions (one factor, one response interaction). An alpha level of $p \leq 0.05$ was used. In the analysis of sex ratio, Δ = 0.5 was added to all cells (Bishop et al., 1975). Analyses of time to attack and numbers of attacks were performed using analysis of variance (ANOVA). Statistical analyses were performed using SYSTAT (Systat, 1999).

4.3 Results

4.3.1 Attacks by Parasitoids

4.3.1.1 No-Choice Experiment. Of the 132 hosts offered to females, approximately 64% were attacked. The frequency of attack was not significantly affected by the instar of the host (L.R.χ^2 = 1.84; d.f. = 2) (Figure 4.3.1), by the experience of the parasitoid (L.R.χ^2 = 0.10; d.f. = 3) or by the interaction of experience and instar (L.R.χ^2 = 5.73; d.f. = 6). The time elapsing from first presentation of the host until attack was influenced by experience (F = 5.23; d.f.

= 3, 80; $p < 0.05$): parasitoid females attacked hosts in less time as they gained experience (Figure 4.3.2).

4.3.1.2 Choice Experiment. Of the 300 hosts offered to female parasitoids, 86% were attacked and received at least one ovipositor probe. The log-linear model selected was based on a marginal fit of the data for the three-way interaction (L.R.χ^2 = 11.85; d.f. = 6; p = 0.065). The frequency of attack was not significantly affected by the instar of the host (L.R.χ^2 = 1.53; d.f. = 2) (Figure 4.3.3) or by parasitoid experience (L.R.χ^2 = 5.86; d.f. = 3). The L.R.χ^2 associated with the three way interaction was partitioned: between less experienced (experience 1 and 2), between more experienced (experience 3 and 4) and the difference between less experienced and more experienced. There was little contribution to the overall L.R.χ^2 of 11.85 between less experienced (L.R.χ^2 = 0.16; d.f. = 2) and between more experienced (L.R.χ^2 = 2.11; d.f. = 2) sub-tables. However, there was a highly significant difference in the response to instar that occurred at the mid-point of the experiment (L.R.χ^2 = 9.58; d.f. = 2; p = 0.0008) (Table 4.3.1). Females with less experience concentrated attacks on instars II and III (L.R.χ^2 = 9.45; d.f. = 2; p = 0.0089) whereas females with more experience attacked instars I, II and III equally (L.R.χ^2 = 1.66; d.f. = 2). However over all instars, more experienced females attacked fewer hosts than less experienced females (L.R.χ^2 = 5.52; d.f. = 1; p = 0.018).

Because *M. mediator* females could attack hosts repeatedly within each experience, the number of attacks per larva could be analyzed. On average, *M. mediator* attacked each larva approximately 1.8 times (Table 4.3.2). The mean number of attacks changed slightly with experience (ANOVA: $F = 2.56$; d.f. = 3, 264; $p = 0.056$) primarily due to a relatively low number of attacks during the third experience. Although there were no differences in the mean number of attacks among instars (ANOVA: $F = 0.14$; d.f. = 2, 264; $p = 0.870$), the interaction of instar over experience was highly significantly different (ANOVA: $F = 3.09$; d.f. = 6, 264; $p = 0.006$) (Figure 4.3.4). As females gained more experience more attacks were concentrated on instar I and less on instars II and III. All three instars had equal probability of being selected for the first attack by *M. mediator* females at the commencement of each of the four experiences (L.R.$\chi^2 = 1.91$; d.f. = 6).

4.3.2 Oviposition by Parasitoids

Of the 258 individual host larvae attacked by females in the choice experiment, approximately 69% contained at least one egg. Neither the interaction of experience and instar (L.R.$\chi^2 = 6.04$; d.f. = 6), nor experience (L.R.$\chi^2 = 4.20$; d.f. = 3) significantly affected the frequency of oviposition in attacked larvae. However, there was a highly significant affect of instar on the frequency of oviposition in attacked larvae (L.R.$\chi^2 = 27.27$; df = 2; $p < 0.001$) (Figure 4.3.5). About 79% of attacked instars I and II contained eggs, but for instar III, only about 49% of attacked larvae contained eggs.

Unlike the number of attacks per larva, the number of eggs per larva was strongly affected by larval instar ($F=7.9$, d.f.=2,264, $p<0.001$) (Table 4.3.2), by experience ($F=2.9$, d.f.=3,264, $P<0.5$) and by the interaction of experience and instar ($F=2.5$, d.f.=6,264, $P<0.05$). Eggs per larva declined from an average of 1.3 ± 0.1 in the first experience to 0.9 ± 0.1 in the fourth experience. As with the interaction for attacks, the main trend is for third instar larvae to receive fewer eggs as parasitoid experience increases (Figure 4.3.6).

4.3.3 Host Suitability

Of the 85 hosts that were attacked in the no-choice experiment, parasitoid cocoons developed from 41%. Attacked larvae in which parasitoid cocoons did not develop showed no evidence of parasitism from dissections. There was no significant effect of the interaction of experience and instar on the frequency of a parasitoid cocoon developing from an attacked larva (L.R.$\chi^2 = 9.67$; d.f. = 6). However, there was a highly significant affect of instar on the frequency of a parasitoid cocoon developing from an attacked larva (L.R.$\chi^2 = 28.53$; d.f. = 2; $p < 0.001$) (Figure 4.3.7). About 76% of attacks on instars I and II resulted in parasitoid cocoons whereas for attacks on instar III, only about 19% resulted in parasitoid cocoons. Although experience had no detectable effect on the frequency of attacks, there was a marginal effect of experience on the probability of a parasitoid cocoon developing from an attacked larvae (L.R.$\chi^2 = 7.87$; d.f. =

3; p = 0.05) (Figure 4.3.8); however this did not show a pattern of behaviour change with increasing experience.

Of the six cocoons produced from instar III, four were female, one was male and one cocoon failed to develop. For instars I and II, 46% of parasitoid cocoons were female. The difference in sex ratio was not significant (L.R.χ^2 = 3.33; d.f. = 2). However, the small number of cocoons that were produced from instar III hosts impaired the sensitivity of this test. There was no significant interaction of experience and host instar with the sex ratio (L.R.χ^2 = 9.67; d.f. = 6).

4.4 Discussion

These studies show that the probability that *M. brassicae* larvae exposed to *M. mediator* females will be attacked, is relatively high. This was especially so in the choice trial. Naive female parasitoids did not discriminate among instars I to III when given either no- choice (Figure 4.3.1) or choice (Figure 4.3.3) of instars. With increasing experience, females attacked larvae in less time in the no-choice trials, and concentrated more single and multiple attacks on first instar larvae in the choice trials.

By concentrating attacks on younger instars, it seems that experienced females are maximizing their reproductive rate. However, multiple attacks for solitary parasitoids are maladaptive, considering that only one immature parasitoid will survive to cocoon formation. For instance, first instar larvae of *M. mediator*

search the haemocel of their host and kill any other parasitoid eggs or larvae found (Arthur and Mason, 1986). Multiple ovipositions by *M. mediator* seem to suggest that the risk of not ovipositing greatly outweighs the risk of wasting eggs by repeatedly attacking a single, available larva. However, multiple attacks on larvae may be an artifact of the experiment that would not occur in the field. Preliminary studies in Switzerland noted that self-superparasitism by *M. mediator* is infrequent in field populations of *M. brassicae* even though up to 5 eggs per host larvae are frequently detected under experimental conditions (Carl and Sommer, 1975).

