

# Heterospecific ovicide influences the outcome of competition between two endoparasitoids, *Encarsia formosa* and *Encarsia luteola*

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**Abstract.** 1. Studies of inter-specific competition in parasitoids have largely focused on the outcome of within-host competition and the behavioural mechanisms by which female parasitoids prevent competition. Another, less well studied, possibility is oviposition preceded by 'heterospecific ovicide', the destruction of the other species' egg. Heterospecific ovicide essentially eliminates within-host competition.

2. This study investigated the mechanisms and outcome of within-host competition in *Encarsia formosa* and *Encarsia luteola*, solitary endoparasitoids of whitefly pests. These species are known to commit ovicide of conspecific eggs.

3. Competition experiments indicated that the offspring of second-ovipositing females had an apparent advantage in competition, regardless of whether the second female was *E. formosa* or *E. luteola*.

4. Observations of ovipositor movement through the cuticle of host whitefly nymphs showed that both species often committed heterospecific ovicide and then oviposited or host-fed. Multiparasitism and heterospecific host discrimination were less common and absent respectively.

5. Heterospecific ovicide appears to explain the second-female advantage in competition between these species. Second-female advantage is contrary to the paradigmatic view of multiparasitism, where the first-ovipositing female has an advantage in competition or one of the species consistently prevails in competition.

**Key words.** *Bemisia tabaci*, intrinsic competition, multiparasitism, whitefly.

## Introduction

Studies of inter-specific competition in parasitoids have largely focused on two phenomena: (1) the outcome of competition between immature parasitoids and (2) the behavioural mechanisms by which female parasitoids prevent immature competition (Godfray, 1994). One behavioural mechanism of particular focus has been 'heterospecific host discrimination', the rejection of hosts previously parasitised by another parasitoid species (Turlings, 1985; Pijls *et al.*, 1995). Heterospecific host discrimination is possible when females are able to detect changes as-

sociated with prior parasitism. Alternatively, female parasitoids may be unable to detect previous parasitism and oviposit, or behaviourally choose to oviposit in hosts already parasitised by the other species. Oviposition in previously parasitised hosts is called 'multiparasitism'.

Multiparasitism and host discrimination are not, however, the only options available to female parasitoids. Another possibility is 'heterospecific ovicide', the mechanical destruction of competitor's eggs. Heterospecific ovicide has been documented in a few species of ectoparasitoids (Infante *et al.*, 2001; Perez-Lachaud *et al.*, 2004). In the case of ectoparasitoid ovicide, the female eats the eggs of the first female or stabs the eggs with her ovipositor. Heterospecific ovicide is interesting because the outcome of competition is fundamentally altered; the second-attacking female eliminates competition for her offspring. Heterospecific ovicide thus reverses the paradigmatic outcome of multiparasitism, where either the first female or one of the

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species has a consistent advantage in competition (Strand, 1986; Godfray, 1994; Quicke, 1997).

Because the eggs of the first female are exposed on the surface of the host, ovicide makes the most sense for ectoparasitoids. Ovicide is much more difficult to document in endoparasitoids, where the movement of the ovipositor is usually hidden. Nevertheless, conspecific ovicide has been documented in a few endoparasitoids (Arakawa, 1987; Netting & Hunter, 2000; Yamada & Kitashiro, 2002; Yamada & Ikawa, 2003). Heterospecific ovicide has not yet been documented in endoparasitoids but may influence the outcome of inter-specific competition between these parasitoids as well.

This study reports on competitive interactions between *Encarsia formosa* Gahan and *Encarsia luteola* Howard, solitary endoparasitoids of whitefly pests. Conspecific ovicide has been observed in both species (Netting & Hunter, 2000; McElveen & Hunter, unpubl. data). *Encarsia formosa* is a cosmopolitan species used for whitefly biological control in greenhouses (Hodde *et al.*, 1998). *Encarsia luteola* is a sibling species of *E. formosa* found in the Southern United States (Polaszek *et al.*, 1992). The two species are sympatric in the Rio Grande Valley of Texas, U.S.A. and occasionally in Southern California, U.S.A., where they may be found on *Bemisia tabaci* (Polaszek *et al.*, 1992).

