The comparative biology of the solitary endoparasitoid *Meteorus gyrator* (Hymenoptera: Braconidae) on five noctuid pest species

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**Key words.** Parasitoid, *Spodoptera*, *Mamestra brassicae*, *Chrysodeixis chalcites*, *Lacanobia oleracea*, insect pests

**Abstract.** The comparative biology of the solitary endoparasitoid *Meteorus gyrator* (Thun.) was investigated in five noctuid pest species. *Meteorus gyrator* parasitized all larval stages of the noctuid pests *Lacanobia oleracea*, *Mamestra brassicae*, *Spodoptera exigua*, *Spodoptera littoralis* and *Chrysodeixis chalcites*. When female parasites were offered host larvae of all developmental stages, host larvae in their third stadium were parasitized most frequently in all species. When the parasitoid was offered a choice of third stadium larvae from each of the five lepidopteran host species, *L. oleracea* was the most frequently parasitized, followed by *M. brassicae*. The growth of *L. oleracea* and *M. brassicae* was markedly reduced when larvae were parasitized by *M. gyrator*, with the effect of parasitism on the remaining species being much less pronounced. In excess of 94% of parasitized hosts gave rise to live wasps in *L. oleracea*, whilst in *M. brassicae* only 52% of parasitized hosts gave rise to a live wasp, the remainder dying (44.6%) or pupating (3.1%).

The larval development of the parasitoid was also strongly influenced by the host species. Thus, the development (egg to cocoon) of female wasps was most rapid in *C. chalcites* (9.7 ± 0.09 days), and longest in *M. brassicae* (17.2 ± 1.08 days). The cocoon weight of wasps was also significantly affected by host species, with the heaviest female cocoons being derived from *C. chalcites* (10.4 ± 0.16 mg) and the lightest female cocoons being derived from *M. brassicae* (7.0 ± 0.14 mg). In all cases, the development times and cocoon weights of male parasitoids were less than those of female wasps.

**INTRODUCTION**

*Meteorus gyrator* (Thun.) (Hymenoptera: Braconidae) is a solitary endoparasitoid which has a wide geographical distribution, occurring throughout the British Isles and northern Europe as well as north Africa and Asia (Thompson, 1953). This parasitoid has a wide host range within the Lepidoptera, and attacks several noctuid, geometrid and lymantriid species (Kotenko, 1976; Askew & Shaw, 1986; Goto et al., 1986). The meteorine wasps constitute a relatively under-researched assemblage, and although some information is available on some other species (Simmonds, 1947; Askari et al., 1977; Thireau et al., 1990), there is very little information on *M. gyrator*. Thus, with the exception of the studies of Bell et al. (2000a) in larvae of the tomato moth, *Lacanobia oleracea* (L.), and those of El-Sheikh et al. (1993) in larvae of *Mythimna loreyi* (Duponchel), no information is available on the performance of this parasitoid against other pest species.

The larvae of a wide range of lepidopteran species attack field and glasshouse crops in the UK and Europe (Foster, 1981; Van de Veire, 1993). For this reason, there is a constant requirement to identify and develop biological control agents. Bell et al. (2000b) indicated that this parasitoid may have potential as a biological control agent against lepidopteran larvae in the glasshouse, although little information is available as to its success on hosts other than *L. oleracea*. Furthermore, a wide range of parasitoid species have been investigated because of their ability to regulate the development of their hosts through the use of venoms, polydnaviruses and teratocytes in order to produce a favourable environment for the development of their larvae (reviewed by Strand & Pech, 1995). Failure to develop within a given host can frequently be attributed to the inability of the parasitoid to successfully regulate their host through disruption of their endocrinology or suppression of the immune response (Vinson & Ivantsch, 1980; Edwards et al., 2001).

