# The biology of *Meteorus gyrator* (Hymenoptera: Braconidae), a solitary endoparasitoid of the tomato moth, *Lacanobia oleracea* (Lepidoptera: Noctuidae)

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**Abstract**

There is a need to identify potential biological control agents for use against lepidopterous pests in greenhouses. The solitary endoparasitoid *Meteorus gyrator* (Thunberg) attacks a range of macrolepidopterous larvae, including those of some important horticultural pest species. Laboratory trials designed to investigate the biology of *M. gyrator* on larvae of the tomato moth, *Lacanobia oleracea* Linnaeus, reveal that this parasitoid is capable of parasitizing all larval stages of its host, third instars being parasitized most frequently. Each female parasitoid lives for up to 40 days (at 25°C), ovipositing into an average of 78 hosts. Preadult development is rapid (~ 2 weeks), and the sex ratio of offspring is 1:1. Parasitism by *M. gyrator* suppresses the growth of both early and late host instars, and there is a concomitant reduction in the amount of food consumed (overall feeding reduction over a 12 day period is 68%). Our results indicate that inoculative releases of *M. gyrator* could provide effective biological control of *L. oleracea* and other noctuid pests of greenhouses.

## Introduction

Greenhouse crops are prone to attack by an array of damaging insects, but in areas of intensive horticulture, the noctuids can comprise in excess of 80% of the macrolepidopterous pest population (van Daele & Pelerents, 1968). Of these numerous species, the tomato moth, *Lacanobia oleracea* Linnaeus (Lepidoptera: Noctuidae) is one of the most common (Ionescu & Pasol, 1987; Jacobson, 2000). *Lacanobia oleracea* is found throughout Europe and Asia Minor to Mongolia (Tkho, 1973). Its larvae are extremely polyphagous, feeding on several hundred different types of food plant, many of which are of economic importance (Kurir, 1982). Although the tomato moth is a significant pest of such diverse crops as tobacco, brassicas and soft fruit (Sannino *et al*., 1993; Benuzzi & Antoniacci, 1995; Molinari *et al*., 1995; Vanparys *et al*., 1995), it is a particularly serious pest of greenhouse tomatoes (Foster, 1980; Griffin & Savage, 1983). *Lacanobia oleracea* caterpillars tend to avoid the defensive chemicals present in tomato leaf tissues and, as a result, they also feed on the pith, stems and on the unripe fruit (Lloyd, 1920). Thus, in addition to extensive defoliation by caterpillars, which leads to stunted plants with reduced yield, scarring of tomato fruits may cause even more serious economic loss.

Because of the high cash value and low insect tolerance that characterize many greenhouse crops, chemical control methods have, until recently, been favoured for tomato moth suppression. However, surveys of pest incidence and crop protection practices in greenhouses reveal that trends in the occurrence of certain insect pests of tomatoes are related to pesticide use and resistance (Foster & Brodie, 1984). Given that the present range of available insecticides includes few products that have not generated resistance, and the increased use of insecticide-sensitive biocontrol agents for the suppression of other glasshouse pests, alternative or integrated methods of pest suppression are now considered to be essential for the long term protection

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of edible crops (Manzaroli & Benuzzi, 1995). The Tomato Growers' Association (TGA) Technical Committee now recommends that biological pest control should be the standard approach to insect pest suppression, and aims for nil use of chemical pesticides within the next ten years (Jacobson, 2000; G. Hayman, TGA, personal communication). Moreover, since the cost of biological control of pests of tomatoes in the UK has been estimated at less than one third that of chemical control (van Lenteren, 1992, and references cited therein), alternative methods of pest suppression can also offer significant economic advantages to the grower.

Parasitic Hymenoptera have had proven success as agents of biological pest control in greenhouses, and there are numerous well-documented examples where their use has afforded significant financial savings (Greathead, 1986; van Lenteren, 1986). Field populations of *L. oleracea* are subject to natural attack by an array of indigenous ecto- and endoparasitic wasps (Thompson, 1953; Herting & Simmonds, 1976; Sannino *et al.*, 1993), but although several of these species have been subject to further research as potential biocontrol agents (Slovak, 1985; Buleza, 1990; Cabballero *et al.*, 1993; Marris & Edwards, 1994; Mosson *et al.*, 1997), only one species, *Trichogramma evanescens* Westwood (Hymenoptera: Trichogrammatidae), is available for use against *L. oleracea* eggs. While *T. evanescens* can undoubtedly prevent tomato moth eggs from hatching, recent field-observations of this widely used greenhouse parasitoid suggest that it is not universally effective in locating and parasitizing discrete egg-clusters (G. Hayman, TGA, personal communication). The presence of an effective larval parasitoid would be especially desirable, since it could offer a means of attacking damaging caterpillars which escape parasitism at the egg stage.