*Encarsia formosa* and *E. luteola* differ in reproductive biology. *Encarsia formosa* is infected with parthenogenesis-inducing *Wolbachia* and so is uniparental (Zchori-Fein *et al.*, 2001). *Encarsia luteola* is a sexual autoparasitoid; females develop as primary endoparasitoids of whiteflies, whereas males develop as hyperparasitoids on conspecific females or primary parasitoids (Gerling *et al.*, 1987).

This study investigated competition between *E. formosa* and *E. luteola* on whitefly (primary) hosts. The first experiment determined the outcome of competition between the two species and how this depended on the order of attack. In the second experiment, behavioural observations were used to directly investigate the role of ovicide in competitive interactions between these species.

## Methods

*Encarsia formosa* was originally obtained from a commercial insectary (Ciba Bunting, Colchester, U.K.). *Encarsia luteola* was collected from *B. tabaci* (Gennadius) in the Imperial Valley of California. Both parasitoid cultures were maintained on *Trialeurodes vaporariorum* (Westwood) on green beans (*Phaseolus vulgaris* L) and were reared at 25–27 °C on a 14:10 h light:dark cycle.

### Experiment 1. Progeny production and the outcome of competition

Experimental arenas were created on excised living cotton leaves infested with *B. tabaci* nymphs. The leaves were held individually in plastic 'leaf boxes', which stood upright with the leaf petioles in  $\approx$  3–4 cm of water. A ring-shaped, self-adhesive foam pad ('Callus Cushions'; Walgreens Co., Deerfield, IL,

U.S.A.; 3 × 16 mm height × interior diameter) was fixed to the lower surface of each leaf. Once an arena was in place, all but 15 early fourth-instar hosts were removed using an insect pin. The arena was covered with a piece of nylon mesh held in place with ski wax. All leaves/arenas were used within 24 h of preparation.

Experimental parasitoids were collected at 24-h intervals from pupae-bearing leaves collected from the cultures and held in Petri dishes. Before the experiment, female *E. luteola* were held in groups for 24 h in vials streaked with honey and containing males. *Encarsia formosa* were held for 24 h in vials with honey.

Female *E. formosa* and *E. luteola* were introduced individually into arenas for 4 h. In the 'competition treatments', *E. formosa* and *E. luteola* were introduced sequentially in both possible orders. In control treatments, hosts were exposed to an individual female *E. formosa* or *E. luteola*, at one of two exposure times, morning or afternoon. These exposure periods corresponded to the first and second female introductions in the competition treatments, respectively, and controlled for time-of-day effects on progeny production. Thus, there were two competition treatments (two orders) and four control treatments (two exposure times × two species). After females had been removed from arenas, the whitefly nymphs were incubated until all wasp progeny had pupated and could be assigned to species (10–12 days).

### Experiment 2. Observations of ovicide

The results of the first experiment indicated that second females reduced the progeny production of first females and emerged from a greater proportion of hosts. Whether heterospecific ovicide might have explained the pattern of second-female advantage was determined directly by making observations of the oviposition behaviour of females following the methods of Arakawa (1987) and Netting and Hunter (2000).

Observations were conducted in arenas consisting of ring-shaped, foam callous pads (6 and 12 mm inner and outer diameters respectively; 3 mm height; Dr Scholl's, Memphis, TN, U.S.A.). The sticky side of the callous pad was affixed to a glass slide. A single early fourth-instar *B. tabaci* nymph was removed from a leaf and affixed to a coverslip with a drop of honey. The coverslip was then placed on top of the callous pad, with the nymph dorsal side down and inside the callous pad arena. Because the ventral cuticle of the whitefly is transparent, the movement of the ovipositor and deposition of eggs could be observed by looking down through the coverslip into the whitefly nymph under 10–50× magnification.

A female of one species was introduced into the arena, observed until she oviposited in the host, and then removed. A test female was introduced into the arena 2 h later and observed. Test females were all  $\approx$  48 h old. Before observations, *E. luteola* were confined with males in vials until mating was observed. Ovicide was characterised by jabbing of the previously laid egg with the ovipositor. Oviposition was recorded when an egg was extruded from the tip of the ovipositor inside the host. Host-feeding was recorded when the female's mouthparts contacted the host cuticle at the ovipositor wound.