The investigation of the success of *M. gyrator* within a range of hosts, and differences in the biology of the parasitoid when developing in different species, is required in order to lay the foundations for the examination of further parasitoid-host interactions aimed at investigating the factors that may contribute to its successful development. The work presented here reports on a series of experiments designed to determine the potential of this parasitoid to parasitize and develop in a range of pest noctuids. Specifically, we have examined some aspects of the basic biology of *M. gyrator* in five noctuid species viz. *Spodoptera exigua* (Hübner), *Spodoptera littoralis* (Boisd.), *Mamestra brassicae* (L.), *Lacanobia oleracea* (L.) and *Chrysodeixis chalcites* (Esper).

**MATERIALS AND METHODS**

**Test insects**

The noctuid larvae used in these experiments were derived from standard laboratory cultures maintained at the Central Science Laboratory (CSL). The procedures for culturing the five test species were all essentially the same, and followed the procedures outlined by Corbitt et al. (1996) for *L. oleracea*. Prior to
use, *L. oleracea* were maintained under constant conditions (20°C, 65% r.h., 16L : 8D). All other species were maintained at 25°C, 70% r.h., 16L : 8D. Larvae of all five species were provided with artificial noctuid diet (Bioserv, New Jersey, USA) based on maize flour (Poitout & Bues, 1974). Developmental stages were distinguished on the basis of head capsule width. *Meteorus gyrator* adults were derived from a laboratory culture (25°C, 70% r.h., 16L : 8D) reared on *L. oleracea* larvae. The origin and culturing of the *M. gyrator* used in these experiments has been described elsewhere (Bell et al., 2000a).

### Host stages selected for parasitism

Five newly-moulted larvae from each of the six larval stadia (i.e. 1st to 6th instar larvae) of each of *L. oleracea*, *S. littoralis*, *S. exigua*, and *M. brassicae* were placed into plastic boxes (150 × 150 × 75 mm) and provided with noctuid diet *ad libitum*. A single, newly-emerged, mated *M. gyrator* female, without prior access to hosts, was released into each box and provided with a 50% v/v aqueous honey solution as a food source. Forty-eight hours after their introduction the parasitoids were removed from the plastic boxes and the host larvae were grouped by stadium and placed in tissue-lined 250 ml plastic pots. The larvae were subsequently supplied with artificial diet *ad libitum* and maintained under constant conditions (25°C, 70% r.h., 16L : 8D). Four days post-parasitism (parasitoid eggs hatch on the 3rd day post oviposition) the host larvae were dissected, and the presence of parasitoid eggs or larvae determined. The number of parasitized larvae from each host stadium was recorded.

### Choice of host species

Five newly-moulted third instar larvae from each of *L. oleracea*, *S. littoralis*, *S. exigua*, *M. brassicae* and *C. chalcites* were placed together in plastic boxes (150 × 150 × 75 mm) and provided with noctuid diet *ad libitum*. This was done for all species. For each of the host species tested, *M. gyrator* overnight in a 12 cm diameter Petri dish. After exposure to the wasp, each larva was placed individually in a 250 ml plastic pot and supplied with artificial diet *ad libitum*. This was repeated twenty times such that a total of 100 larvae of each moth species were exposed to *M. gyrator* in this way. All larvae were subsequently monitored for parasitoid emergence, death or pupation. On death or pupation, hosts were dissected to determine the presence of parasitoid eggs or larvae. Similarly, the frequency of superparasitism was investigated by dissecting moribund hosts following the egression of the parasitoid larvae to determine the number of parasitoid first instar head capsules present (indicative of the number of parasitoid eggs that had hatched within each host) and for the presence of remaining live parasitoid larvae within them.

### Parasitoid success in different hosts

To determine the proportion of parasitized hosts that successfully yielded live wasps, groups of five larvae of each of the test species (excluding *C. chalcites*) were exposed to a single female *M. gyrator* overnight in a 12 cm diameter Petri dish. After exposure to the wasp, each larva was placed individually in a 250 ml plastic pot and supplied with artificial diet *ad libitum*. This was repeated twenty times such that a total of 100 larvae of each moth species were exposed to *M. gyrator* in this way. All larvae that were subsequently monitored for parasitoid emergence, death or pupation. On death or pupation, hosts were dissected to determine the presence of parasitoid eggs or larvae. Similarly, the frequency of superparasitism was investigated by dissecting moribund hosts following the egression of the parasitoid larvae to determine the number of parasitoid first instar head capsules present (indicative of the number of parasitoid eggs that had hatched within each host) and for the presence of remaining live parasitoid larvae within them.