Based on the number of attacks in the no-choice trials, the selection behaviour we observed with *M. mediator* fails to support the prediction that parasitoids will select only hosts that maximize fitness since not all attacked larvae were equally suitable for immature parasitoid development. This was particularly notable for attacks made on instar III where only 19% of attacks resulted in a parasitoid cocoon (Figure 4.3.7). By dissecting attacked larvae in the choice experiment we were able to address whether this result was due to differences in the survival of developing immature parasitoids in different host instars or whether *M. mediator* females failed to oviposit, especially in instar III. Since the dissections did not show any evidence of egg encapsulation within the first three days after attack, our results suggest that not all attacks result in oviposition. Highest ratios of egg to attack occurred most frequently with instar I and to a lesser extent, instar II. Again the largest discrepancy was that seen for instar III where only 45

and 49% of single and multiple attacks respectively, resulted in oviposition (Table 4.3.2 and Figure 4.3.5 respectively).

Failing encapsulation within the first three days after an attack, it is unclear why the number of eggs per attack was low in instar III and substantially higher in instar I and II. Host selection strategies of parasitoids have been shown to be influenced by visual (Eller et al., 1990; Hailemichael et al., 1994; Wackers and Lewis, 1994; Battaglia et al., 1995; Howard et al., 1998; Powell et al., 1998; Wackers and Lewis, 1994), chemical (Dicke, 1999) and behavioural attributes of the host (Gross, 1993; Brodeur et al., 1996; 1998; Lei and Camara 1999; Meyhofer and Casas, 1999; Potting et al., 1999). Female parasitoids have been reported to assess the suitability of larvae during an attack by probing the host with their ovipositor, which is equipped with specialized sensillae (Fisher, 1971). Though experienced *M. mediator* females did show some degree of avoidance of instar III in our analysis of attacks and in our analysis of multiple ovipositions, it is unlikely that *M. mediator* exclusively assesses suitability in this manner. It seems that host assessment by *M. mediator* is imperfectly related to suitability since females oviposited more frequently than expected from the low cocoon production in instar III.

A second possibility is based on the assortment of host defensive behaviours of *M. brassicae* larvae. In both experiments, third instars tended to be more physically aggressive with female parasitoids than either first or second instars,

and were often observed biting approaching female parasitoids. Such aggressive behaviour has been shown to repel attacks and oviposition attempts in female parasitoids (Brodeur et al., 1996), increase parasitoid grooming time (Lei and Camara, 1999) and increase the risk of parasitoid injury or death (Iwasa et al., 1984; Potting et al., 1999). Instars I and II did not respond to parasitoid attacks in the same manner as instar III. This could account for the high frequency of successful attacks seen in instars I and II relative to instar III. Some host defensive behaviours (Gross, 1993), such as escape responses, may have been inhibited by the conditions of our experiments.

Based on the eggs deposited per attack in the different instars in the choice experiment, it is possible to evaluate the reasons for the low cocoon production in the no-choice experiment. This can be done by using the number of eggs to attacks from Table 4.3.2 to predict the number of attacks in the no-choice trial that resulted in oviposition. This prediction can be compared with the observed cocoon emergence from Figure 4.3.7. It is notable that, for instars I and II, the observed percentage of attacked hosts producing cocoons is very similar to the predicted percentage of attacked hosts in which eggs were laid (Table 4.4.1). However, there is a considerable discrepancy in the observed and predicted values for the third instar: 6 of the 30 attacked larvae produced cocoons, whereas it is predicted that 13 of the attacked larvae would have received eggs. This suggests that the low frequency of cocoon production for instar III may be a result of the failure of immature parasitoids to develop to cocoon formation.

Parasitized hosts can exhibit immunological responses that result in encapsulation of the developing parasitoid (Vinson and Iwantsch, 1980a) or other means of destruction of the developing parasitoid such as by cuticular encystment (Arthur and Ewen, 1975) or inadequate nutrition (Vinson and Iwantsch, 1980b)

The present study indicates that instar I and to a lesser extent, instar II are most suitable hosts for *M. mediator*. The frequency of their acceptance nearly matches their suitability, even though the high frequency at which instar I and II were attacked may be an artifact of the experimental design. In contrast, instar III is only marginally suitable as a host for *M. mediator*. The low production of parasitoid cocoons from instar III appears to be a result of the failure of *M. mediator* to oviposit during an attack and the failure of immature parasitoids to develop to maturity. However, *M. mediator* females showed little discrimination among instars when attacking and ovipositing within larvae. This suggests that *M. mediator* is not an optimal forager according to classical models of host selection.

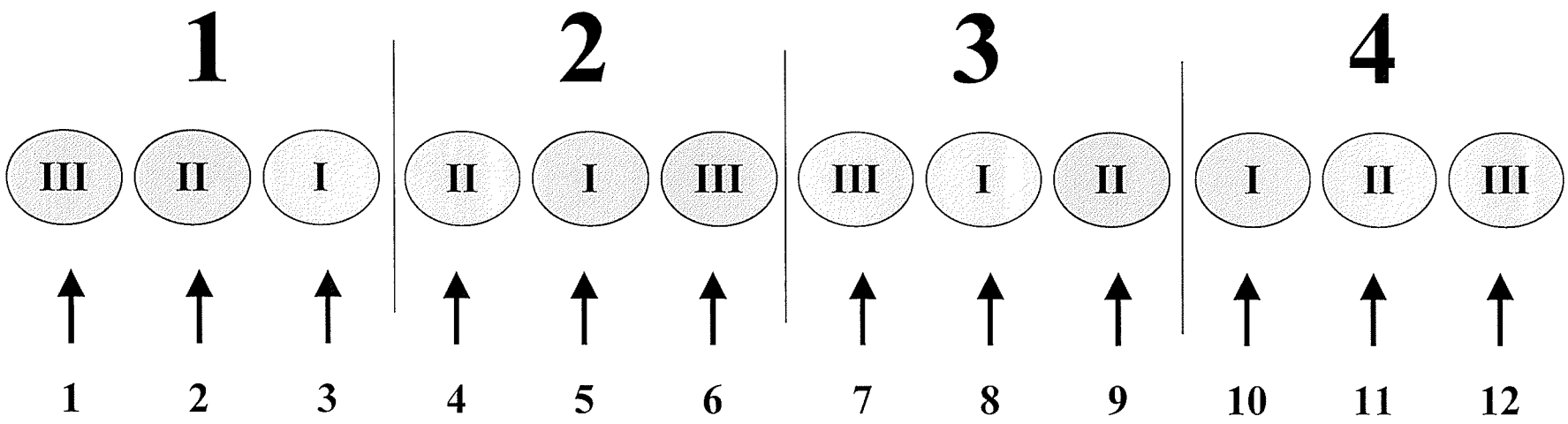
The selection of marginal hosts carries some negative consequences. For example, a reduced probability that offspring will survive (Vinson, 1976), a diminished egg load (Heimpel et al., 1996), lost searching opportunities for more suitable hosts (Sait et al., 1997) and the risk of injury while the parasitoid is attempting to subdue the host (Brodeur et al. 1996). However, the selection of

marginal hosts by parasitoid females is not an unusual one in the laboratory (Temerak, 1983; Shepard et al. 1983; Caballero et al., 1993; Hailemichael et al. 1994; Ngi-Song et al. 1995; Brodeur and Vet 1995; Oliveira et al. 1999). Researchers have hypothesized that female parasitoids equate larger sized hosts with a higher quality of resource for the developing immature parasitoids (Vinson and Iwantsch, 1980b; Charnov et al., 1981). According to Charnov et al.'s (1981) hypothesis, this is most pronounced for the development of female progeny. The results from this study provide some support for this, since female progeny developed from four out of the five developing cocoons emerging from instar III larvae.