*Meteorus gyrator* Thunberg (= *scutellator* (Nees)) (Hymenoptera: Braconidae) is a common solitary endoparasitoid of macrolepidopterous larvae. It occurs throughout the British Isles and northern Europe, Japan and North Africa (Thompson, 1953). Hosts are primarily noctuids (Askew & Shaw, 1986; Goto *et al.*, 1986), but this parasitoid also utilizes geometrids and lymantriids (Thompson, 1953; Kotenko, 1976). In spite of the widespread distribution of *M. gyrator*, information regarding its general biology, or any characteristics which might equip it to perform well as an agent of biological pest control, is very scarce. Nothing has been documented regarding the biology of *M. gyrator* on larvae of *L. oleracea*, but in other host species, *M. gyrator* lays a single egg through the host integument. The egg hatches into a larva which feeds internally until immediately prior to pupation. The final instar larva then exits the host and spins a distinctive cocoon, which hangs from a line of silk, like a 'meteor', hence the generic name (Huddleston, 1980). It has been demonstrated that parasitism by *M. gyrator* does suppress food consumption of parasitized hosts (El-Sheikh *et al.*, 1993) and it is therefore possible that this parasitoid may have a similar effect on the crop damaging potential of *L. oleracea*. Proper elucidation of the relationship between pest and natural enemy is critical to any biological control project (Orr & Suh, 1998). The following study therefore describes a series of laboratory experiments designed to provide comprehensive data on the biology of *M. gyrator* on *L. oleracea*. Such information will allow preliminary assessment of the likelihood that populations of *M. gyrator* could become established in greenhouses, and whether this parasitoid might prove efficient against this plant pest.

## Materials and methods

### *Preparation of experimental organisms*

The origin and culturing of the *L. oleracea* used in these experiments has been described previously (Corbitt *et al.*, 1996). Prior to use, all *L. oleracea* individuals were maintained under constant conditions (20°C, 70% r.h., 16L:8D). Larvae were provided with an artificial semi-solid noctuid diet (Korano, La Balme-les Grottes, France) based on maize flour (Poitout & Bues, 1970). Developmental stages were separated, for use in experiments, on the basis of stadium-specific differences between widths of their larval head capsules (Corbitt *et al.*, 1996).

An initial population of *M. gyrator* was collected from the field (Yorkshire, UK) in 1998, from parasitized specimens of the noctuid species *Euplexia lucipara* Linnaeus (small angle shades) and *Autographa gamma* Linnaeus (silver Y), and from *L. oleracea* baits, established on artificially-infested sugarbeet. Additional adult wasps were obtained by Malaise trapping. *Meteorus gyrator* was subsequently established in the laboratory on mixed instars of *L. oleracea* larvae and kept at 25°C, 70% r.h., 16L:8D. On emergence, adult wasps were supplied with a 50% v:v aqueous honey solution as a food source. Sexes were distinguished on the basis of the obvious morphological differences which exist between males (ovipositor absent) and females.

### *Host stages selected for parasitism by* M. gyrator

Immature *L. oleracea* were divided into 15 equal groups, such that each group was comprised of five larvae from each of the six larval stadia (first instar to sixth instar) and five prepupae. In order to ensure that larvae would remain within these selected stages for as long as possible, only the most-recently moulted caterpillars, which had therefore only just entered their particular stadium, were used. Similarly, prepupae were collected at least 72 h before metamorphosis would normally begin. *Lacanobia oleracea* groups were placed into plastic boxes (150 × 150 × 75 mm) and provided with noctuid diet. A single mated female *M. gyrator* (24–48 h old) was introduced into each box, such that 15 female parasitoids were provided with a choice of 35 potential hosts. Parasitoids were provided with a 50% v:v honey solution food source, and were left to forage for 72 h. This time interval was sufficient to allow *M. gyrator* to attack at least one host, but was not long enough to enable the *L. oleracea* to moult to their next larval stadium or to pupate (Corbitt *et al.*, 1996). After this period, parasitoids were removed. Hosts were grouped according to stadium, placed in these groups into 200 ml plastic pots, and maintained at 25°C, 70% r.h., 16L:8D. Each group of larvae was furnished with noctuid diet *ad libitum*, and inspected daily until the emergence of parasitoids. The proportion of *L. oleracea* which had been successfully parasitized from each developmental stage, by each female wasp, was recorded. Since initial observations revealed that some parasitized hosts continued to moult, the developmental stage of each host at the time of emergence of each parasitoid was also recorded. This would allow the relationship between the original stadium of the host, at the time of parasitism, and its eventual stadium, at the time of parasitoid emergence, to be assessed.

### *The lifespan of and mean number of hosts parasitized by* M. gyrator*; the sex ratio of offspring and the duration of parasitoid development*

Fifteen male/female pairs of *M. gyrator* (< 24 h old) were placed into separate plastic boxes (150 × 150 × 75 mm), each containing ten newly-moulted third instar *L. oleracea*, a standard volume (1 $cm^3$) of noctuid diet and a 50% v:v aqueous honey solution food source. Honey food sources were replenished, *ad libitum*, throughout the experiment, to ensure that wasps had continuous access to a fresh food supply. After 24 h of host-exposure (25°C, 70% r.h., 16L:8D), each pair of parasitoids was retrieved and introduced to a fresh batch of ten third instar caterpillars for the next 24 h period. This procedure was repeated using successive groups of new potential hosts until the female parasitoid had died. All parasitoid-exposed *L. oleracea* larvae were placed, in their groups of ten, into 200 ml plastic pots, and provided with noctuid diet *ad libitum*. They were subsequently maintained (25°C, 70% r.h., 16L:8D) until they had either pupated or yielded a parasitoid cocoon. Cocoons were separated into individual glass vials (50 × 12 mm) until adult parasitoids emerged. The following information was recorded: the lifespan of each male or female *M. gyrator*; the number of offspring produced by each female parasitoid (in total, and per day of her life); the sex of each live wasp obtained; the duration of parasitoid development within the host caterpillar, and the duration of parasitoid development externally within the cocoon.