### Data analysis

Datasets were analysed using two-way ANOVA (Minitab V13.3). Where necessary, proportions were subjected to angular transformation prior to analysis. Following ANOVA, differences between datasets were determined using Tukey-Kramer *post hoc* tests and the accepted level of significance was *P* < 0.05 in all instances. For the comparison of two means, Student’s t-test was used.

## RESULTS

### Host stages selected for parasitism

For each of the host species tested, *M. gyrator* successfully parasitized all developmental stages presented to it and for all hosts significant differences were apparent in the proportions of the different instars parasitized (one-way ANOVA, *P* < 0.05) (Table 1). In all cases, the third larval stadium was the most frequently parasitized host stage - always representing more than 50% of the total number of hosts parasitized for each of the test species. In the cases of *L. oleracea*, *S. littoralis* and *S. exigua*, the fourth stadium was the next most frequently
parasitized stage (15.7%, 19.7% and 19.2% respectively) followed by the second stadium (9.4%, 8.5% and 15.1% respectively). However for *M. brassicae* this trend was reversed, the second stadium being the next most readily parasitized (23.3% of total parasitism) followed by the fourth stadium (8.3% of total parasitism). In all species tested, although the 1st, 5th and 6th stadia were parasitized, parasitism of these stadia was generally less frequent.

Insufficient numbers of *C. chalcites* were available to conduct a comparable assessment of the most frequently parasitized stadium for this host. However, pilot studies (not reported here) also indicated that the third larval stadium of *C. chalcites* was also the stage most frequently parasitized by this wasp.

**Host species selected for parasitism**

Significant differences were recorded between the frequencies of parasitism of the different host species (one-way ANOVA, $F = 35.1$, df = 4, 145, $P < 0.05$). Of the five host species presented to *M. gyrator* females in choice tests, *L. oleracea* larvae were the most frequently chosen for parasitism, with an average 3.3 ± 0.23 hosts parasitized per wasp (Fig. 1). However, all other test species were parasitized by *M. gyrator*, albeit to a lesser extent. *Mamestra brassicae* was the next most frequently parasitized host, with an average of 2.7 ± 0.15 hosts parasitized per wasp, whilst *S. littoralis, S. exigua* and *C. chalcites* gave averages (± SEM) of 0.8 ± 0.12, 1.7 ± 0.16 and 1.1 ± 0.13 parasitized hosts per wasp, respectively.

The development of *M. gyrator* on different hosts

The development time (egg to cocoon) of *M. gyrator* developing within hosts parasitized as third instars was significantly affected by host species ($F = 73.15$; df = 4, 322; $P < 0.001$ (Table 2). Similarly, the sex of the parasitoid also had a significant effect on development time ($F = 8.29$; df = 4, 322; $P < 0.01$) and, irrespective of host species, male parasitoids developed more rapidly than their female counterparts. By the same token, the weight of the cocoons spun by the parasitoids following egression from the host was also significantly affected by the host species ($F = 55.15$; df = 4, 323; $P < 0.0001$) and the sex of parasitoid ($F = 15.15$; df = 4, 323; $P < 0.0001$). Wasps developed most rapidly in *C. chalcites* (9.3 ± 0.11 and 9.7 ± 0.09 days for male and female parasitoids, respectively).