In the field, it is likely that other attributes of the host are important regulators of host acceptance behaviour for *M. mediator*. Recent models of host selection predict that host selection behaviour of parasitoids will change with the availability of hosts. Because the availability of suitable host stages varies temporally and spatially, female parasitoids are expected to develop host selection strategies that ensure reproductive success. Hence the acceptance of a marginal host can be viewed as favorable to the individual parasitoid when the frequency of host encounters is low, which is likely to occur during periods of low host abundance (Strand and Obrycki, 1996). Of vital importance is the synchrony of the parasitoid with predominantly suitable stages of the host, which is likely to occur for parasitoids with long-standing association with a host.

In Central Europe, *M. mediator* is the predominant parasitoid reared from early instar larvae in two generations of *M. brassicae*. In both generations, female parasitoids searching in the field are likely to be confronted with choice situations in which several instars of host larvae are available simultaneously and no-choice situations in which a single instar is available. If the laboratory results are applicable to this situation then it appears that in no-choice situations and for inexperienced females in choice situations there may be inefficiency of reproduction and killing power associated with the lack of differentiation among host instars. If the parasitoid is not synchronized with suitable host stages, as is likely to occur when introduced to a new host under a new climatic regime this may contribute to the difficulty of establishing *M. mediator* for the biological control of bertha armyworm in Canada. If this is so, synchronization of host and parasitoid generations is of paramount importance, and initial releases at the time of a bertha armyworm outbreak may also be helpful.

Figure 4.2.1 Schematic illustration of the methodology used to investigate the number of *Mamestra brassicae* larvae attacked by *Microplitis mediator* in no-choice exposures. Shaded circles represent the experimental arena. Numbers contained within shaded circles represent *M. brassicae* instars I-III. Numbers above shaded circles (1-4) represent a maximum 30-minute experience with host instars. Numbers below arrows (1-12) represent a maximum 10-minute experience with host instars and the sequence of offerings to *M. mediator* females.


1
2
3
4
III
II
I
II
I
III
III
I
II
I
II
III
1
2
3
4
5
6
7
8
9
10
11
12

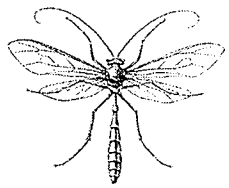
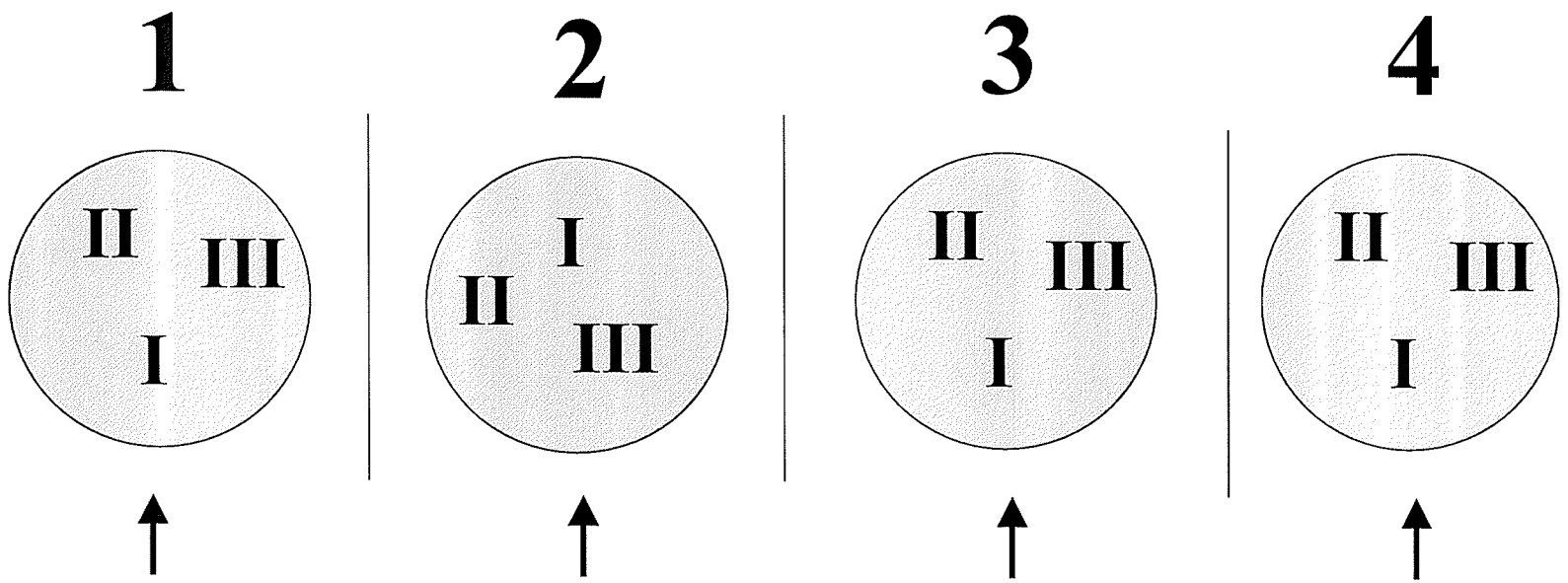


Figure 4.2.2 Schematic illustration of the methodology used to investigate the number of *Mamestra brassicae* larvae attacked by *Microplitis mediator* in choice exposures. Shaded circles represent the experimental arena. Numbers contained within shaded circles represent *M. brassicae* instars I-III. Numbers (1-4) above shaded circles represent a 30-minute experience with host instars and the sequence of offering to *M. mediator* females.


1
II
III
I
2
I
II
III
3
II
III
I
4
II
III
I

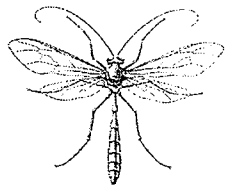


Figure 4.3.1 Percent (± S.E.M) of first, second and third instar larvae of *Mamestra brassicae* attacked by *Microplitis mediator* females in the no-choice experiment. Numbers above S.E.M. bars represent the number of attacks from a potential 44 for each host instar.