### Statistical analyses

Analyses consisted of the following comparisons: (1) the number of progeny produced by individual females in the control treatments; (2) the number of progeny produced by a focal species in the control treatment versus each of the two competition treatments; (3) the proportions of progeny attributed to each species in the competition treatments when first versus second in the arena; (4) the relative frequency of different oviposition behaviours observed when females of the two species encountered heterospecific-parasitised hosts.

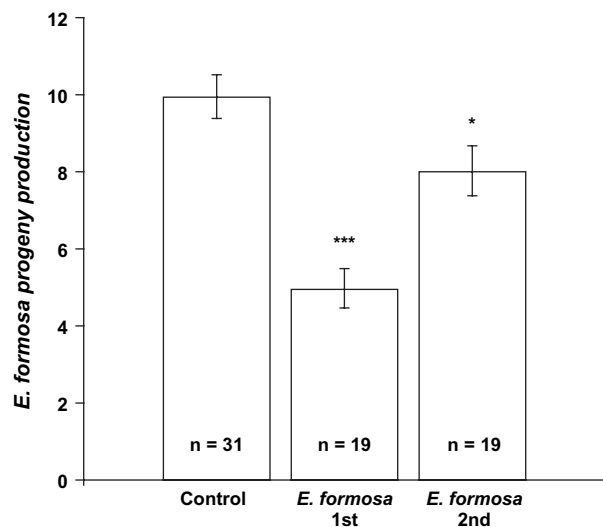
Analyses used generalised linear models in the statistical package GLIM (Crawley, 1993). Analyses involving the number of progeny assumed Poisson distributed errors, which are generally appropriate for count data. The appropriateness of Poisson errors was checked, however, by comparing residual deviance with the residual degrees of freedom. When the residual deviance was much greater than the residual degrees of freedom, indicating overdispersion or greater-than-Poisson variance, the model was corrected to yield a more conservative test (Crawley, 1993). The proportion of progeny produced and the influence of order on the proportion of progeny were analysed using logistic analysis of deviance with binomial errors. To determine whether one species produced significantly more than 50% of the wasp progeny, the competition treatments were pooled and the mean proportion of *E. formosa* ( $\pm 95\%$  binomial confidence interval) was calculated. Order of attack was also placed in the model as an explanatory variable. For the behavioural observations, the frequency of ovicide relative to multiparasitism was compared for *E. formosa* versus *E. luteola* using a  $2 \times 2$  G-test (Sokal & Rohlf, 1981).

## Results

### Experiment 1. Progeny production and the outcome of competition

In the absence of competition, both *E. formosa* and *E. luteola* produced similar numbers of progeny when exposed to hosts in the morning versus the afternoon. *E. formosa* produced a mean (SE) of 10.1 (0.66) and 9.6 (0.39) progeny in the morning and afternoon respectively ( $n_{AM} = 20$ ,  $n_{PM} = 11$ ;  $\chi^2_1 = 0.15$ ,  $P > 0.05$ ). *Encarsia luteola* produced a mean of 6.8 (0.6) and 4.8 (0.66) progeny in the morning and afternoon respectively ( $n_{AM} = 19$ ,  $n_{PM} = 11$ ;  $\chi^2_1 = 2.87$ ,  $P > 0.05$ ). Controls for each species were therefore pooled across time of exposure for further analyses. *Encarsia formosa* produced somewhat more progeny than *E. luteola* in the absence of competition (Figs 1 and 2;  $\chi^2_1 = 19.73$ ,  $P < 0.001$ ).