### *The larval development of* M. gyrator

Thirty groups of 30 third instar *L. oleracea* were placed in plastic boxes (150 × 150 × 75 mm), and exposed to mated *M. gyrator* females. In order to ensure that the majority of potential hosts were subsequently parasitized, each box contained a ratio of one wasp to five caterpillars. Twenty four hours after initial exposure, parasitoids were removed. Hosts were maintained under standard conditions (25°C, 70% r.h., 16L:8D) and supplied with fresh noctuid diet, as necessary, until required for dissection. Hosts were dissected, in batches of 60, at daily intervals over a period of 15 days post parasitoid-exposure. All dissections were carried out in sterile phosphate buffered saline, on the stage of a binocular microscope. The number and duration of the larval instars of *M. gyrator* were recorded, and the morphological characteristics of each developmental stage were noted. Measurements were made using an eye-piece graticule (± 0.01 mm).

### *The effect of parasitism by* M. gyrator *on the growth of* L. oleracea *at different stages of host development*

Fifty newly-moulted *L. oleracea* from either the third or fifth larval stadium, respectively, were placed, in groups of 25, into plastic boxes (150 × 150 × 75 mm). Five newly-emerged, mated *M. gyrator* females were subsequently released into each box for a period of 24 h. This duration of parasitoid-exposure, at this ratio (one *M. gyrator* to five hosts) ensured that a significant proportion, but not all, of the available hosts were parasitized. After wasps had been removed, larvae were placed into individual 200 ml plastic pots, supplied with artificial diet *ad libitum*, and maintained under standard conditions (25°C, 70% r.h., 16L:8D). At 24 h intervals, all larvae were weighed, inspected and any developmental events (moulting, pupation, etc.) recorded. Those *L. oleracea* individuals which had escaped parasitism, and remained healthy, served as controls. (Other caterpillars which yielded no parasitoids, but which subsequently failed to pupate, were discarded as they might have been stung).

### *The effect of parasitism by* M. gyrator *on the food consumption of* L. oleracea

Thirty newly moulted fifth instar *L. oleracea* were exposed to six mated *M. gyrator* females for a period of 24 h. This duration of parasitoid-exposure, at the ratio of one parasitoid to five hosts, was chosen to ensure that most, but not all, of the available caterpillars would be parasitized. Fifth instar hosts were used, since at this stage in their development *L. oleracea* normally feed very actively (Corbitt *et al.*, 1996), thus making any differences between food consumption achieved by healthy or parasitized individuals readily apparent. After 24 h, parasitoids were removed and caterpillars were placed into individual plastic pots (200 ml). Each larva was provided with a pre-weighed volume of noctuid diet of sufficient size (> 0.5 g) to ensure that the amount of food provided would be greater than the amount eaten during the course of two days. After 48 h (25°C, 70% r.h., 16L:8D), any diet remaining in each pot was collected and replaced with a fresh pre-weighed portion of food. This procedure was repeated at 48 h intervals until all parasitized hosts had produced wasps and subsequently died, and all non-parasitized *L. oleracea* had pupated.

In order to estimate the dry matter content of the food supplied to *L. oleracea* larvae at each feeding, five reference samples of diet (approximately 1–2 g) were weighed, then dried in an oven (90°C, 48 h) and reweighed. These data were used to produce a standard curve. By comparing the wet weight of any given sample with the standard curve, its equivalent dry weight could be calculated. In this way, the wet weight of each portion of food supplied to each *L. oleracea* larva at the start of each 48 h period was converted into its equivalent dry weight. All pieces of uneaten diet collected during the course of the experiment were dried in the same way as the reference food samples. The dry weight of food consumed by each larva during each successive 48 h interval was then determined by subtracting the dry weight of the food remaining from the dry weight of food initially provided.

## Results

### *Host stages selected for parasitism by* M. gyrator

Of the six host-types presented to *M. gyrator*, all developmental stages, with the exception of prepupae were successfully parasitized (fig. 1). Third instar larvae were parasitized most frequently, forming 38.4% of the total parasitism. However, second and fourth instars were also readily attacked, together contributing almost 50% of the final number of parasitoid cocoons produced. The remaining instars of *L. oleracea* (first, fifth and sixth instars) were only parasitized infrequently (at between 2% and 6% of the total recorded parasitism).

Irrespective of the developmental stage of a host at its time of parasitism, parasitoid larvae did not exit their dying host's remains until the latter stages of *L. oleracea's* larval

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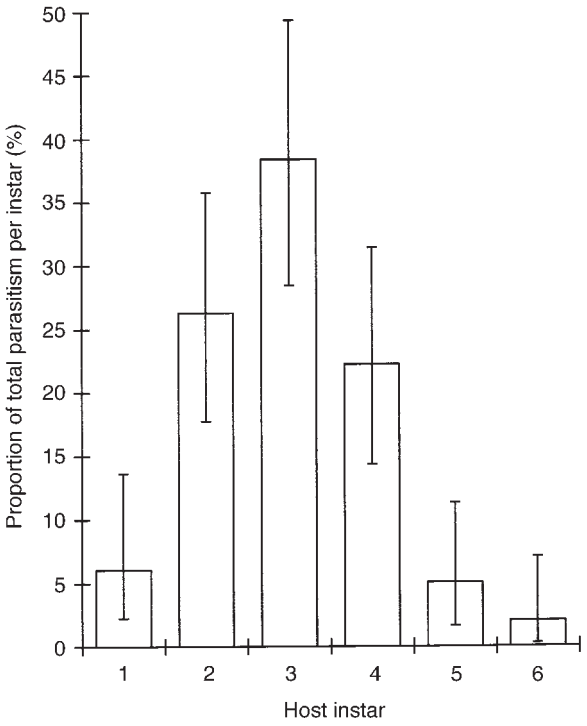