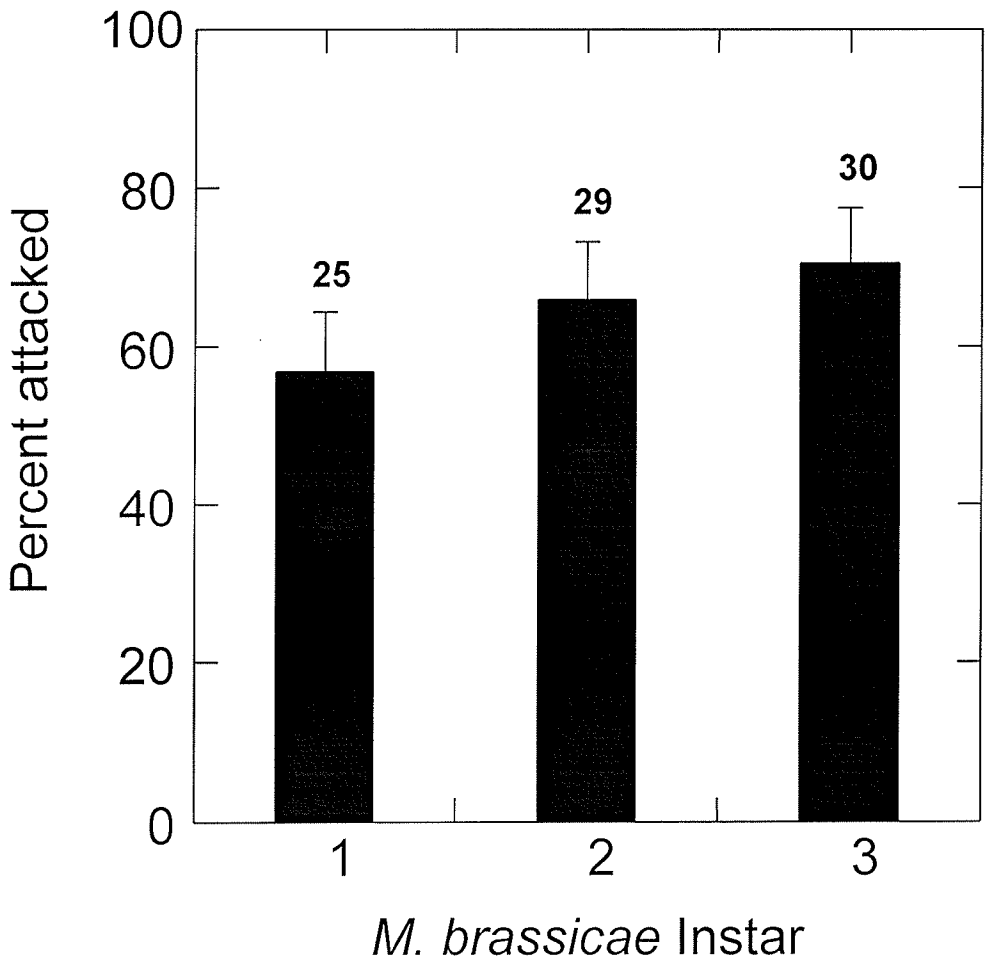

100
80
60
40
20
0
Percent attacked
25
29
30
1
2
3
M. brassicae Instar

Figure 4.3.2 Average time (s) (± S.E.M) in each of four experiences for *Microplitis mediator* to attack one larva of *Mamestra brassicae* in the no-choice experiment.

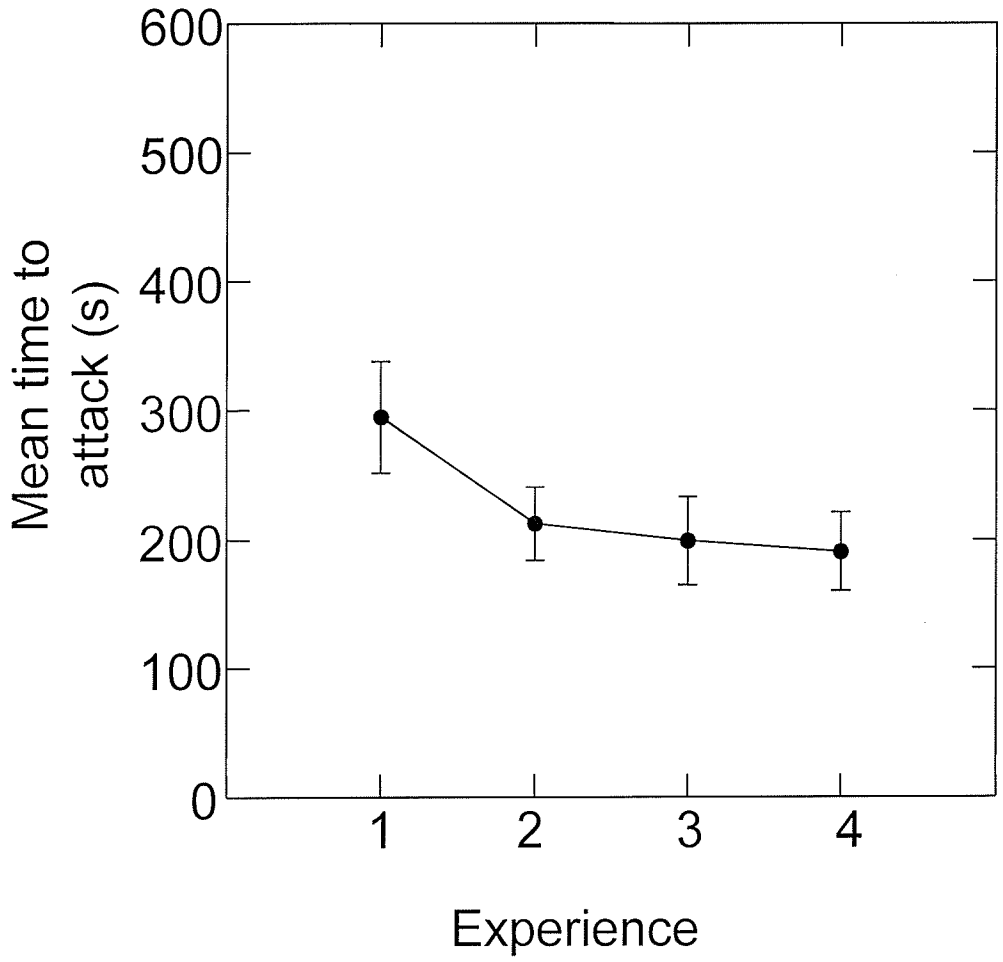

600
500
400
300
200
100
0
Mean time to attack (s)
1
2
3
4
Experience

Figure 4.3.3 Percent (± S.E.M) of first, second and third instar larvae of *Mamestra brassicae* attacked by *Microplitis mediator* females in the choice experiment. Numbers above S.E.M. bars represent the number of attacks from a potential 100 for each host instar.