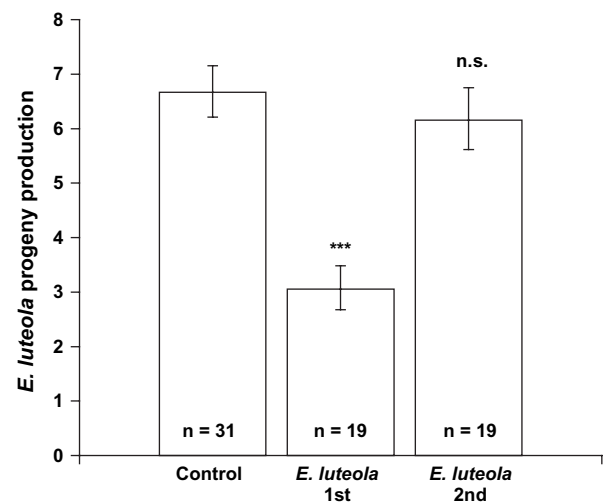
Competition reduced the progeny production of both *E. formosa* and *E. luteola* and the order of exposure affected progeny production (Figs 1 and 2). In particular, second females reduced the number of progeny produced by the first female regardless of species. When *E. formosa* was followed in the arena by *E. luteola*, the number of *E. formosa* progeny produced was reduced by 50% (Fig. 1;  $\chi^2_1 = 39.11$ ,  $P = 4.0 \times 10^{-10}$ ). When *E. luteola* was followed in the arena by *E. formosa*, the number of



**Fig. 1.** Effect of competition from *E. luteola* on *E. formosa* progeny production. Competition with *E. luteola* reduced progeny production of *E. formosa* when *E. formosa* was first (\*\*\*)  $P < 0.001$  and, to a lesser degree, when *E. formosa* was second (\* $P < 0.05$ ) in the arena. Numbers inside the bars indicate the number of replicates.

*E. luteola* progeny produced was reduced by 46% (Fig. 2;  $\chi^2_1 = 24.53$ ,  $P < 0.001$ ).

Progeny production of the second female was less affected by competition than the progeny production of first females. When *E. formosa* followed *E. luteola* in the arena, the number of *E. formosa* progeny produced was reduced relative to the control treatment by  $\approx 20\%$  (Fig. 1;  $\chi^2_1 = 4.88$ ,  $P = 0.027$ ). When *E. luteola* followed *E. formosa* in the arena, the number of *E. luteola* progeny produced was not significantly reduced compared with controls (Fig. 2;  $\chi^2_1 = 0.41$ ,  $P = 0.525$ ).



**Fig. 2.** Effect of competition from *E. formosa* on *E. luteola* progeny production. Competition with *E. formosa* reduced progeny production of *E. luteola* when *E. luteola* was first (\*\*\*)  $P < 0.001$  but not when *E. luteola* was second (NS at  $\alpha = 0.05$ ) in the arena. Numbers inside the bars indicate the number of replicates.

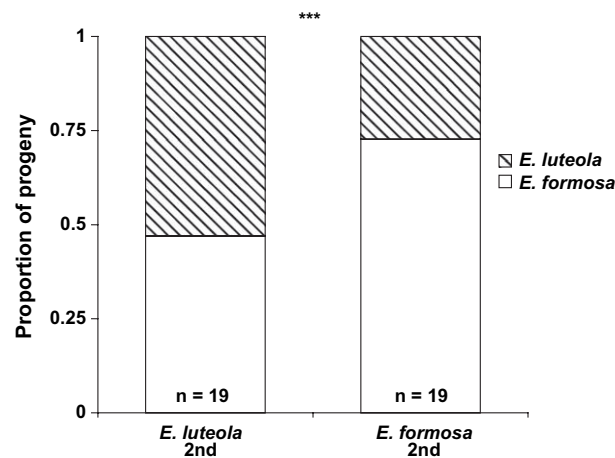
This pattern of second-female advantage in progeny production was also reflected in the proportions of progeny produced. Both *E. formosa* and *E. luteola* produced a greater proportion of offspring when second in the arena than when first in the arena (Fig. 3; analysis of deviance;  $\chi^2_1 = 16.48$ ,  $P < 0.001$ ). Overall, *E. formosa* produced a slightly but significantly greater proportion of offspring in the competition treatments. For the two competition treatments combined, the mean proportion of *E. formosa* was 0.58 (95% binomial confidence limits: 0.53, 0.63).