<table>
<thead>
<tr>
<th>Host Species</th>
<th>Mean No. Hosts Parasitized per Wasp (± SEM)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. oleracea</em></td>
<td>3.3 ± 0.23 (40)a</td>
</tr>
<tr>
<td><em>M. brassicae</em></td>
<td>2.7 ± 0.15 (40)a</td>
</tr>
<tr>
<td><em>S. littoralis</em></td>
<td>0.8 ± 0.12 (24)ad</td>
</tr>
<tr>
<td><em>S. exigua</em></td>
<td>1.7 ± 0.16 (26)ad</td>
</tr>
<tr>
<td><em>C. chalcites</em></td>
<td>1.1 ± 0.13 (23)ae</td>
</tr>
</tbody>
</table>

**Table 2.** The mean development times of *M. gyrator* (egg-cocoon), and cocoon weights, in different candidate host species (days ± SEM). For each parameter, values followed by different letters are significantly different (two-way ANOVA followed by Tukey-Kramer post hoc tests, $P < 0.05$).

<table>
<thead>
<tr>
<th>Development time from egg – cocoon (Days ± SEM) (n)</th>
<th>Mean cocoon weight (mg ± SEM) (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td>Females</td>
</tr>
<tr>
<td>L. oleracea</td>
<td>10.6 ± 0.17 (46)ab</td>
</tr>
<tr>
<td>M. brassicae</td>
<td>15.1 ± 1.06 (23)c</td>
</tr>
<tr>
<td>S. littoralis</td>
<td>11.5 ± 0.10 (26)be</td>
</tr>
<tr>
<td>S. exigua</td>
<td>9.8 ± 0.14 (23)ab</td>
</tr>
<tr>
<td>C. chalcites</td>
<td>9.3 ± 0.11 (40)a</td>
</tr>
<tr>
<td>Females</td>
<td>11.6 ± 0.28 (51)b</td>
</tr>
<tr>
<td></td>
<td>17.2 ± 1.08 (27)d</td>
</tr>
<tr>
<td></td>
<td>11.6 ± 0.10 (24)b</td>
</tr>
<tr>
<td></td>
<td>9.9 ± 0.15 (26)ab</td>
</tr>
<tr>
<td></td>
<td>9.7 ± 0.09 (46)ac</td>
</tr>
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</table>
respectively), and also gave the greatest mean cocoon weights at emergence (10.1 ± 0.16 and 10.4 ± 0.16 mg for male and female parasitoids, respectively) in this host. In contrast, wasps developing in *M. brassicae* showed the slowest larval development time for both male (15.1 ± 1.06 days) and female wasps (17.2 ± 1.08 days) and also gave the smallest mean cocoon weights (6.1 ± 0.16 and 7.0 ± 1.5 mg for male and female parasitoids, respectively). In the remaining species, cocoon weights were largely similar (8–9 mg).

**Effect on host growth**

The growth of hosts was significantly affected by parasitism in all host species examined when compared with unparasitized larvae (Student’s t-test, *P* < 0.05). Fig. 2 shows the maximum weights attained by parasitized and unparasitized hosts for each of the test species. In *L. oleracea*, *M. brassicae* and *C. chalcites*, growth was rapidly suppressed such that parasitized hosts were markedly smaller than unparasitized hosts after 4–5 days. However, for both *S. littoralis* and *S. exigua* no reduction in growth was observed during the parasitoid’s developmental period. The difference in the growth of parasitized and unparasitized larvae was most pronounced in the case of *L. oleracea*, where the mean maximum weight attained by parasitized larvae was only 6.9% of that of non-parasitized hosts. Similarly, parasitized *M. brassicae* larvae reached a maximum weight only 7.6% of the weight reached by non-parasitized larvae, whilst *C. chalcites* grew to 26.1% of the weight of unparasitized hosts. However, in the case of *S. exigua* and *S. littoralis* the mean maximum weight reached by parasitized larvae was 62.0% and 34.5% respectively, of the maximum weights reached by non-parasitized controls. In both these cases, these differences were largely due to growth of unparasitized hosts after the time when parasitoids had emerged from the parasitized hosts, and not due to suppression of growth during parasitism (growth curves not shown).