Fig. 1. The relative frequencies (as a percentage of total parasitism) at which different pre-adult stages of *Lacanobia oleracea* were selected for parasitism by *Meteorus gyrator*. Bars represent 95% confidence limits for percentages (Rohlf & Sokal, 1981).

lifespan: 100% of hosts which had been parasitized as first, second or third instars continued to develop until at least their fourth stadium, before parasitoid larvae emerged; up to 50% of these hosts survived to reach their penultimate, fifth, larval stadium before yielding their parasitoid burden. When hosts were parasitized as fourth or fifth instars, they did not always moult again before the parasitoid was ready to exit. Hosts which had reached their final (sixth) instar at the time of initial attack yielded parasitoids while remaining within the same developmental stage. This inverse correlation between the host's developmental stage at initial parasitism, and its instar at the end point of parasitism is typical of larval endoparasitoids that need to let the host grow sufficiently before completing their own development.

### *The lifespan of and mean number of hosts parasitized by* M. gyrator*; the sex ratio of offspring and the duration of parasitoid development*

Female *M. gyrator* outlived their male counterparts, surviving for an average of approximately 31 days, compared to approximately 20 days for males (table 1). The mean numbers of hosts parasitized per parasitoid per day are shown in fig. 2. There was no pre-oviposition period, such that parasitoids readily attacked hosts within 24 h of eclosion. The maximum rate of host attack was recorded on the fourth day, when females successfully parasitized an average of 4.8 hosts per day. From this point onwards, the oviposition curve appears to display two elements: Firstly, there is a general decline in the rate of parasitism, as highlighted by the addition of a regression curve (fig. 2); *M. gyrator* subsequently continued to parasitize 2–4 hosts per day up till day 17, and from day 22 onwards, individual females averaged less than two parasitized hosts per day. Secondly, it seems that this steady linear decline in oviposition performance was punctuated by regular troughs in rates of parasitism: parasitism fell on days 9, 13, 17, 22 and 26, respectively, only to rise again in the intervening intervals.

The mean total number of wasps that emerged from hosts was 78 per *M. gyrator* female (table 1). However, a proportion (~16%) of these immature parasitoids either failed to spin a cocoon, or died during pupation. As a result, each *M. gyrator* female ultimately produced an average of just under 66 live offspring (table 1). Overall, the sex ratio of emergent adult parasitoids was biased toward males (1♀:1.5♂) (table 1). However, of the 15 females used in this experiment, three individuals produced only male offspring, and were assumed to have remained unmated. The female parasitoids that had mated produced both female and male offspring, at a sex ratio of 1♀:1♂. The sex ratios of the offspring that emerged from hosts parasitized on each day of any female's life are shown in fig. 3 (mated females only). Ratios were initially biased towards males but became mostly female biased from day 6 to day 23. In the latter part of the parasitoids' lives, however, female offspring became rare, or absent, as the parasitoids aged.

Male offspring emerged from the host after an average of 10.9 ± 0.08 days, significantly quicker than females that emerged after 11.3 ± 0.10 days (Student's t-test, $P < 0.01$) (table 1). Similarly, the interval between emergence from the host, to eclosion of the adult parasitoid from its cocoon, was significantly shorter in males (6.5 ± 0.03 days) than in females (7.2 ± 0.04 days). However, prior to pupation, parasitoid larvae took up to 24 h to complete the spinning of the cocoon, void their meconium and form a prepupa. This meant that the

Table 1. The mean number of hosts successfully parasitized per *Meteorus gyrator* female, developmental time and longevity in the presence of hosts.

| | No. hosts producing emergent parasitoid larvae | No. hosts producing live adult parasitoids | Sex ratio (% females) | Larval development (within host) (days ± SEM) | | External development (within cocoon) (days ± SEM) | | Longevity (days ± SEM) | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Female | Male | Female | Male | Female | Male |
| Mean (n) | 78.2 ± 3.4 (1173) | 65.7 ± 2.7 (1019) | 40 (1019) | 11.3 ± 0.09 (406) | 10.9 ± 0.08 (613) | 7.2 ± 0.04 (406) | 6.5 ± 0.03 (613) | 30.9 ± 1.7 (15) | 20.1 ± 2.6 (15) |

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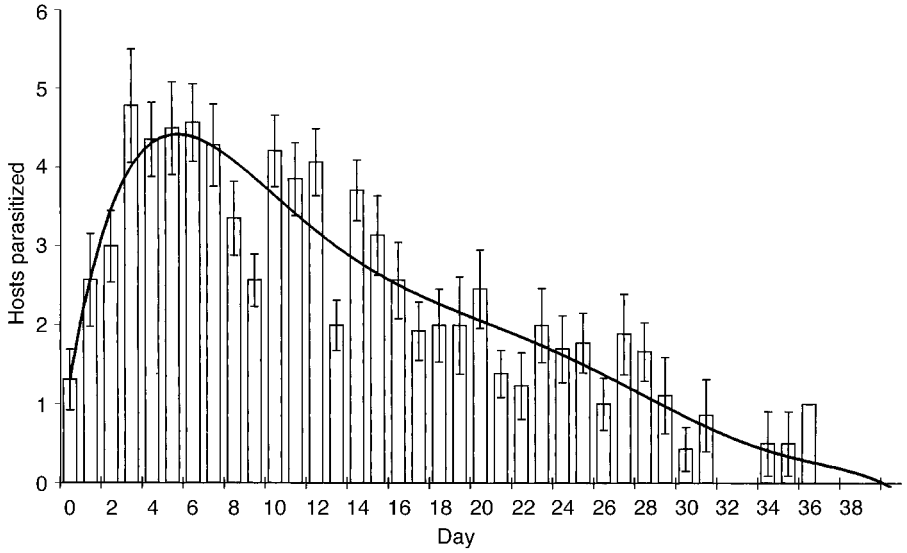


Fig. 2. The mean number of *L. oleracea* hosts parasitized per day during the lifetime of each *Meteorus gyrator* female. Bars represent mean ± s.e. The solid line illustrates a sixth order polynomial regression ($y = -8E\text{-}08x^6 + 1E\text{-}05x^5 - 0.0007x^4 + 0.0211x^3 - 0.316x^2 + 2.0933x - 0.4779$. $R^2 = 0.8878$).