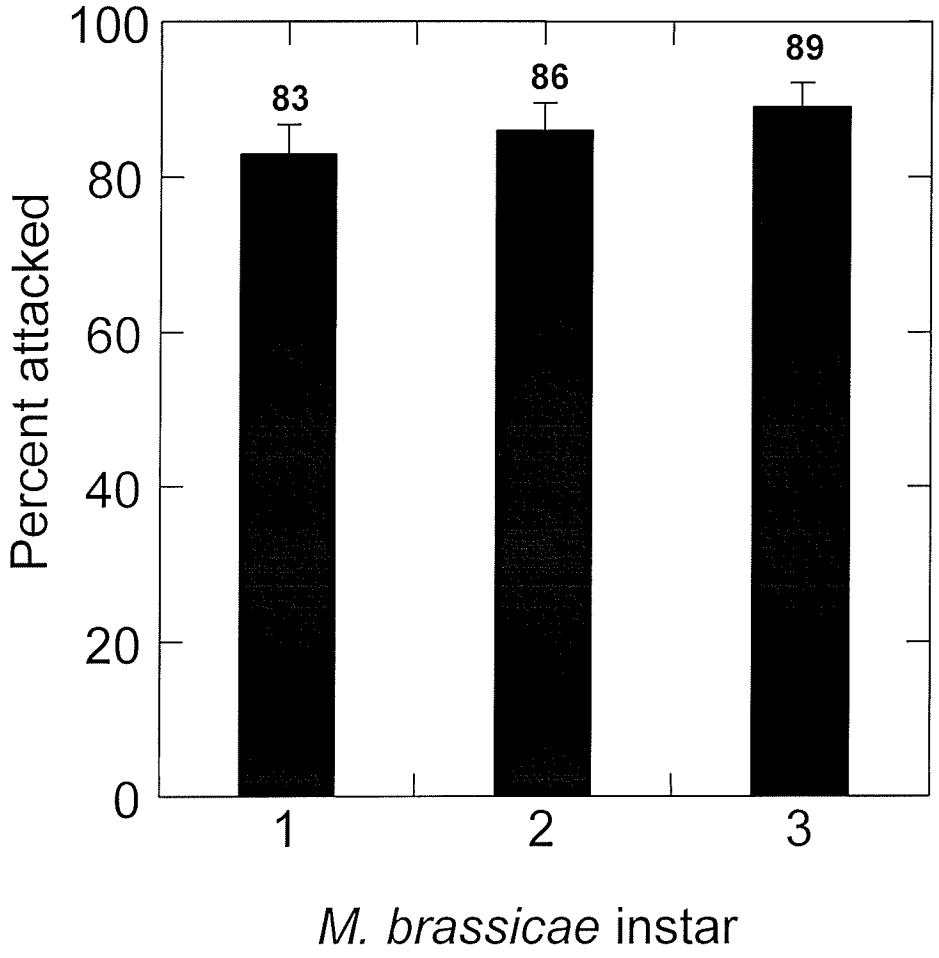

100
80
60
40
20
0
Percent attacked
83
86
89
1
2
3
M. brassicae instar

Table 4.3.1 Effect of experience with *Mamestra brassicae* larval instars on the number of attacks out of a possible 100 (± S.E.M) by *Microplitis mediator* in the choice experiment.

Experience	Instar			Average
	1	2	3	
Less (1 and 2)	80±0.06	96±0.03	96±0.03	91±0.02
More (3 and 4)	86±0.05	76±0.06	82±0.06	81±0.03

Table 4.3.2 Effect of *Mamestra brassicae* larval instar on the number of attacks, the number of eggs laid and eggs laid per attack by *Microplitis mediator* in the choice experiment.

Instar	Number of attacks/larva (Mean ± S.E.M.)	Number of eggs/ larva (Mean ± S.E.M.)	Eggs/attack (Mean ± S.E.M.)
1	1.9±0.2	1.3±0.1	0.75±0.05
2	1.7±0.2	1.2±0.1	0.69±0.06
3	1.7±0.1	0.8±0.1	0.42±0.06
Average	1.8±0.1	1.1±0.1	0.62±0.03

Figure 4.3.4 Effect of *Microplitis mediator* experience with *Mamestra brassicae* instars on the mean number of attacks (± S.E.M) for each larva in the choice experiment.

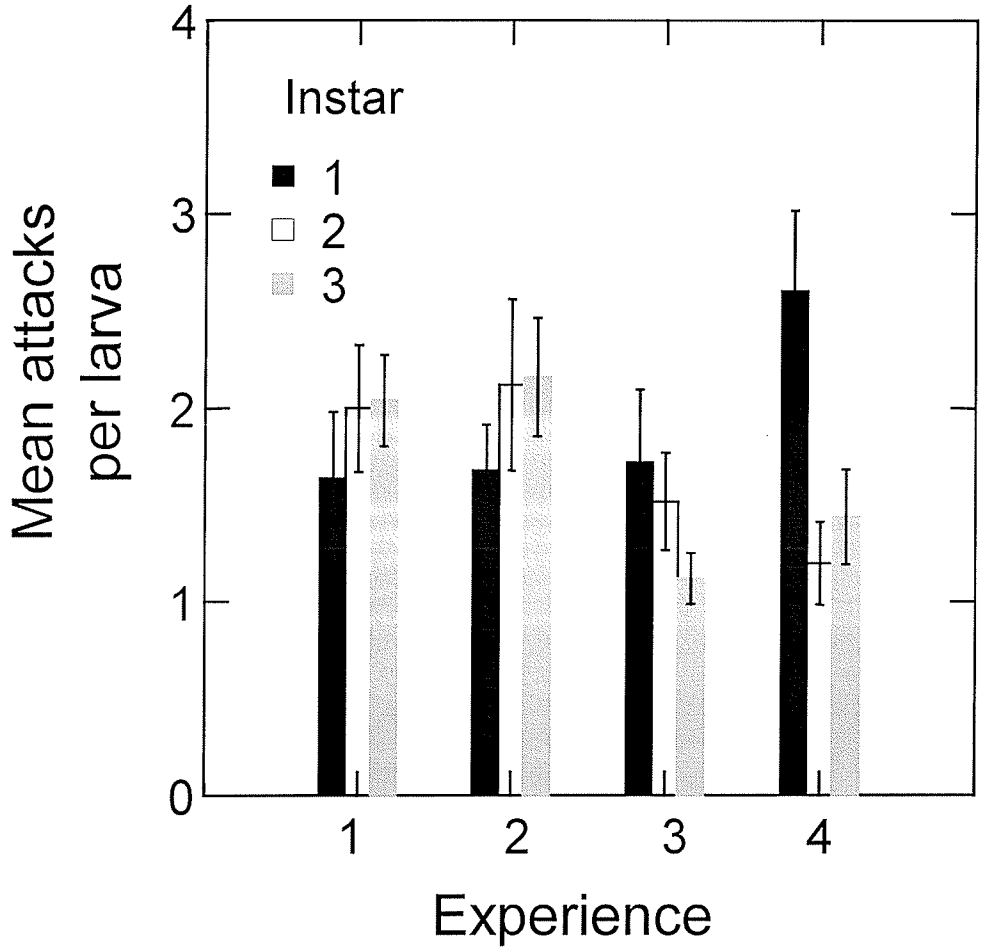

Mean attacks per larva
Instar
1
2
3
0
1
2
3
4
1
2
3
4
Experience

Figure 4.3.5 Effect of instar on percent (± S.E.M.) attacked *Mamestra brassicae* larvae that contained at least one parasitoid egg in the choice experiment. Numbers above S.E.M. bars represent the number of attacked larvae with parasitoid eggs (compare with numbers above error bars in Figure 4.3.3).

