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# The response of an insect parasitoid, *Ormia ochracea* (Tachinidae), to the uncertainty of larval success during infestation

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**Abstract** *Ormia ochracea* is a parasitoid fly which lays its larvae on its hosts, the field crickets *Gryllus integer* and *Gryllus rubens*, in two distinct modes: (1) directly on the host and (2) around the host. In the field, 12.7% of male crickets were parasitized and 3.2% were superparasitized. Despite the disadvantages of parasitizing infested hosts, there was no evidence that *O. ochracea* avoided superparasitism. This and other experiments suggest that the host assessment ability of *O. ochracea* is less than that reported for many hymenopteran parasitoids. By manipulating the number of larvae in each cricket, we determined that four to five larvae per host resulted in the largest number of adult flies. However, as larval number per host increased from one to six, pupal size, and hence adult size, declined. In the field, hosts were found with a mean of 1.7 ± 1.0 (SD) larvae per cricket, suggesting that there may be some selection pressure against larger clutch sizes. Nevertheless clutch sizes larger than the host can support were sometimes found in the field. During the first mode of larviposition, gravid flies deposited no more than three larvae directly onto the host. Larvae deposited directly on the host had a high probability of infesting it. During the second mode of larviposition, gravid flies laid a larger number of larvae around the host (6.1 ± 5.2). Larvae that were laid around the host were less likely to infest a cricket than were larvae that were deposited directly onto it. *O. ochracea* is unique in that its two different modes of larviposition have different probabilities of larval success. Even though the success rate for larvae laid during the second mode of larviposition was low, the possibility of parasitizing more hosts appears to have selected for flies laying more larvae (e.g. increasing clutch size) than is optimal if all the larvae successfully entered a single host.

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## Introduction

Lack (1947), in his influential hypothesis, suggests that animals should be selected to produce the number of offspring that will maximize their reproductive fitness (known as Lack's solution). One of the key assumptions of mathematical formulations of this hypothesis is that an animal will have the ability both to control its clutch size and to assess environmental variables such as patch quality in order to lay an optimal number of eggs (see Godfray et al. 1991). Recently a few theoretical studies have attempted to determine how the estimates of an animal's optimal clutch size change as the limitations of an animal's abilities are taken into account (Godfray and Ives 1988; Mangel 1990). Analysis of such models indicates that an inability to control the number of progeny deposited in a host will lead to the selection for either larger or smaller clutch sizes than would produce the largest number of fertile offspring per host (Godfray and Ives 1988). However no study that we know of has experimentally determined the uncertainty in the number of progeny deposited into a host, studied how this may differ during ovi- or larviposition, and then examined how this actually effects the number of eggs or larvae laid. In this paper we examine this phenomenon in a tachinid insect parasitoid.

In the last decade many studies have used insect parasitoids to explore the factors important for determining clutch size (e.g., Charnov and Skinner 1984; Skinner 1985; Hubbard et al. 1987; Mangel 1989; Hardy et al. 1992). As predicted from Lack's hypothesis and later refinements of it (see Godfray et al. 1991; Wilson and Lessells 1994), many parasitoids regulate clutch size according to host size (Hardy et al. 1992), host species [even when the larva of different species

are the same size (Vet et al. 1993)], or host search time (Strand and Godfray 1989). Furthermore superparasitism occurs in such a way that it can be viewed as having adaptive value (Hubbard et al. 1987; van Alphen and Visser 1990).

In virtually all theoretical and experimental studies of clutch size in insect parasitoids it has been assumed that the parasitoid has the ability to assess host quality and accurately control clutch size (Mangel 1989; Wilson and Lessells 1994). These studies have focused on the hymenopteran parasitoids that use an oviposition strategy in which the female handles and/or inserts her ovipositor into the host. This strategy gives these species the potential to control clutch size as well as to assess the host's external and internal condition. Using these assumptions several workers have determined the theoretical optimum as well as the actual clutch sizes for a number of species (see Godfray 1987, 1994).

Not all parasitoids are hymenopterans, however. The tachinids, a very large and diverse group of dipteran parasitoids, rarely deposit eggs directly into a host (Wood 1987). Most lay their eggs or larvae either on or around the intended host. Given their method of ovi-or larviposition, it is possible that they will not be able to assess accurately host quality or control clutch size.