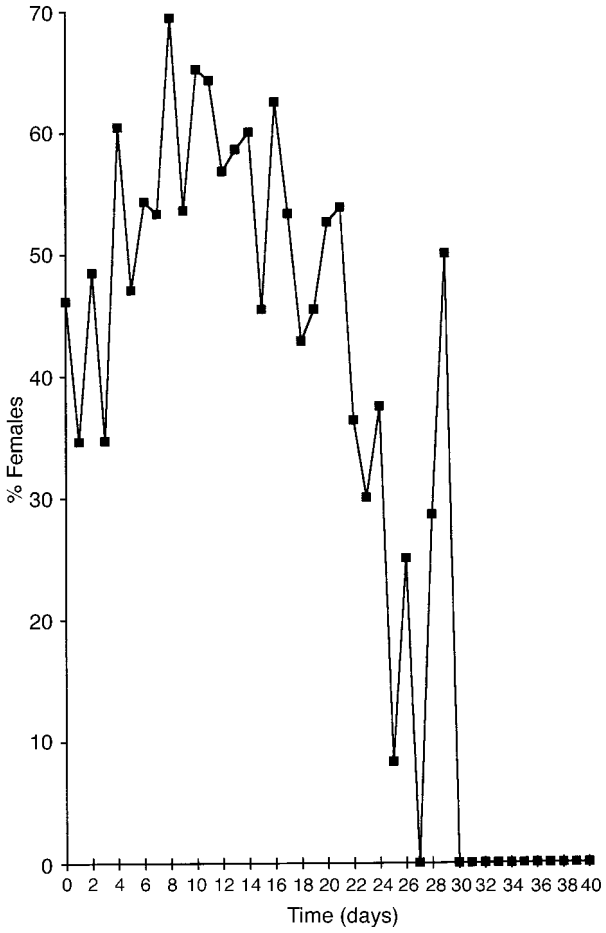


Fig. 3. The sex ratio (mean % female) of offspring produced per day by each *Meteorus gyrator* female during the course of her lifetime.

true pupal period of the parasitoids was approximately a day shorter than the total period spent within the cocoon.

### *The larval development of* M. gyrator

*Meteorus gyrator* eggs remained unhatched for 2–3 days post-oviposition. Newly-laid eggs were oval, completely clear and each had a prominent egg-stalk, the petiole. Each egg was generally found with its petiole embedded in the mid- or hind-gut of the host, although some were occasionally found floating free in the haemolymph. Immediately after oviposition, eggs measured, on average 0.30 ± 0.009 mm long (including the petiole) and 0.13 ± 0.002 mm wide (n = 10). The petiole measured approximately 0.10 ± 0.006 mm. Eggs swelled greatly prior to hatch, such that 24 h post-oviposition the average length was 0.61 ± 0.03 mm (n = 10), and by two days post oviposition they were, on average, 0.68 ± 0.07 mm long (n = 10 eggs) and contained the fully developed parasitoid larvae that were clearly visible inside. Hatching occurred when the parasitoid embryo straightened, causing the chorion to split. First instar parasitoid larvae were caudate, the caudal appendage making up approximately one third of the total length of the larva (mean = 2.24 ± 0.12 mm, n = 10) on the day of hatching. The head capsules of first instar larvae were heavily sclerotized, and mandibles were prominent. On several occasions, dissection revealed that hosts contained more than one parasitoid larva, indicating that superparasitism had occurred. However, by seven days after parasitoid-exposure, only one parasitoid larva was usually found. Moulting to the second stadium occurred from the sixth day post-parasitism although, in some of the hosts dissected, first instars persisted until 12 days after oviposition. Second instar larvae were hymenopteriform, having a much reduced caudal appendage and a largely non-sclerotized head capsule. On no occasion was more than one live larva found inside a host which contained a second instar. The second stadium lasted for 2–3 days, after which they moulted (9 days post-oviposition). Although morphologically similar to the

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previous developmental stage, third instars were readily identified by their opaque appearance, the presence of more heavily-sclerotized mouth parts and the virtual absence of cauda. The third stadium persisted for approximately one day within the host, before emerging through the body wall to begin metamorphosis. On leaving the host, the third instar larva rapidly spun a cocoon that was suspended from a pensile silk thread. The larva continued to strengthen its cocoon for approximately 20 h, after which time the prepupa began to form, and the eyes of the parasitoid became visible as reddish patches beneath the parasitoid cuticle. The meconium was voided 1–4 h after the onset of the prepupal stage, and pupation occurred shortly after.