#### Experiment 2. Behavioural observations

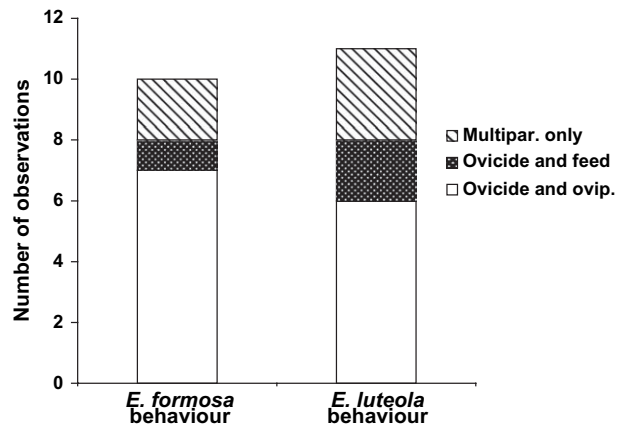
Both *E. formosa* and *E. luteola* attacked heterospecific-parasitised hosts. In only one case, a test female *E. formosa* walked off a host after antennating but then immediately returned to commit ovicide and host feed. For both species, the majority of encounters with heterospecific-parasitised hosts included ovicide (Fig. 4). Female *E. formosa* and *E. luteola* committed ovicide and oviposited in 70% of 10 observations and 55% of 11 observations respectively. Multiparasitism without ovicide occurred in 20% and 30% of observations of *E. formosa* and *E. luteola* respectively. In all cases of host-feeding, ovicide preceded the act of feeding. There was no significant difference between the two *Encarsia* species with respect to the frequency with which they committed ovicide or multiparasitised ( $G_1 = 0.154$ ,  $P > 0.05$ ; Fig. 4).

#### Discussion

The results of Experiment 1 indicate that the offspring of second-ovipositing females had an apparent advantage in within-host competition. *Encarsia luteola* that followed *E. formosa* in arenas produced about as many progeny as they did in control



**Fig. 3.** Effects of order of *E. formosa* and *E. luteola* in experimental arenas on the proportion of total progeny produced by each species. Both *E. formosa* and *E. luteola* produced a greater proportion of progeny when second in the arena than when first ( $***P < 0.001$ ). Numbers inside the bars indicate the number of replicates.



**Fig. 4.** Absolute frequency of heterospecific ovicide followed by oviposition, heterospecific ovicide followed by host feeding and multiparasitism alone (oviposition with no ovicide). Each observation represents the behaviour of an individual female parasitoid. A single observation of antennal host rejection followed by re-encounter and ovicide with host feeding is included as host feeding. *Encarsia formosa* and *E. luteola* committed heterospecific ovicide and multiparasitism with similar frequency ( $G$ -test,  $P > 0.05$ ).

arenas. Second-ovipositing *E. formosa* produced 80% of the progeny that they would have produced under no competition with *E. luteola*. By contrast, the number of progeny produced by first-ovipositing females was reduced by  $\approx 50\%$  relative to no-competition controls for both *E. formosa* and *E. luteola*. Females of both species also produced a greater proportion of progeny when they were second in the arena than when they were first.

The mechanism producing this pattern was probably heterospecific ovicide. Observations indicated that when a female *E. formosa* or *E. luteola* encountered a heterospecific-parasitised host, the most common response was to kill the previously laid egg with the ovipositor and then oviposit. Ovicide followed by destructive host feeding by second females, which commonly occurred in the behavioural observations, might also have led to a reduction in the progeny production of first females in Experiment 1 (see Collier & Hunter, 2001). However, the competition treatments averaged less than one additional dead whitefly relative to the control treatments (data not shown), suggesting that destructive feeding on parasitised hosts did not appreciably reduce the progeny production of first females.

The results for *E. formosa* and *E. luteola* contrast with two previous studies of competition between other *Encarsia* species. Collier *et al.* (2002) and Pedata *et al.* (2002) studied interactions between *E. formosa* and *Encarsia pergandiella*, although cultures of both species were from different populations. Neither of these studies documented second-female advantage. Both Collier *et al.* (2002) and Pedata *et al.* (2002) found that *E. pergandiella* prevailed in within-host competition. Potential mechanisms of *E. pergandiella*'s superiority were explored by Donnell and Hunter (2002), who observed that *E. formosa* hatches before *E. pergandiella* but are much smaller at hatching. These authors suggested that the larger size of first-instar *E. pergandiella* helped the latter prevail in competitive interactions in the host.