**Developmental success of *M. gyrator***

Live parasitoids emerged from over 94% of parasitized *L. oleracea*, with no parasitized hosts pupating (Fig. 3). However, in *M. brassicae* only 52% of parasitized hosts gave rise to live wasps with the remainder either dying during development, or pupating. Moreover, whilst live parasitoid larvae were never found in *L. oleracea* following the egression of the first wasp, in *M. brassicae* 45% of hosts that had produced a live parasitoid had at least one live wasp larva remaining within the moribund host. In *S. littoralis*, whilst fewer hosts were parasitized (as determined by dissection of dead hosts or by wasp emergence), only 7.5% of hosts that produced live wasps still contained a live wasp larva and in only one instance was evidence of parasitism found in a host that had pupated. The majority of parasitized *S. exigua* hosts gave rise to live wasps (ca. 83%) and no hosts contained live parasitoid larvae following egression of the first parasitoid or showed evidence of parasitism on dissection following pupation.

Dissections of all hosts following egression of the parasitoid revealed that self-superparasitism was common and had occurred in all species. The number of parasitoid first instar head capsules was used as a measure of the number of eggs that had been oviposited within each host. An average of 1.4 ± 0.08 head capsules were found in parasitized *L. oleracea* with 80% of exposed hosts being parasitized. However, in *M. brassicae* an average of 4.3 ± 0.44 were counted with 66% of total number of exposed hosts...
being parasitized. *Spodoptera littoralis* was the most heavily superparasitized with an average of 5.0 ± 0.89 head capsules present in each parasitized host, despite only 40% of exposed hosts being parasitized whilst *S. exigua* gave a value of 2.2 ± 0.25 head capsules per host (35% parasitism).

**DISCUSSION**

In these experiments we have shown that the parasitoid *M. gyrator* was able to attack all larval stages of the five noctuid species tested. In all of these species, the third larval stadium was the most frequently parasitized developmental stage. *Lacanobia oleracea* was the most frequently parasitized species in host choice tests. However, it has been postulated that wasps reared on a particular host may subsequently preferentially parasitize the same host species (Smith & Cornell, 1979; Cortesero & Monge, 1994). It has been suggested that parasitism of the same host species in which the parent wasp developed may have an adaptive advantage as such behaviour could contribute towards ensuring the successful development of a wasp’s offspring (Rojas et al., 1999). To a degree, the levels of parasitism relative to the other test species observed in *L. oleracea* may be a reflection of this fact and this phenomenon requires further investigation.

Parasitism by *M. gyrator* resulted in a rapid reduction in the growth rate of host larvae of three of the noctuid species tested, with the ultimate weight achieved by all parasitized host species being significantly lower than unparasitized insects. In the case of *S. littoralis*, however, no effect on the growth of parasitized hosts was detected during the period of the parasitoid’s larval development although unparasitized hosts did grow significantly larger subsequent to the time that parasitoids had emerged from parasitized hosts. For *S. exigua*, the difference in the ultimate weights achieved between parasitized and unparasitized hosts was relatively small, whereas in the other host species the growth rates were markedly different. *Spodoptera exigua* is naturally the smallest of the hosts tested here, and it is possible that the observed reduced impact of parasitism on the growth of this species may have been consequence of the smaller size of this host. It would therefore appear that *M. gyrator* allows hosts to grow to a largely similar size, irrespective of the species parasitized, in order for there being sufficient resource available for its successful development.

The developmental times and cocoon weights for *M. gyrator* reared on different host species may give some indication of the suitability of the different host species for this parasitoid. In general, as the suitability of a host decreases, so the developmental time of the parasitoid increases, and the resulting cocoon weight decreases (Harvey et al., 1999). It was, however, noted that the development times of the parasitoid within the different host species appeared to be correlated with the speed of development of the host; most rapid wasp development was observed in *C. chalcites* which shows the most rapid larval development, whilst development was slowest in *M. brassicae*, the moth with the longest larval development. A further indication of the suitability of a host may be derived by examining the survival of the host following parasitism. When the survival of parasitized hosts was assessed, only 5% of parasitized *L. oleracea* hosts died during parasitism whilst approximately 45% of parasitized *M. brassicae* died before the egression of the parasitoid larvae. The *Spodoptera* species were intermediate in their ability to support parasitoid development, with 68% and 83% of parasitized host producing live wasps for *S. littoralis* and *S. exigua*, respectively. It must be noted, however, that these values for the successful
development of the parasitoid were derived from hosts that were determined to be parasitized by the presence of parasitoid larvae and head capsules and do not take into account the possibility that some eggs may have been encapsulated before hatching. The complete absence of encapsulated eggs on dissection of the hosts indicates that this may be, however, a rare event.