### *The effect of parasitism by* M. gyrator *on the growth of* L. oleracea *at different stages of host development*

The growth of parasitized or healthy third and fifth instar *L. oleracea* larvae, respectively, is shown in fig. 4. Parasitized fifth instar *L. oleracea* continued to grow normally for three days post-parasitism. However, from the fourth day onward, a very marked difference between the respective weights of healthy or parasitized hosts became apparent. Although parasitized larvae achieved further weight gain for another two days, the maximum average weight attained by larvae parasitized as fifth instars was 0.27 ± 0.01 g (n = 18), which corresponds to only just over half the weight of similar control caterpillars of the same age (0.48 ± 0.04 g, n = 25). Hosts which had been parasitized as third instars continued to increase in weight for longer than those individuals which were parasitized later, as fifth instars (fig. 4), reaching their maximum average weight of 0.06 ± 0.003 g (n = 16) at 11 days post-parasitism. However, non-parasitized third instars on the same day weighed, on average, 0.37 ± 0.04 g (n = 18).

### *The effect of parasitism by* M. gyrator *on the food consumption of* L. oleracea

Parasitized fifth instar hosts consumed an average of 0.2 ± 0.02 g dry matter (n = 13) (*c.* 1 g wet weight of diet) post-parasitism whilst the control larvae, which completed development, consumed 0.63 ± 0.04 g of dry matter (n = 13)

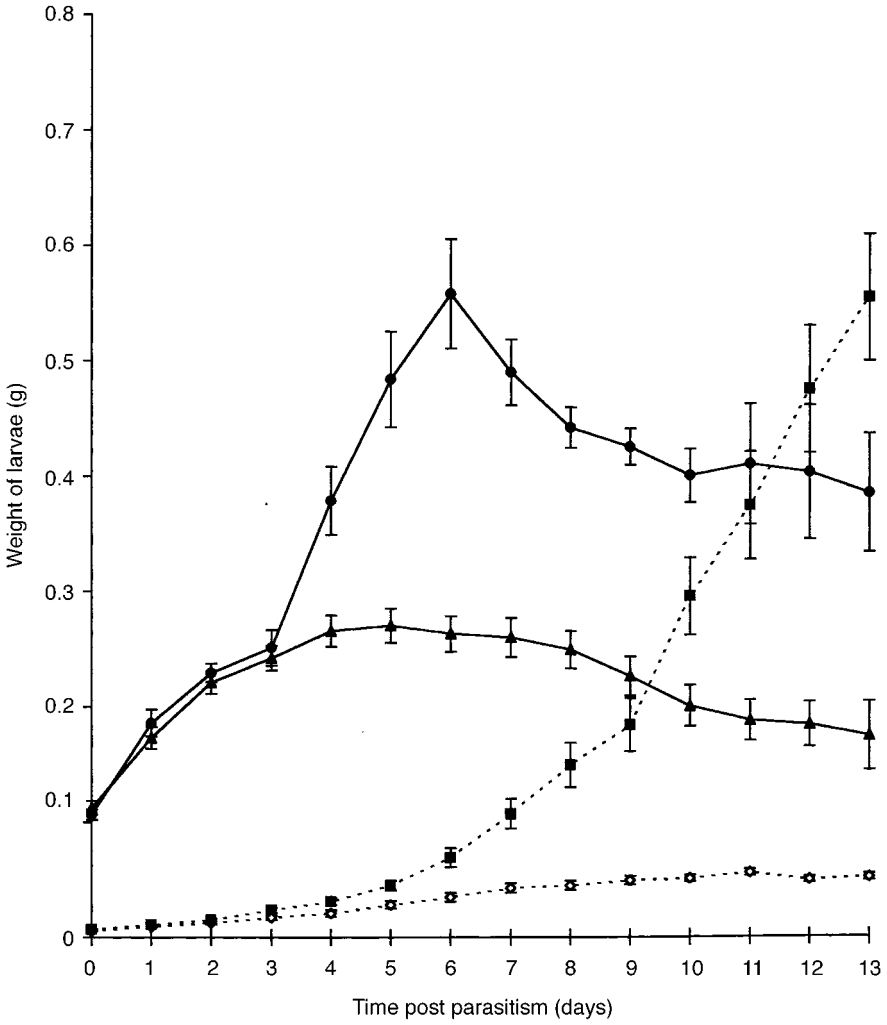


Fig. 4. A comparison between the rate of growth of parasitized and non-parasitized third and fifth instar *Lacanobia oleracea*, respectively. Bars represent mean ± s.e.; --◇--, parasitized third instars; --■--, non-parasitized third instars; --▲-- parasitized fifth instars; --●--, non-parasitized fifth instars.

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over the same period (*c*. 3 g wet weight of diet) (fig. 5). This corresponds to an overall reduction in the food consumption of parasitized larvae of 68%. The difference in dry matter consumption became apparent 2–4 days after parasitism, whilst 4–6 days after parasitism food consumption, at 0.031 ± 0.006 g dry matter, was approximately one-sixth that of the controls. Parasitoid larvae emerged 9–11 days post-parasitism. Post-parasitoid emergence, vacated hosts continued to consume very small quantities of food until their death, at 10–12 days post parasitism.