*Ormia ochracea* is a parasitoid fly that attacks field crickets in both Texas, where it parasitizes *Gryllus integer* (Cade 1975) and Florida (Walker 1986) where it attacks *G. rubens*. Gravid flies are attracted by the calling song of male crickets (Cade 1975) (female crickets do not sing). The ear of the female fly is sensitive to the frequency of the cricket calling song (Robert et al. 1992). Once a gravid fly has located a cricket, it larviposits in two different modes; directly onto the cricket, as well as on the ground around it (Cade 1975). Typically this results in larvae being placed both directly on the host, as well as on the ground surrounding it. The number of larvae laid during these two larviposition events is examined in this paper. Once the larvae are on the cricket, they immediately burrow into it. The first instar larvae embed into the host's muscle for the first 3 days; they then migrate to the abdomen. Larvae emerge from the host approximately 7 days after infestation. The host dies within 1 day of larval emergence (Adamo et al. in press).

Females lay live larvae and contain 65–517 mature first instar larvae, (with a mean of 219 $\pm$ 38 (SE) from field collected females, Wineriter and Walker 1990) in their larviparium. Females usually contain both mature and immature larvae, as well as eggs, suggesting that they mature eggs over time and probably do not exhaust their supply of larvae during larviposition.

In this study we determine the number of larvae per host that produces the largest number of adult parasitoids. This number is compared with the number of larvae laid by the flies in the laboratory and the field during both modes of larviposition. We compare the relative uncertainty of successful host infestation between the two modes of larviposition and examine how this has influenced the clutch size strategy of *O. ochracea*.

## Methods

### Animals

#### *Crickets*

*G. integer* and *G. rubens* were collected from the field (Austin, Texas, or Gainesville, Florida, respectively) just prior to the start of our experiments. Briefly, crickets were kept at 28°C and at approximately 65% humidity with a 14:10 h L/D cycle and they were maintained as previously described (Adamo and Hoy 1994).

#### *Flies*

*O. ochracea* were collected in Gainesville, Florida and Austin, Texas for the following experiments. The flies from Texas and Florida were maintained in separate cages and were not allowed to interbreed. *O. ochracea* from Texas were used to infest *G. integer*, their natural host in Texas, while *O. ochracea* from Florida were used to infest *G. rubens*.

Flies were maintained using the procedures described by Wineriter and Walker (1990). Flies were kept at 28°C and at 65% humidity with a 14:10 h L/D cycle in the same room in which the crickets were reared. To maintain the fly colony, crickets were hand-infested with first instar larvae. The larviparium of gravid females was removed and larvae were transferred onto the soft tissue behind the posterior margin of the host's mesothorax using a fine glass probe. This allowed us to control the number of larvae deposited per host. Larvae emerged from their hosts after 7 days when kept at 28°C.

### Definition of clutch size

In hymenopteran parasitoids, clutch size is defined as the number of eggs deposited in or on the host. Because *O. ochracea* has two distinct modes of larviposition, it also has two "clutch sizes". In the first mode, clutch size refers to the number of larvae that are placed on the host. In the second mode, clutch size refers to the number of larvae that are placed around the host. In other parasitoid systems, uncertainty in clutch size refers to the inability of a parasitoid to lay an exact number of eggs (see Godfray 1987). This results in the female's lack of control over the number of eggs that are actually deposited in the host. In *O. ochracea*, the uncertainty in clutch size in the second mode of larviposition refers to the uncertainty in the number of larvae that will actually enter a host after being deposited, not in the fly's ability to control the number of larvae placed around the cricket. This uncertainty constrains the ability of the fly to control the number of larvae that will infest a host. The fly can only set the upper limit for the number of larvae per host.

### Description of larviposition in *O. ochracea*

#### *Field observations*

To identify factors which may be important in controlling clutch size in *O. ochracea*, larviposition was observed and filmed while collecting flies in Austin, Texas at the Brackenridge Field Station. Flies were collected over a 2-week period from 7 to 21 October 1992. Flies were attracted to a loudspeaker which played a tape of *G. integer* calling song. On top of the loudspeaker was a plastic funnel, at the bottom of which was a live male *G. integer*. The behaviour of the fly and the cricket were filmed using a videocamera. Crickets used as "bait" had been kept in the laboratory for several days prior to the

experiment and were therefore known not to be carrying parasitoids. After having interacted with the flies that were attracted to the speakers, these crickets were dissected to determine if they were parasitized and, if so, with how many larvae. The number of larvae that were deposited on the funnel were also counted.

We also collected calling crickets and male and female crickets that flew towards the speaker. Specimens were preserved in ethanol, and their size and the size and number of any *O. ochracea* larvae were noted. Specimens collected from the area in June–September 1991 were also examined for *O. ochracea* larvae.