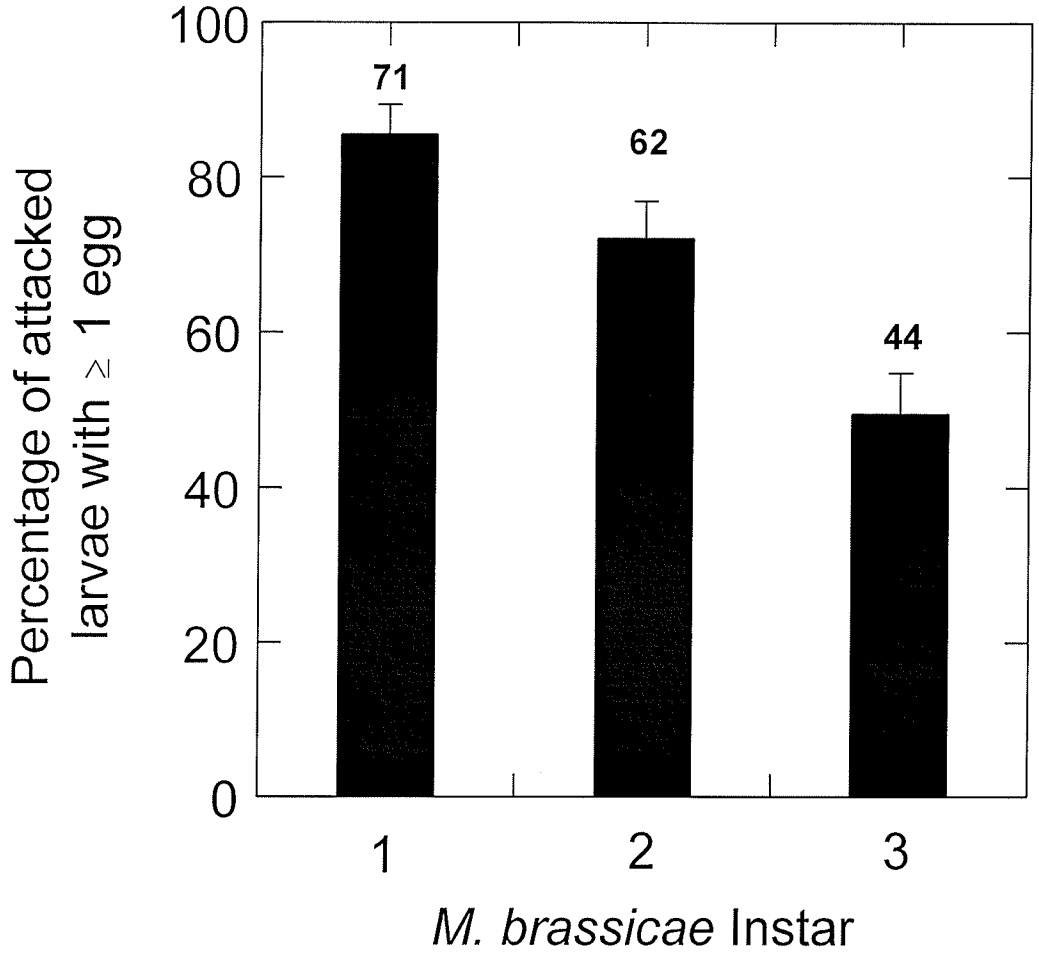

100
80
60
40
20
0
71
62
44
1
2
3
Percentage of attacked larvae with ≥ 1 egg
M. brassicae Instar

Figure 4.3.6 Effect of *Microplitis mediator* experience with *Mamestra brassicae* instars on the mean number of eggs (± S.E.M) oviposited within each larva attacked in the choice experiment.

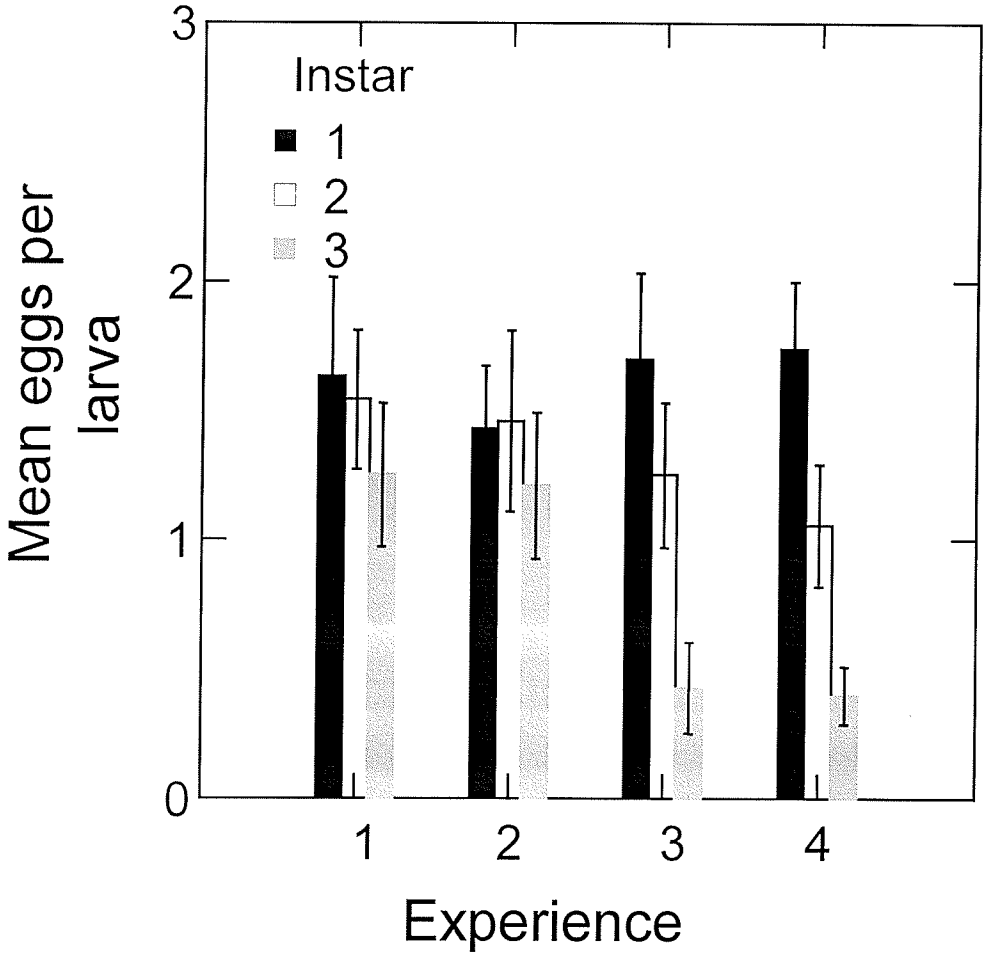

Mean eggs per larva
3
2
1
0
Instar
1
2
3
1
2
3
4
Experience

Figure 4.3.7 Effect of host instar on percent (± S.E.M.) of attacked *Mamestra brassicae* larvae that produced a parasitoid cocoon in the no-choice experiment. Numbers above S.E.M. bars represent numbers of attacked larvae producing cocoons (compare with numbers above error bars in Figure 4.3.1).

