

# The Biology of *Encarsia tricolor*: An Autoparasitoid of Whitefly

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*Encarsia tricolor* Förster (Hym.: Aphelinidae) is an autoparasitoid of a number of whitefly pest species. Females develop as primary endoparasitoids, whereas males develop hyperparasitically in other whitefly endoparasitoids including conspecific females. Under a constant regime of 25°C and 16:8 h L:D, the biology of *E. tricolor* was investigated using the Cabbage whitefly, *Aleyrodes proletella*, as host. The following results were obtained. (1) A significant positive linear correlation was detected between size and longevity for both sexes, given a honey diet. Mean ( $\pm$ SE) longevity was  $16.9 \pm 0.62$  days for females and  $13.8 \pm 0.66$  days for males. Females were significantly larger than males. (2) Female *E. tricolor* could develop in all host instars. Development times were slowest in first instar nymphs ( $22.3 \pm 0.34$  days) and fastest in fourth instar nymphs ( $18.7 \pm 0.25$  days). Female development times were not overtly variable. (3) Male *E. tricolor* could hyperparasitize all stages of conspecific female larvae and pupae offered. When parasitizing larvae, male development times were longer, indicating that male development is delayed until the host approaches pupation. (4) Mean ( $\pm$ SE) lifetime fecundity of *E. tricolor* laying female eggs was  $85.36 \pm 13.85$  at a mean rate of  $7.31 \pm 0.27$  eggs/female/day. (5) In a study of sex ratio dynamics in the parasitoid culture, emergent sex ratios were a function of the period of parasitism. The emergent sex ratio (percentage male) from individual leaves increased from 44% after 2 weeks in the culture to 76% after 4 weeks. A concurrent increase in the overall percentage parasitism was also recorded:  $23 \pm 3.4\%$  at 2 weeks to  $87 \pm 4.1\%$  at 4 weeks. (6) Observations on oviposition behavior indicated a clear preference to exploit late instar nymphs for female production. All whitefly instars were used for host feeding. Oviposition times for male eggs (in conspecific pupae) were significantly greater than for female eggs (in late instar whitefly nymphs). © 1995 Academic Press, Inc.

**KEY WORDS:** *Encarsia tricolor*; *Aleyrodes proletella*;

autoparasitoid; reproduction; development; host selection; sex ratio dynamics.

## INTRODUCTION

Aphelinid parasitoid wasps have been among the most effective agents in programs of biological control. Against homopteran pests such as whiteflies and scale insects, this family of parasitoids has achieved an unparalleled consistency of control in diverse agrosystems. Perhaps the best known example of this is the thelytokous aphelinid, *Encarsia formosa*, and the whitefly, *Trialeurodes vaporariorum*, which has become a textbook success of biocontrol in glasshouses. Of the 860 established releases for classical biocontrol using parasitoids listed by Greathead (1986), the highest number, 185, involved aphelinids, of which half succeeded in maintaining their target host below economic threshold densities.

The reproductive biology of many aphelinid species is remarkable. As well as showing conventional, bisexual endo/ectophagous development, aphelinids have been divided into three groups according to their host relations (Walter, 1983). Females always develop as primary endoparasitoids of Homoptera. Males, however, develop in one of three ways: (i) as primary ectoparasitoids of Homoptera (diphagous parasitoids), (ii) as a hyperparasitoid of an homopteran endoparasitoid (heteronomous hyperparasitoids), or (iii) as a primary endoparasitoid of lepidopterous eggs (heterotrophic parasitoids).

Heteronomous hyperparasitoids have been further divided into varieties of autoparasitoids according to the details of male development, but the general term, autoparasitoid, is often used, as it is here. Such deviant host relations have marked implications for the use of these parasitoids in control programs, not least because, in heteronomous hyperparasitoids, for example, males can develop hyperparasitically in conspecific females. Consequently, male production has a negative impact on the rate of growth of the parasitoid population.

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The autoparasitoid, *Encarsia tricolor* Förster, has been reported from 10 whitefly species across Europe and Russia, most commonly *Aleyrodes proletella* (Butler, 1936; Gomez-Menor, 1943), *Aleurotrachelus jelinekii* (Laudonia and Viggiani, 1984), and *T. vaporariorum* (Albajes *et al.*, 1980; Arzone, 1976, 1977). As usual, females develop as primary endoparasitoids, whereas males have been recorded as hyperparasitoids of seven endoparasitoid species including conspecific females (Vet and van Lenteren, 1981; Viggiani, 1984, 1987; Williams, 1989, 1991; Avilla *et al.*, 1991). Because of their minute size (ca. 1 mm) and the divergent ontogeny of autoparasitoid species, fundamental studies on the biology and reproduction of *E. tricolor* are few. An early study by Stüben (1949) described the larval development, mating, oviposition, and host feeding behaviors. Stüben was, however, unaware of sex-linked differences in development and the ability, as with most parasitic Hymenoptera, of virgin females to lay haploid male offspring. Later studies have focused on the potential of the species as a biocontrol agent, particularly in temperature regimes in which *E. formosa* is not effective, or against *T. vaporariorum* on field crops in southern Europe (Arzone, 1976; Isart, 1977; Castresana Estrada *et al.*, 1979; Bordas *et al.*, 1981; Christochowitz *et al.*, 1981; Vet and van Lenteren, 1981). Recent studies of *E. tricolor* have focused primarily on larval development in *T. vaporariorum* and conspecific or other male hosts (Avilla and Copland, 1987; Artigues *et al.*, 1992a,b) or host selection and sex ratio (Avilla *et al.*, 1991; Williams, 1991). This work has focused on the relevance of an understanding of the biology (longevity, fecundity, rates of development, sex ratio dynamics, etc.) of the parasitoid for application to pest control.