To determine if a relationship between clutch size and host size existed in the field, we measured the thorax width and body length of crickets caught in the field. Simmons (1986) has shown that these measures are a good estimate of size (e.g., weight) for a related field cricket *Gryllus bimaculatus*. We then counted the number of larvae present.

*Indoor arena*

We placed a speaker (Panasonic model RQ2735) in an indoor arena ($2.2 \times 1.8 \times 1$ m). The arena was kept at room temperature (22°C) and on a 12:12 h L/D cycle with food and water ad libitum. Dusk was simulated by turning on a shaded 40-W bulb for 30 min when the overhead lights were switched off. One gravid *O. ochracea* was placed in the arena the day prior to the experiment. The arena always contained two *G. integer* male crickets (at least one of which produced calling song after each trial) and one female *G. integer*, therefore the flies were not deprived of hosts between trials. A live *G. integer* male cricket was tethered (glued) onto white paper on top of the speaker that played *G. integer* calling song. The volume setting of the speaker remained the same for all the trials. We found that in the field the flies were most responsive to the speakers for about half an hour after sunset. Therefore we observed the speaker for the 30 min of simulated dusk, or until the fly contacted the cricket. The tethered crickets as well as the white paper were then collected. We examined the cricket both internally and externally to determine the number of larvae both on and in it. We also counted the number of larvae on the white paper. Flies were used a maximum of 3 consecutive nights before being replaced.

During three different trials in the indoor arena, gravid flies were given dead, plastic-coated (Krylon clear acrylic spray coating) crickets instead of live crickets as targets for larviposition. The number of larvae deposited on and around the model were counted.

The effect of larval number on pupal size and viability

To calculate the number of larvae per host that results in the highest number of surviving adults, *G. integer* and *G. rubens* crickets were hand infested with one to ten larvae. The number of larvae that emerged and pupated was recorded. The width of the resulting pupae was measured using vernier calipers and the number of pupae that yielded live flies was also recorded. The sex and size of the resulting flies was recorded.

Superparasitism

To determine if superparasitism occurs in field populations, we examined field caught samples (1992 sample only). We only considered a host to be superparasitized if it had two distinct size classes at different stages of development (i.e., one group still embedded in thoracic muscle while the others had implanted in the abdomen—see Adamo et al. in press for details).

Because we did find evidence of superparasitism in the field (see Results), we studied the fate of larvae that are laid in a parasitized host in the laboratory. We manually placed larvae onto crickets which had been preinfested with three larvae 10 min, 1 day and 3 days before. A randomly selected subset of crickets was dissected 2 and 5 days (unless larvae had emerged from the host) after the second infestation and the size, number and position of all the larvae were recorded. The larvae were allowed to emerge from the remaining crickets and their number and the viability of the pupae were noted.

To determine if there is any evidence that gravid flies will avoid depositing larvae on already parasitized hosts, a gravid fly was placed in a cage (64 cm high, 30 cm wide) with one healthy male cricket for 1 day. The next day the cricket was removed and replaced with a male that had been infested 3 days before but which was still producing calling song. In some of the trials ($n = 10$) crickets had been parasitized by placing them in a cage with an *O. ochracea* female which was allowed to larviposit on it. This gave *O. ochracea* an opportunity to mark the host, in the way that some hymenopteran parasitoids do (Strand 1986). The fly that was used to infest the crickets was never the same gravid fly that was used in the subsequent test. In the other trials ($n = 20$) the males were hand-infested. The next day a female cricket was placed in the cage. The order with which each of the three groups of crickets were presented to the fly was randomly chosen for each trial. The number of crickets parasitized in each of the three groups (healthy, parasitized and female crickets) was noted.

The crickets were left for only 1 day with the fly because that seemed to decrease the chance that the flies would show abnormal larviposition because of a lack of suitable hosts. For example, we found that *O. ochracea* will deposit larvae on singing *G. bimaculatus*, which has a very different calling song from that of *G. integer* and *G. rubens*. but this only occurred after the crickets had been in the same cage with the fly for 3–4 days (*O. ochracea* larvae can successfully develop inside *G. bimaculatus*, Adamo et al. in press).

Statistical analysis

We analyzed our results using ANOVA with the appropriate post hoc tests when the data were found to be homoscedastic and normally distributed (Sokal and Rohlf 1981). Data that were not normally distributed or needed to be tested using ranks were analyzed using non-parametric procedures (Meddis 1984). Most calculations were done using SYSTAT.