## Discussion

A variety of organisms have received research attention as candidates for biological control of *L. oleracea*, including parasitic protozoa (Efimenko *et al*., 1990), parasitic nematodes (Williams & Walters, 1996), pathogenic fungi (Daricheva & Koval, 1983), and baculoviruses (Foster & Crook, 1983). While these alternative control agents have shown promise, they cannot, as yet, be obtained for commercial use. Other biological methods for the suppression of *L. oleracea*, which are available, include *Bacillus thuringiensis* (Bt) and parasitic Hymenoptera. Although treatment with Bt can be very successful (Burges & Jarrett, 1980; Benuzzi & Antoniacci, 1995), it is sometimes necessary to make repeated applications to achieve good control (Burges & Jarrett, 1976), and not all preparations are effective (Ionescu & Beratlief, 1985). Moreover, *L. oleracea* larvae are less susceptible to Bt than those of other pest Lepidoptera, such as *Pieris brassicae* (Linnaeus) (Lepidoptera: Pieridae) or *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae) (Langenbruch, 1984). The most widely used egg parasitoid, *T. evanescens* can also be applied against the tomato moth (Slavchev, 1984), but the fact that *L. oleracea*

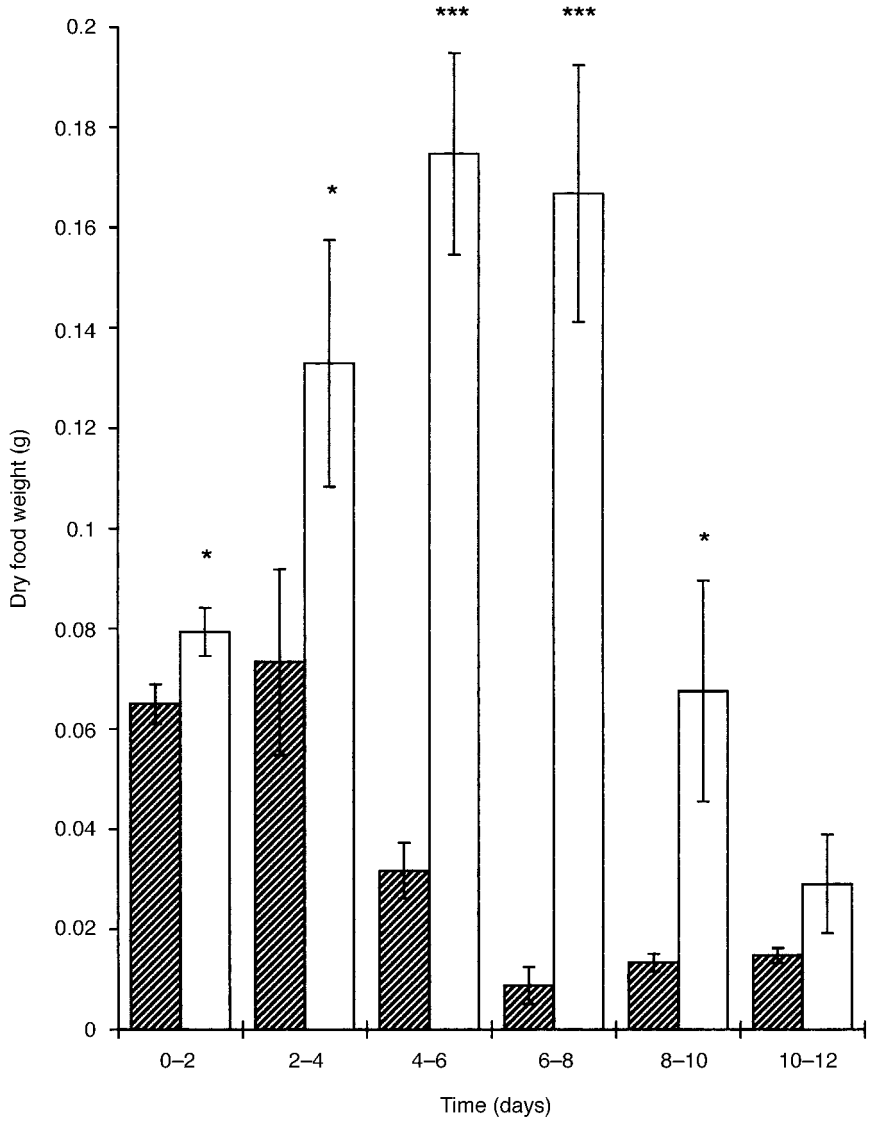


Fig. 5. The dry matter consumption achieved by parasitized (▨) and non-parasitized (□) *Lacanobia oleracea*, respectively. *, ** and *** indicate significant differences at $P < 0.05$, 0.01 and 0.001 respectively (Student's t-test). Bars represent mean ± s.e.

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deposits its eggs in discrete clutches, in layers up to three eggs deep, prevents parasitoids from encountering all but the most exposed eggs within a clutch.

In the light of the strengths and limitations of existing noctuid suppression measures used in greenhouses, the traits shown by the parasitoid *M. gyrator* may be particularly beneficial. Unlike some meteorine wasps, which avoid certain larval stages of their particular host, all larval stages of *L. oleracea* are acceptable to *M. gyrator*. Whereas *Meteorus rubens* (Nees) (Braconidae) does not attack any of the early larval instars of *Agrotis ipsilon* (Hufnagel) (Noctuidae), and *Meteorus autographae* Muesebeck (Braconidae) cannot develop in the final larval instar of the soybean looper *Chrysodeixis includens* Walker (Noctuidae) (Grant & Shepard, 1984), *M. gyrator* can parasitize any tomato moth caterpillar encountered in an infested crop, irrespective of its age, stadium or size. The fact that *M. gyrator* shows a preference for intermediate stadium caterpillars is especially advantageous, since pests are attacked while they are still relatively small and have not yet started to consume large quantities of plant material (Corbitt *et al*., 1996).