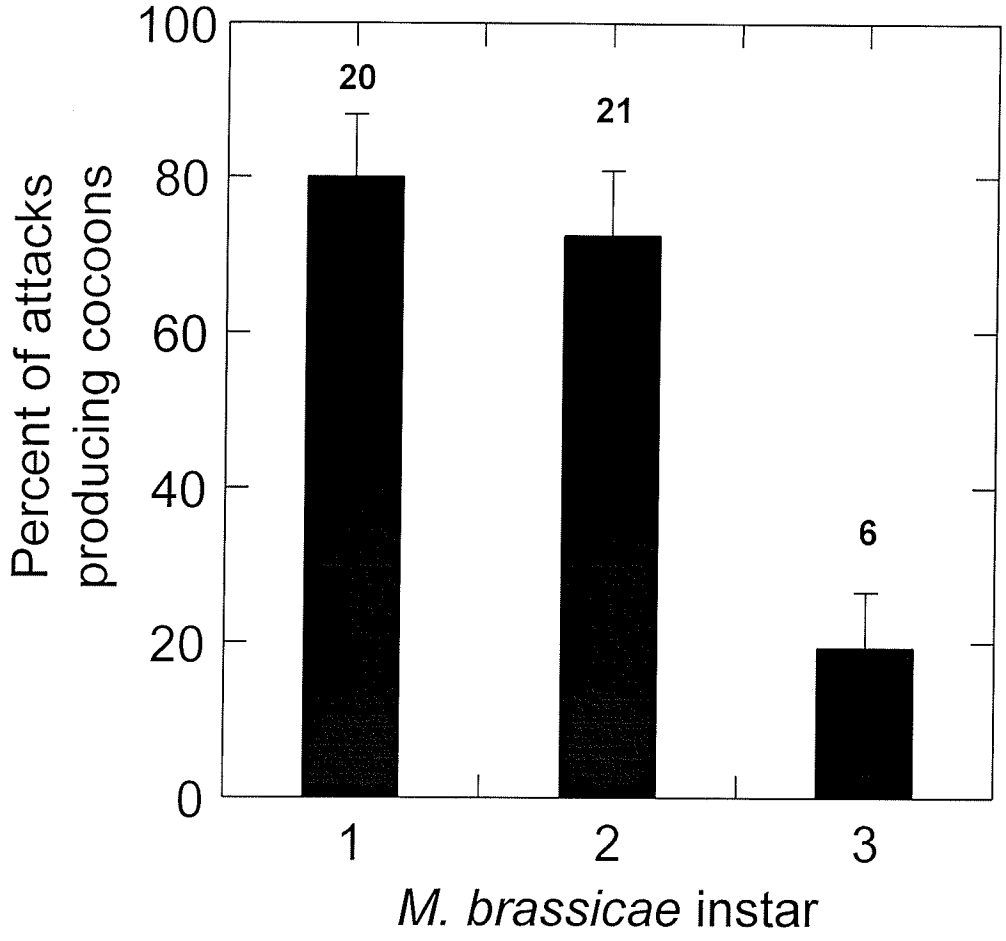

100
80
60
40
20
0
Percent of attacks producing cocoons
20
21
6
1
2
3
M. brassicae instar

Figure 4.3.8 Effect of parasitoid experience on percent (± S.E.M.) of attacks resulting in parasitoid cocoons developing from *Mamestra brassicae* larvae attacked in the no-choice experiment.

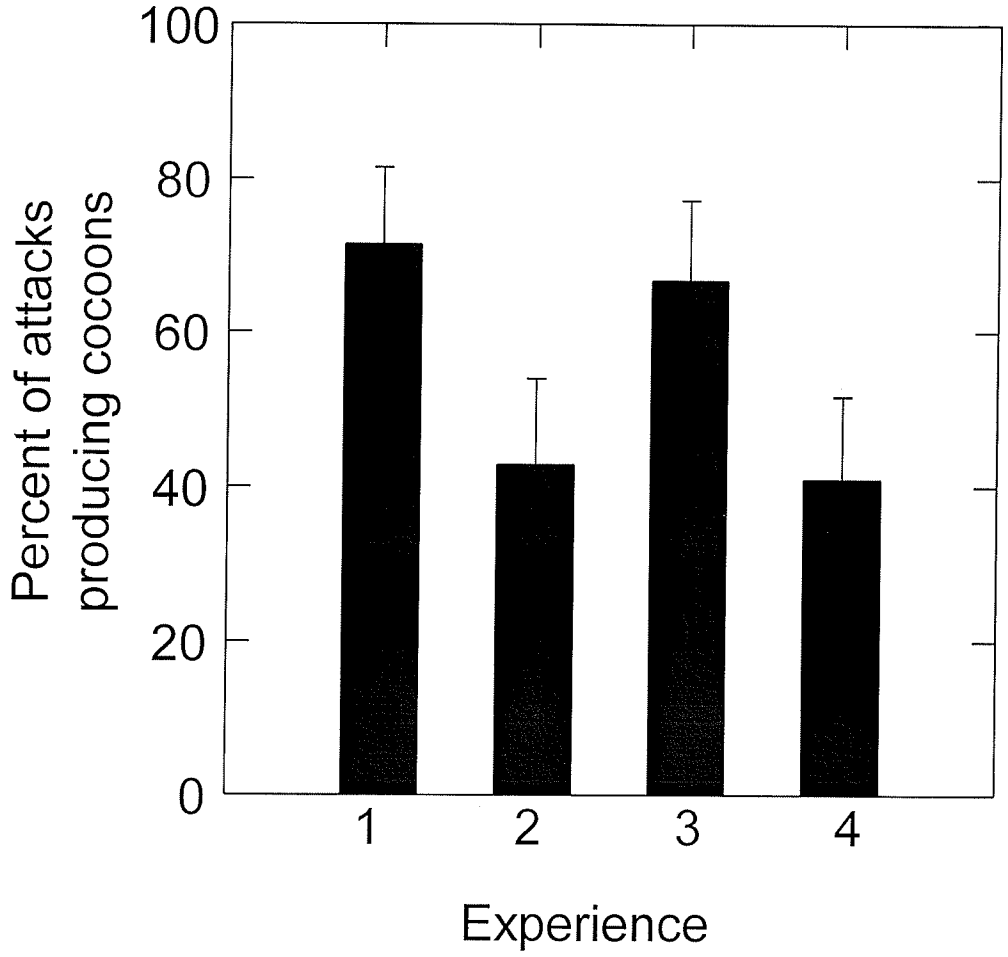

100
80
60
40
20
0
Percent of attacks producing cocoons
1
2
3
4
Experience

Table 4.4.1 Comparison of observed and predicted percentage of attacked larvae that received eggs and observed percentage of attacked hosts that produced parasitoid cocoons in the no-choice experiment.