## Results

### Description of larviposition in *O. ochracea*

#### Description of the behaviour in the field

In the field, the flies approached the speaker at dusk and continued to arrive at the speaker for about 35 min. Once the speaker was turned on, flies arrived in less than 30 s. In many cases the flies did not approach the cricket, but sat at the edge of the funnel, or walked around its rim. A total of eight crickets were exposed over 6 nights to the flies and of these six were parasitized. One of the crickets that was not parasitized began intense grooming behaviour after being contacted by the fly. In five cases the fly landed briefly (less than 1 s) on the cricket. In three of these cases the cricket was later found to be parasitized. In another 3 cases crickets were parasitized without being touched by a female fly. Parasitized crickets had $1.8 \pm 0.7$ SD (N = 6 males) larvae per host.

When the funnel was subsequently examined, it contained three to eight larvae after the fly had left the cricket (mean $5.2 \pm 2.8$, $n = 8$ trials). The larvae ranged from 3 to 8 cm from the cricket.

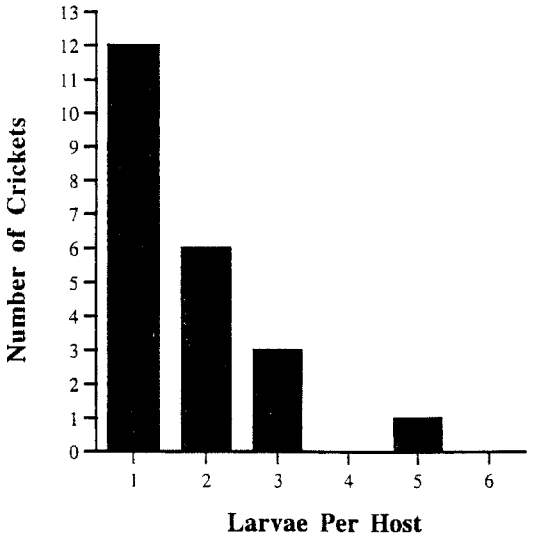


**Fig. 1** The number of larvae per host in the field

**Table 1** Rate of parasitism in field samples from Austin, Texas

| | No. collected | No. parasitized | % Parasitized |
|---|---|---|---|
| 1991 | | | |
| Males | 210 | 14 | 6.7 |
| Females | 147 | 6 | 4.1 |
| 1992 | | | |
| Males | 63 | 8 | 12.7 |
| Females | 42 | 0 | 0 |
| Total | | | |
| Males | 273 | 22 | 8.1 |
| Females | 189 | 6 | 3.2 |

There is no evidence that *O. ochracea* alter their clutch size based on host size. There was no significant correlation between host size and clutch size in field samples (Spearman's $r = 0.137$, $n = 13$, $P > 0.1$).

Figure 1 shows the distribution of clutch sizes observed in the field for male *G. integer* crickets. In total, 8.1% ($n = 273$) of males were parasitized (Table 1). In the sample collected in 1992, 12.7% ($n = 63$) of males were parasitized. Females were parasitized less frequently than males (3.2%, $n = 189$; *G*-test, $G = 5.1$, $P < 0.03$), but the largest clutch size, 6, was found in a female cricket.

## Larviposition in the arena

The flies landed on the speaker, walked towards the tethered crickets, usually walked quickly around the thorax and upper abdomen, then walked around the cricket, about 3–5 cm from it. Crickets were never parasitized with more than two larvae under these conditions, and extra larvae were not found on any of the parasitized crickets when they were examined immediately after the fly had left. The mean clutch size was $1.3 \pm 0.5$ ($n = 5$ flies and 8 crickets). There was no significant difference in clutch size (Mann–Whitney, $P > 0.1$) between the laboratory and field trials, though the sample sizes were small. The number of larvae found on the white paper (i.e., the number of larvae that were laid around instead of on the cricket) varied from 2 to 18. The mean was $6.1 \pm 5.2$ ($n = 8$). They were deposited 3–10 cm from the cricket.

In the indoor arena, all three of the flies presented with a dead, plastic coated cricket larviposited on it. The flies also laid larvae around the model. On inspection of the model, we found two flies had deposited two larvae, and one fly had deposited one larva. The flies deposited five, five, and three larvae around the model, respectively.

## Effect of larval number on pupal size and viability

Pupal size declined as the number of larvae per host increased in both species (Fig. 2). Not only did pupal size decrease with increasing larval number, but larval mortality tended to increase as well (Fig. 3). Of the larvae that were placed singly on the cricket's pronotum (*G. integer*, $n = 30$) 90% eventually pupated, while only 60% of the larvae placed on the cricket in clutches of six eventually pupated ($n = 15$ crickets).