Whilst M. gyrator is a solitary endoparasitoid, with only one parasitoid ever emerging from a given host, it was observed that in M. brassicae and, to a lesser extent, S. littoralis, live wasp larvae were frequently found within hosts from which a parasitoid larva had already egressed. It is generally thought that parasitoid larvae in superparasitized hosts eliminate all competing parasitoid larvae before moulting to the second stadium, however in the case of these two "poorer" hosts this did not always occur and perhaps further indicates that the parasitoid is less well adapted to these host species. In all of the species tested superparasitism was seen to occur, as determined by the dissection of hosts after egression of the parasitoid larva. It was noted that superparasitism was lowest in the host species that gave the highest success rate in terms of parasitoid development (L. oleracea and S. exigua), whilst in M. brassicae and S. littoralis, where poorer rates of survival were recorded post-parasitism, superparasitism was higher. These high levels of superparasitism may have been a contributory factor in the higher levels of mortality observed in these hosts and may indicate that the parasitoid is less well adapted to these hosts. Superparasitism is generally considered to be mal-adaptive for solitary parasitoids (Godfray, 1994) although it has frequently been observed in M. gyrator, even when a large excess of unparasitized hosts are available (H. Bell, unpublished observations) and may indicate that this parasitoid is unable to distinguish hosts previously parasitized by self or conspecifics. The small number of hosts available to the ovipositing parasitoid (5 per host for 24 hours) may have exacerbated the occurrence of superparasitism although it was noted that, particularly in the case of the Spodoptera species, unparasitized hosts were available to the majority of wasps at the end of the experiment. However, there is the potential that superparasitism may be a consequence of the strategy of this wasp to parasitize any suitable host that it encounters, regardless of its developmental stage or whether it is already parasitized. Further studies into the ovipositional behaviour of M. gyrator are currently ongoing in order to clarify this aspect of the parasitoids behaviour.

Bell et al. (2003) reported that this parasitoid could parasitize and develop in all larval stages of L. oleracea that it was presented with. However, the potential for this parasitoid to parasitize a range of hosts had not been investigated. Here we report that this parasitoid is capable of parasitizing all larval stages of a range of economically important species that frequently occur as glasshouse pests in Europe. Field studies, not reported on here, also indicate that this parasitoid can parasitize Autographa gamma (L.), Euplexia lucipara (L.) and several Mythimna species (H. Bell, unpublished data). It has also been reported to parasitize Trichoplusia ni (Hübner) (C. Bloemhard, personal communication).

The results would suggest that this parasitoid is best adapted to parasitizing L. oleracea, and S. exigua, with high host mortality reducing its success in S. littoralis and M. brassicae. Atypical parasitoid larval development in these latter species further point to the fact that they are perhaps less suitable hosts than the former species. However, despite having varying degrees of success when parasitizing different species, this wide host range may prove a useful attribute when one considers the effectiveness of other parasitoids reported on as potential biocontrol agents in the glasshouse, such as Eulophus pennicornis (Marris & Edwards, 1995; Bell et al. 2001) and Cotesia marginiventris (Cresson), that are both highly restricted with respect to the range of hosts they will parasitize, and the stages of those species that they can develop on or within. Interesting aspects of this parasitoid's behaviour, such as its readiness to superparasitize and the persistence of supernumerary larvae within less favourable hosts strongly indicate that further investigations into the behaviour and interactions of M. gyrator with its various host species are warranted.

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