Instar	Observed attacked larvae (%)	Predicted attacked larvae with eggs (%)	Observed attacked hosts producing cocoons (%)
1	57	75	80
2	66	69	72
3	70	42	19

Chapter 5: General Discussion

In this study *M. brassicae* egg masses and larvae were collected from organically managed field plots in Switzerland to characterize the moth's seasonal abundance, spatial distribution and incidence of parasitism. Additionally I have focused on one parasitoid of *M. brassicae* larvae, the solitary endoparasitoid *M. mediator* in a laboratory study that investigated the choice of host instars by parasitoid females and the consequences of those choices for parasitoid survival. In a broad context, this research was designed to provide insight into the difficulty in establishing *M. mediator* in Canada to control *M. configurata*.

Microplitis mediator was first recognized as a potential candidate in 1974 after field surveys and mass collections of *M. brassicae* larvae showed that it was the most dominant and constantly reared parasitoid (Carl and Sommer, 1975). Following twelve years of study of the parasitoid, it was proposed that *M. mediator* be released into Canada until either it established or the reasons for the failure of establishment be determined (Carl et al., 1986). Between 1990-1993 (Mason and Youngs, 1994) and again in 1999 (Mason, 1999) several releases of the parasitoid were made in Canada in canola fields infested with *M. configurata*. As of yet, success of establishment is unknown (Mason et al., 2001). I have attempted to address the issue of establishment by returning to Central Europe and focusing on some of the relevant interactions of *M. mediator* with its native host *M. brassicae*.

Host Selection by *Microplitis mediator*

The selection of first to third instars of *M. brassicae* larvae by *M. mediator* females was studied under laboratory conditions. Female parasitoids attacked a high rate of larvae regardless of the host instar available for attack and regardless of whether the parasitoid had a choice of instars. Although this result suggests that *M. mediator* is a highly motivated parasitoid, the dissections of larvae showed that not all attacks resulted in the oviposition of an egg. Highest egg to attack rates were found in instars I and II whereas only half of the attacks on instar III resulted in oviposition. The question is whether *M. mediator* females are actively accepting instars I and II while in turn, actively rejecting instar III. Optimal foraging theory predicts that *M. mediator* females will reject instar III as a host since the results from our suitability analysis show that attacks on instar III were not profitable in terms of reproductive fitness; only 19% of all attacks on instar III resulted in the development of parasitoid cocoons. This result is an unexpected one and indicates that the host selection strategies of *M. mediator* females are imperfectly related to the suitability of hosts.

The differential incidence in oviposition among host instars is likely a result of the differences observed in host defensive behaviour. Our observations of the experiment showed that host instar III were more aggressive with attacking parasitoids than either instar I and II, and would frequently bite and spit regurgitant at the approaching parasitoid. It seems therefore that parasitoid females are not rejecting host instar III but instead failing to oviposit within them.

The main conclusion from the experiment is that the low rate of successful attacks in instar III is a combination of the parasitoids failure to oviposit within larvae and the unsuitability of the host for immature parasitoid development. Of greater importance is the evidence that female parasitoids continue to attack instar III even though the probability of success is reduced.

Parasitism in Field Plots

If the host selection behaviour observed in the laboratory extends into the field, it would suggest that the effectiveness of *M. mediator* would be compromised since the field study shows that field plots are often infested with both suitable and, in the case of instar III, marginally suitable instars of *M. brassicae* at the same time. The selection of marginal hosts is disadvantageous in view of the investment in handling time of the host and low reproductive output. Additionally, the handling of an aggressive host is risky in terms of parasitoid injury and survival. Alternatively, the selection of instar III as a host can be viewed as moderately advantageous since female offspring emerged from 80% of developing cocoons. However, even though the successful parasitization of marginal hosts would effectively add to the female parasitoid population in the field, the addition would be substantially less than if the parasitoid exclusively selected suitable instars, such as instar I and II of *M. brassicae*.

Although larval instars ranging in suitability are available in field plots at the same time, the susceptibility of instars to parasitism by *M. mediator* is not equal.

Differences in spatial distribution and abundance of *M. brassicae* larvae may influence parasitism in the field. In 1999, instar I and to a lesser extent instar II of *M. brassicae* larvae were aggregated within field plots and this progressively shifted towards random distribution for later instars. The transition in spatial distribution for instars was paralleled with a progressive reduction in larval abundance, which was seen in both generations of *M. brassicae* and in both years of the study. This suggests that the rate of host encounter with less suitable instars is likely to be more rare for *M. mediator* females than encounters with suitable host instars. The results from our study of field parasitism in 1998 and 1999 show that *M. mediator* females do encounter suitable host instars on a continuous basis and in fairly high percentages in both generations of *M. brassicae*. Whether this trend in parasitism is a result of random host encounters with strictly suitable instars is unclear from this study since percent parasitism was determined through laboratory rearing of field collected larvae. In this manner, parasitism could be associated with instar I to instar IV larvae of *M. brassicae*; however it is not possible to indicate which instar was encountered by *M. mediator* at the time of attack and oviposition. This finding would provide fundamental insight into the choices female parasitoids make in the field and the timing of the encounter and would require an additional study that associates the host instar of *M. brassicae* with the development stage of the immature parasitoid.

The results from the binomial logistic regression analysis indicate that parasitism by *M. mediator* differed among field plots sampled in 1999. Highest estimates of parasitism were most commonly obtained for field plots with a relatively high overall abundance of host larvae. Within field plots, parasitism was negatively associated with the number of larvae of the same instar per plant. The mechanisms for the response are largely unknown.

The guild of parasitoids attacking *M. brassicae* was small in both years of this study; only six parasitoid species were reared from egg masses (2 species) and larvae (4 species). *Microplitis mediator* was clearly the dominant parasitoid reared from field collected instars I-IV, while other larval parasitoids were either infrequent or rare in field plots infested with *M. brassicae*. Parasitism of early stages of *M. brassicae*, including fairly high parasitism rates of egg masses, was coupled with the abundance of early instar larvae remaining below the reported economic threshold (Anon, 1998) in both years of this study. This result is important when considering the potential effectiveness of *M. mediator* in combination with other parasitoid species associated with *M. configurata* in Canada. It is not possible to conclude whether the dominance of *M. mediator* would change in combination with other parasitoid species such as with the larval endoparasitoid *Banchus flavescens* (Hymenoptera: Ichneumonidae) under field conditions in Canada.

In Canada, *Mamestra configurata* is a cyclical pest varying between periods of high host abundancy and periods where the host is rare in fields (Turnock, 1988). It has been suggested that a generalist parasitoid should be introduced into this habitat (Mason and Young, 1994). A generalist parasitoid could utilize alternative hosts when the pest and its habitat were unavailable. *Microplitis mediator* has been reported to attack over 40 lepidopterous hosts spanning two families: Noctuidae and Geometridae (Nixon, 1970; Shenefelt, 1973). In this study only one other species, *Autographa gamma* was parasitized by *M.mediator*. However this was during the second, more abundant generation of *M. brassicae*. The results from this study indicate that the host range of *M. mediator* within fields infested with a high abundance of *M. brassicae* is narrow. Studies should focus on examining habitat that is known to harbour *M. brassicae* but at the time of the study is rare in samples.

Chapter 6: List of References

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