Pupae that failed to metamorphose into flies tended to be smaller ($2.95 \pm 0.47$, $n = 176$) than pupae that successfully developed into adults ($3.21 \pm 0.42$, $n = 237$; *t*-test, $P < 0.001$, Fig. 4). As would be

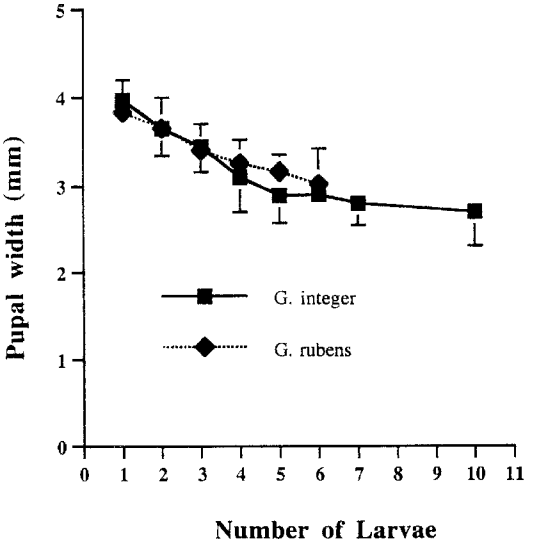


**Fig. 2** Pupal size decreased as larval number per host increased *Gryllus integer*, sample size (crickets) for each larval number: 8, 22, 21, 5, 8, 7, 27, ANOVA test for trends, $F(1, 142) = 103.4$, $P < 0.001$; *G. rubens* $n = 8$, 30, 17, 36, 10, 6, ANOVA test for trends, $F(1, 102) = 31.9$, $P < 0.001$). All *values* are given as means with SDs

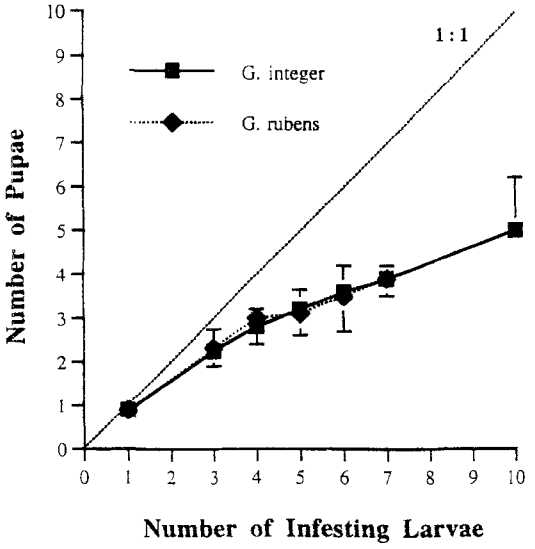


Fig. 3 Larval mortality increased as larval number per host increased (frequency table test for trends, $Z = 2.53$, $P < 0.01$, Meddis 1984). The sample sizes (number of crickets) were *G. integer*—30, 33, 10, 28, 15, 10, 20; *G. rubens*—10, 10, 10, 15, 10, 10

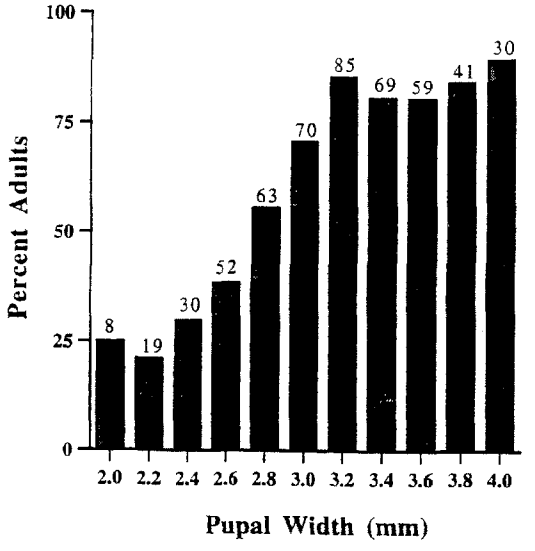


Fig. 4 Smaller pupae were less likely to metamorphose into adults (*G. integer*, Spearman's correlation, $r = 0.88$, $n = 11$). The *number* above each *bar* denotes the number of pupae per group

predicted, fewer pupae metamorphosed into flies from large clutches than from smaller ones (*G*-test, $P < 0.01$, alpha error adjusted for multiple comparisons). For both *G. integer* and *G. rubens*, we counted the number of adults produced by each clutch size: four or five larvae per host produced the largest number of adults in *G. integer*, four larvae produced the largest number in *G. rubens* (Fig. 5).