Nevertheless, Pedata *et al.* (2002) may have observed evidence of ovicide by *E. formosa*. These authors did not attempt to directly observe ovicide, but found dead *E. pergandiella* eggs in host dissections. They speculated that *E. formosa* may have 'accidentally' laid eggs inside *E. pergandiella* eggs, causing the destruction of the latter, but also raised the possibility of directed ovicide by *E. formosa*. Whether accidental or intentional, ovicide by *E. formosa* was insufficient to overcome the superiority of *E. pergandiella* in multiparasitism. In their dissections, Pedata *et al.* (2002) found no evidence of heterospecific ovicide by *E. pergandiella*.

Under what conditions should heterospecific ovicide be favoured? Species that win in multiparasitism, such as *E. pergandiella*, should not be under strong selection to commit ovicide. Instead, the pay-offs of heterospecific ovicide should be greatest for species that tend to lose in multiparasitism. By committing ovicide, a female parasitoid increases, if not guarantees, the failure of the first female's progeny and the success of their own. A female's propensity to commit heterospecific ovicide should be greatest when parasitised hosts containing ovicide-killed eggs are similar in quality to unparasitised hosts and greater in quality than hosts containing living competitor's eggs. A female's propensity to commit ovicide may therefore also depend on the inter-encounter interval of the females (which was not investigated in this study). This interval can profoundly influence the outcome of multiparasitism (Strand, 1986; Godfray, 1994; Quicke, 1997) and so might be expected to affect the propensity of heterospecific ovicide.

Time costs may also affect a female's propensity to commit ovicide, at least in species that are time-limited (Strand & Godfray, 1989). Studies of conspecific ovicide in *E. formosa* and the ectoparasitic bethylid *Laelis predatus* (Say) showed that handling time associated with ovicide and oviposition was essentially the same as the handling time associated with oviposition alone, suggesting that the time costs of ovicide are negligible for these species (Mayhew, 1997; Netting & Hunter, 2000). Yamada and Kitashiro (2002) also suggested very low time costs of conspecific ovicide in the dryinid *Haplogonatopus atratus* Esaki and Hashimoto. There is considerable debate about whether parasitoids are time-limited or egg-limited in the field (e.g. Rosenheim, 1999; Eilers *et al.*, 2000; West & Rivero, 2000); however, the available evidence suggests that additional handling time is not a major cost to ovicide.

There seem to be clear benefits to individual females to committing heterospecific ovicide, yet it is not completely clear how heterospecific ovicide might affect inter-specific competition between parasitoid populations in the field. Some authors have argued that ovicide is important in interactions between ectoparasitoids, particularly species in the Bethylinidae (Infante *et al.*, 2001; Perez-Lachaud *et al.*, 2004). The present study is the first to document heterospecific ovicide clearly in endoparasitoids. For both ectoparasitoids and endoparasitoids, heterospecific ovicide essentially means that the parasitoid species that most often commits ovicide last will be the species that most often emerges from multiparasitised hosts. The potential effects of this scenario are not well represented in population-dynamic models, which typically assume that the competing parasitoid species attack different stages of the host, and/or one species

emerges from multiparasitised hosts (reviewed by Hassell, 1978; Mills & Getz, 1996; Murdoch *et al.*, 2003).

In part because of a lack of appropriate theory, it is difficult to predict how heterospecific ovicide might affect competition between *E. luteola* and *E. formosa* under field conditions in Southern California and the Rio Grande Valley of Texas. In addition, interactions between these species are likely to be complicated by phenomena other than ovicide, especially autoparasitism by *E. luteola*. Autoparasitism would be expected to confer a strong competitive advantage to *E. luteola* (Briggs & Collier, 2001; Hunter *et al.*, 2002). Other aspects of parasitoid life history and the environment are also likely to be crucial in determining competitive outcomes between these species (Murdoch *et al.*, 2004). The complexity of predicting competitive outcomes notwithstanding, heterospecific ovicide may play a significant role in inter-specific competition in parasitoids, and represents an interesting alternative to the physiological mechanisms of parasitoid competition.

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