The extent to which larval development is able to continue post-parasitism is closely correlated with the stage of development of each *L. oleracea* host at the time of attack; while early stadium caterpillars continue to pass through up to four further moults before parasitoid emergence, later stadia yield their parasite burden much more rapidly. However, irrespective of the stage of host development at the time of initial attack, the rate of weight gain of *L. oleracea* is suppressed soon after initial parasitism. In the case of third instar hosts, although these may reach their fifth instar before parasitoid emergence, they do not make any significant weight gain beyond the fourth day post-parasitism. This effect is more pronounced in later stadia, such that fifth instars cease growth within 72 h of initial parasitism. While hosts do not actually die until up to two weeks after attack by *M. gyrator*, the rapid onset of suppressed growth implies a correspondingly early reduction in food requirements. Observations of large, and normally voracious, late instar caterpillars confirm that their food consumption is noticeably reduced (~ 20%) within two days of initial attack. This difference between the weight of diet consumed by healthy and parasitized individuals, respectively, increases during the course of parasitism; eight days after first attack by *M. gyrator*, feeding is suppressed by 95%. Such differences are highly statistically significant ($P < 0.001$), and represent an overall reduction in the destructive capacity of *L. oleracea* of over 68%.

*Meteorus gyrator* appears to show two patterns within the levels of oviposition achieved during each female's lifespan: firstly, a peak in oviposition occurs on the third day after emergence, followed by a general decline in the daily rate of parasitism; secondly, oviposition rates undergo a regular series of comparatively marked depressions, which occur at approximately four-day intervals. The reason for this secondary cyclical oviposition pattern is unclear. Peaks and troughs in rates of parasitism do not, however, reflect variations in the availability of fresh food for the wasps, since honey solution was renewed throughout the trial. Neither do they reflect any innate cycle in *M. gyrator*'s egg maturation capabilities, since this parasitoid is pro-ovigenic, and thus emerges with a fixed egg load (Flanders, 1950). This interesting observation requires further elucidation, and is currently the subject of further research.

*Meteorus gyrator*'s lifetime fecundity is comparable to, or even higher than, that recorded in other parasitoids of *L. oleracea* which have been identified as having potential as agents of biological pest control (Marris & Edwards, 1995; Mosson et al., 1997). Compared to other *Meteorus* species, the fecundity of *M. gyrator* appears to be relatively low (Grant & Shepard, 1984; Fuester et al., 1993). However, previous studies have measured oviposition performance in terms of total number of eggs dissected from parasitized hosts, rather than as numbers of hosts successfully parasitized. This means that a meteorine which lays a very high number of eggs may, in fact, have a low fecundity because many potential progeny are victims of superparasitism or of host death. Since we only recorded successful parasitisms, our value for the maximum number of *L. oleracea* that can be attacked by a single parasitoid (78 individuals) is, therefore, a much more reliable measure of the number of hosts that a parasitoid will kill during her lifespan, and of her reproductive capacity.

Each female parasitoid produces in excess of 60 progeny during her lifespan, of which approximately half will be female. A single *M. gyrator* female is therefore capable of contributing approximately 30 new control agents to the parasitoid pool within three weeks of initial exposure to *L. oleracea*. Under these circumstances, timed inoculative releases of *M. gyrator* could quickly produce a self-sustaining parasitoid population, thus providing a level of crop protection over successive pest generations. *Lacanobia oleracea* undergoes two generations a year (the first adults appear in April or May, and the second in late summer), so it is critical to time control measures to coincide with the peak of activity of first generation larvae, if more serious, late-season, damage is to be avoided (Jacobson, 2000). In order to target early instars, it is envisaged that timed releases of *M. gyrator* would need to begin in May. This might be repeated approximately one week later, to ensure that an active population of ovipositing wasps coincides with the third and subsequent developmental stadia of any *L. oleracea* which escaped parasitism when younger. Although this programme of releases should produce a synchronized population of wasps, which would theoretically persist long enough to affect the second generation of tomato moth caterpillars, a second inundative release might be necessary by the end of the summer.

While these laboratory findings reveal that *M. gyrator* does possess several traits which could allow it to act as an effective agent of biological control against *L. oleracea*, all data were collected under standard environmental conditions. Several aspects of meteorine performance may be affected by the fluctuating temperatures, humidities and photoperiods that parasitoids will encounter in the greenhouse and this may, in turn, influence the number of wasps required to achieve significant pest suppression. For example, *Meteorus leviventris* (Wesmael) (Braconidae), a gregarious endoparasitoid of the black cutworm, *A. ipsilon* mainly oviposits in darkness (Grafton-Cardwell, 1982), and it is possible that the oviposition performance of *M. gyrator*, which was never observed foraging in daylight, will depend heavily on the photoperiod regime used in the greenhouse. Although, in the present study, approximately equal numbers of male and female progeny were recorded, there are many cases of the sex-ratio of parasitoids being altered by environmental conditions and/or the fitness of the host (Charnov *et al*., 1981; King, 1987). While it is clear that

ecological factors need to be properly taken into account in the future design of any trial releases, preliminary studies are now ongoing to assess the performance of *M. gyrator* on a range of noctuids, both in the laboratory, and in artificially-infested tomato plants under small-scale greenhouse conditions. Moreover, in the light of recent interest in the use of transgenic plants with enhanced resistance to *L. oleracea* caterpillars (Fitches *et al*., 1997; Gatehouse *et. al*., 1997, 1999), there is a need to examine the tritrophic effects of genetically modified crops on biocontrol agents, including *M. gyrator* (Bell *et al*., 1999). This is especially relevant, given the increasing importance of integrated control measures for use in greenhouses (Manzaroli & Benuzzi, 1995).

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