On dissecting the crickets of both species that failed to produce the expected number of pupae, there was

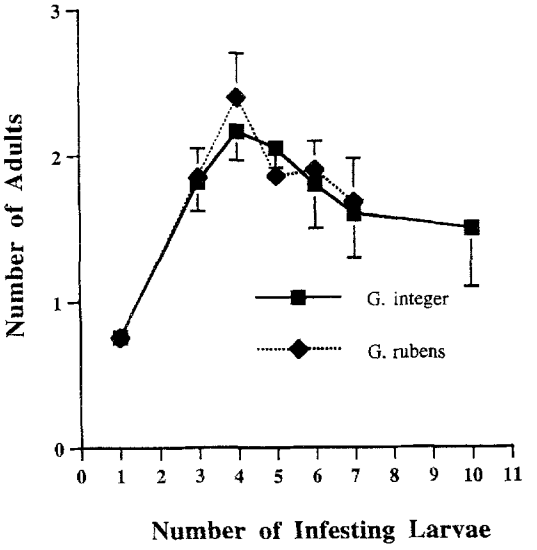


Fig. 5 The number of adult flies that resulted from different numbers of larvae per host. (*G. integer*, ANOVA F (7, 112) = 5.96, $P < 0.01$ with Bonferroni a posteriori comparisons, 4 larvae result in significantly more adults than 3 to 6 larvae, $P < 0.05$; *G. rubens*, ANOVA $F(5, 89) = 6.32$, $P < 0.01$ with Bonferroni a posteriori comparisons, 4 larvae result in significantly more adults than do 3 or 5 larvae, $P < 0.05$). G. integer $n = 10, 12, 20, 10, 10, 10, 20, 27$; *G. rubens* $n = 10, 20, 18, 18, 18, 10$. The *data values* represent the means and the *error bars* the SD

often no trace of the missing larvae, although in others there were dead larvae at all stages of development. There was no obvious sign why some larvae survived and why others did not. There was no evidence of cannibalism or fighting amongst the larvae (e.g., the presence in the host abdomen of larval parts, obviously damaged larvae, or larvae feeding on other larvae), although the possibility cannot be ruled out.

The sex ratio of the flies at emergence was not significantly different from 1:1 (*G. rubens* 21 males, 26 females, *G. integer* 54 females, 45 males; $G = 0.01$, $P > 0.1$). Male flies (thorax width = 3.07 ± 0.32 mm) were significantly larger than female flies (2.78 ± 0.24, *t*-test, $P < 0.01$).

## Superparasitism

Of male crickets found in the field 3.2% ($n = 63$) were superparasitized (no female crickets were found to be superparasitized). Given that the rate of parasitism in the field was 12.7%, 25% of parasitized males were superparasitized. However, because we can identify with certainty only those cases of superparasitism in which the two clutches were more than 3 days apart, the rate of superparasitism in the field is likely to be higher than the field data suggest.

In the laboratory trials, male crickets that were already parasitized were as likely (26/30) to be infested as were previously unparasitized males (19/20; *G*-test,

$G = 1.00$, $P < 0.05$). Gravid flies larviposited on both hand-infested crickets (17/20) and fly-infested (9/10). Females were not parasitized (0/10, $G$-test, $P < 0.01$, alpha error adjusted for multiple comparisons), suggesting that calling song was an important cue for releasing larviposition in *O. ochracea*.

Larvae that parasitized crickets 24 h or more after the initial infestation never successfully emerged from the host (*G. integer* $n = 28$ crickets; *G. rubens* $n = 10$ crickets). The younger larvae grew normally but when the older larvae emerged, the host died and the younger larvae died with the host. Therefore 24 h after the first infestation, secondary infestations yielded no adults. There was no evidence that the older larvae were smaller because of the presence of the second infestation. *G. integer* that were infested with a second group of larvae 1 day later yielded larvae that were not significantly smaller than those that were in singly infested hosts (doubly infested *G. integer* with three surviving larvae—pupa width, $3.32 \pm 0.26$, $n = 13$ crickets; singly infested *G. integer* with three surviving larvae—pupa width, $3.44 \pm 0.28$, $n = 21$ crickets, $t$-test, $P > 0.1$).

If hosts were parasitized by a second group of larvae within 20 min of the first infestation, both groups of larvae successfully emerged from the host. The resulting pupae were the same size as pupa from a host parasitized by a single fly with the same number of larvae (doubly infested *G. integer* with five surviving larvae—pupal width, $3.02 \pm 0.31$, $n = 7$ crickets; singly infested *G. integer* with 5 surviving larvae—pupal width, $2.89 \pm 0.39$, $n = 8$ crickets, $t$-test, $P > 0.1$).

## Discussion

### Superparasitism

It is possible that some of the superparasitized males may have acquired larvae during an agonistic encounter with a parasitized male, although this has never been observed in the field. However even if this does occur, it is unlikely that it could account for all of the superparasitism found in males. Agonistic encounters are not more common than interactions with females, at least in the related field cricket, *Gryllus pennsylvanicus* (Souroukis and Cade 1993) and as the rate of parasitism in females is only 3.2%, it is likely that at least some of the superparasitism seen in the field in male crickets was caused by double infestation by gravid flies.

In *O. ochracea* all larvae that were deposited one day or more after a host's initial infestation did not survive. Therefore it would probably be valuable if flies could avoid parasitized hosts. Flies are likely to encounter parasitized hosts in the field because parasitized crickets do not show a significant decrease in their calling behaviour even 3 days after infestation (Cade 1984). However, there was no evidence that *O. ochracea* can avoid parasitized hosts in either the field or the laboratory, although this still needs to be rigorously tested. Nevertheless, a related ormiine which infests katydids, *Ormia lineifrons*, also appears not to be able to identify previously parasitized hosts (T. Burk., unpublished work).

Most of the calling male hosts of *O. ochracea* are not parasitized even towards the end of the field season (in 1992, 85% of calling males were not parasitized). This suggests that host availability is probably not a limiting factor for the flies, and therefore superparasitism in *O. ochracea* is unlikely to be an adaptation to exploit a rare host.

In the indoor arena, female flies larviposited on dead, plastic coated crickets. This was also observed by Cade (1975). The flies deposited the same number of larvae on the dead models as they did in the field and in other arena trials with live crickets. The apparent inability of *O. ochracea* to discriminate between live and dead hosts or between parasitized hosts and unparasitized hosts is in striking contrast to the ability of many hymenopteran parasitoids (Spiers et al. 1991). The hymenopteran parasitoids that have been studied use a modified ovipositor to directly inject eggs and/or venom into the host which gives these species an opportunity to sample the host's internal environment. However, few gravid tachinids contact the inside of their progeny's potential host (Wood 1987) which may place a constraint on their ability to perform detailed host assessment.

Although some hymenopterans mark their hosts to prevent superparasitism, host marking has not been previously reported in tachinids (van Alphen and Visser 1990) and appears not to exist in *O. ochracea*. At first glance, it might seem that the inability of most tachinids to assess internally their host would favour the evolution of host marking behaviour. However it seems likely that female flies would gain few benefits from marking their hosts. Because the presence of a younger clutch inside the host does not appear to effect the size or mortality of a clutch that is at least a few hours older, there may be little selection pressure for *O. ochracea* females to develop a marking system to repel conspecifics (see Roitberg and Mangel 1988). Whether marking may be adaptive to prevent self-superparasitism would depend upon the female flies' re-encounter rate with the same host (see Roitberg and Mangel 1988). Given the low rate of parasitism in the field, this factor is also unlikely to exert much selection pressure towards the evolution of marking behaviour.

### Optimal clutch size

A first estimate of Lack's solution in *O. ochracea* is the clutch size that produces the maximum number of surviving adults, which is four in *G. rubens* and four or

five in *G. integer* (Fig. 5). More realistically, calculating a better estimate of the optimal clutch size requires a measure of the fecundity of the resulting offspring. In *O. ochracea*, larger clutches do produce more adult flies, but these flies tend to be smaller. We do not know the effect of size on adult fitness for either male or female *O. ochracea*. *O. ochracea* do not breed well in the laboratory (only about 20% become gravid: personal observations; Wineriter and Walker 1990), therefore testing the fitness of the progeny in the laboratory is problematic, and testing it in the field has not yet been attempted. Nevertheless, we have good circumstantial reasons to think that decreased adult size decreases a fly's fitness. Female fecundity declines as female size declines in other parasitoids (Waage and Ng 1984; Hardy et al. 1992). There may also be a cost to being a small male. Male ormiine flies appear to form mating aggregations around tall landmarks (Lederhouse et al. 1976). Whether large size would increase a male's success in these aggregations remains unknown, but the observation that males are larger than females suggests that larger size may bestow some competitive advantages to males. The optimal clutch size will decrease if small flies have lower adult fitness (Godfray 1987). This may partly explain why *O. ochracea* directly deposit no more than three larvae on their host.

Although we lack the data needed to calculate the optimum clutch size, the optimal number of larvae per host cannot be greater than the host can support. Therefore for both *G. integer* and *G. rubens* the optimal number of larvae per host cannot be more than four or five. Nevertheless, hosts are occasionally found with clutch sizes above this maximum (our data; Walker, personal communication). This also occurs in the field in Hawaii, where the cricket *Teleogryllus oceanicus* can be found with one to six *O. ochracea* larvae per host, even though Zuk et al. (1993) found that only two larvae successfully emerge and pupate from a parasitized host. We suggest that this "non-optimal" clutch size occurs because of the lack of the fly's ability to control the number of larvae that will infest a cricket during the second mode of larviposition. For example, if a parasitized host moves around its burrow (perhaps while courting a female) it may pick up extra larvae. A female cricket may approach the male (or more than one male) in such a way that it picks up a large number of larvae. This would explain the occasional observation of clutch sizes above that which the host can support.

## Uncertainty in *O. ochracea*

*O. ochracea* has an unusual method of larviposition which has two distinct modes. In the first stage, gravid flies deposit a small (range 1–3) number of larvae directly on the host. The larvae that are laid directly on the host appear to have a high probability of infesting it (Fig. 4). Therefore the uncertainty in her clutch size is relatively low. As would be predicted, during this mode of larviposition the fly lays less than four larvae (the number of larvae that produces the largest number of adult flies). When the uncertainty in the number of larvae entering the host is low, the fly does not lay more than the host can support. During the second mode of larviposition, the female lays larvae around the cricket. This second larviposition event is often larger than one host could support (five to eight is the range found in the field experiments). These larvae do not appear to be intended for the cricket that the fly has more directly infested but for any females that may be attracted to the male (Cade 1975). Female crickets are parasitized in the field in both Texas and Florida (Walker and Wineriter 1991) supporting this hypothesis. (Because female crickets do not sing, they are not parasitized directly by the fly). The probability of these larvae infesting a cricket will partly depend on the number of conspecifics that the calling male attracts. In *G. integer*, a calling male mates $0.8 \pm 0.1$ SE times per night (Cade and Cade 1992). However, Wineriter and Walker (1990) found that *Ormia depleta* larvae that are placed on the sand near a cricket, instead of directly on a soft membrane, were less likely to infest the cricket, suggesting that not all of the arriving conspecifics will be parasitized. These observations suggest that there is greater uncertainty about the final number of larvae that will enter a host from the fly's second mode of larviposition than from the first. Even the number of potential hosts cannot be known by the fly in advance.

Mathematical models describing parasitoid oviposition assume one host per oviposition event (see Godfray and Ives 1988). In *O. ochracea* this may not always be the case, which will both increase the possible pay off of laying larger clutches, but will also increase the possible cost (e.g., all the larvae will die if no host appears). The basic mathematical description of fitness, $W = \sum f_i(c_i)\, c_i g(c_i)$, where $W$ is the gain in fitness to the female fly, $f_i$ is the probability that $c_i$ offspring will be found in the host, and $g$ is the fitness function, will be similar for *O. ochracea* as for other parasitoids, though the fitness function will be complex because of the stochastic processes involved.

Mathematical models that attempt to incorporate stochasticity in the number of eggs or larvae introduced into a host into optimal clutch size estimates often require more data than is available for any one species (Godfray and Ives 1988). For example, in the model of Godfray and Ives (1988), whether uncertainty in clutch size should raise or lower Lack's solution depends critically on the shape of the fitness function. Knowing the exact fitness function requires a knowledge of the fecundity of male and female progeny, and this is not known for any insect parasitoid, although there have been estimates made for some hymenopteran parasitoids (see Godfray 1994). *O. ochracea* is unique in that the certainty of the number of infesting larvae per host

varies within the same animal because it has two different modes of larviposition. For this species, the decline in the precision with which the female can control the number of larvae that enter the host correlated with an increase in the number of larvae that the fly deposited. Although the exact fitness function is not known for this species, it does support the analysis of Godfray and Ives (1988) that parasitoids will sometimes be selected to deposit more than the larval number that will yield the optimum number of surviving adults. The cost to this strategy is that sometimes hosts will be "over-parasitized" as is seen in the field with *O. ochracea.*

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