#### MATERIALS AND METHODS

Cabbage whiteflies, *A. proletella*, were collected from Brussels sprout plants (var. winter harvest) during January 1986 at Imperial College, Silwood Park, Ascot, Berkshire, UK. Whiteflies were cultured at  $25 \pm 1^\circ\text{C}$  (16:8 h L:D) in muslin-walled cages containing Brussels sprout plants 20–30 cm tall, bearing approximately 10 leaves. Parasitoids were collected by placing plants heavily infested with all stages of *A. proletella* beneath local Viburnum bushes infested with the Viburnum whitefly, *A. jelinekii*, which is parasitized at low levels by *E. tricolor* (Southwood and Reader, 1988). After 14 days, the plants were returned to the rearing rooms and examined daily for parasitized scales. Additional males were obtained by allowing newly emerged *E. tricolor* females to oviposit in *E. formosa* pupae on tomato leaves from a local glasshouse. Male *E. tricolor* emerged approximately 14 days later and were used to

mate females. Parasitoids were cultured in conditions identical to whitefly, using Brussels plants infested with *A. proletella*, added to the culture cage as necessary. All studies were carried out at  $25 \pm 1^\circ\text{C}$  (16:8 h L:D), using *A. proletella* nymphs on Brussels sprout leaves unless otherwise stated.

#### Longevity

Parasitoid pupae were taken from the culture and allowed to emerge in muslin-lidded butter tubs containing dampened cellulose sponge. Each 24 h, wasps were collected, sexed, and transferred to glass vials containing honey. Vials were examined daily for mortality and fresh honey was added as required. Upon death, the parasitoid head capsule was measured at its widest point to an accuracy of 0.01 mm. This was used as an index of parasitoid size.

#### Female Development

Female pupae were placed individually into gelatin capsules and upon emergence were allowed to mate with a young male at room temperature. Females were then confined with an abundance of whitefly nymphs of a particular instar beneath a clip cage. Clip cages were constructed of half a plastic petri dish 35 mm in diameter, 5 mm deep, sealed to the leaf by foam draught excluder around the edge of the dish and held in place against the leaf using an elastic band. After 24 h, the parasitoid was removed and the parasitized scales were allowed to develop. The number of emerging females was recorded daily.

#### Male Development in Conspecific Hosts

Leaves bearing third instar whitefly nymphs were exposed to 10 mated females from the culture for 24 h to give a high ratio of parasitized to unparasitized hosts of uniform age. The female parasitoid larvae so produced were allowed to develop until early larvae (2–3 days old), mature larvae (6–7 days old), or young pupae (10–11 days old). Each leaf was then offered to a virgin female less than 24 h old. Each virgin female could lay male eggs hyperparasitically in the parasitized hosts, but could only utilize the unparasitized hosts for host-feeding. All replicates were allowed to develop until the primary (female) parasitoids were 12–13 days old, whereupon they were transferred individually to gelatin capsules, checked daily for emergence, and sexed. Parasitized scales which failed to emerge were dissected to determine the fate of their contents.

#### Fecundity

Single mated female *E. tricolor* were offered an abundance of third instar whitefly nymphs and transferred

to fresh leaf patches at 48-h intervals until death. To ensure successful mating, a young male was also present in the clip cage for the first 48 h of the experiment, but not thereafter. Parasitized scales were allowed to develop and emerge as above. Pupae which failed to emerge were included in the fecundity data. Only female eggs were laid during the trial.

#### *Sex Ratio Dynamics in the Culture*

Leaves bearing all stages of whitefly and parasitoids were removed from the culture cage on a routine basis: two leaves per plant per week, with an additional whitefly infested plant being added to the culture cage every 2 weeks. The number and sex of *E. tricolor* adults emerging from each leaf were monitored daily thereafter. Each plant was labeled such that its period of exposure to parasitism could be recorded. Apart from the routine leaf samples, plant material was not removed from the culture cage, except when completely dead and devoid of viable parasitoid pupae. As a result of leaf sampling, most plants were defoliated by 4 weeks exposure. The culture sampling began with three plants each separated by a 1-week interval (exposed to parasitism for 1, 2, or 3 weeks) and the addition of a single whitefly infested plant marked the commencement of the formal sampling. The period of monitoring lasted 30 weeks.

#### *Oviposition Behavior*

Young mated females (24–48 h old) with no ovipositional experience were placed in pairs on a leaf area containing an abundance of all host stages. Each pair was observed for the following hour and ovipositional times were recorded using a stopwatch to an accuracy of 1 s. When laying female eggs (unparasitized hosts), all whitefly stages were offered simultaneously in varying proportions. A plan was drawn of the clip cage arena which allowed those nymphs which had been probed and rejected to be distinguished from nymphs parasitized successfully. The sequence and frequency of host discovery by each wasp was also noted. Parasitism was determined by dissection of probed hosts 3–5 days after the observations were made. The experiment was replicated 12 times.

When laying male eggs in parasitized hosts, female *E. tricolor* were offered leaf areas containing only conspecific pupae and prepupae. All pupae which received ovipositional probing during the observation period were transferred individually to gelatin capsules and were dissected 3–5 days later for the presence of hyperparasitic male larvae. The experiment was replicated five times.

## RESULTS

#### *Longevity*

The mean ( $\pm$ SE) longevity of males was 13.8 ( $\pm$ 0.66) days ( $n = 58$ ) compared to 16.9 ( $\pm$ 0.62) days ( $n = 96$ ) for females. The mean ( $\pm$ SE) head width was significantly larger in females (0.243  $\pm$  0.003 mm) compared to males (0.207  $\pm$  0.003 mm) ( $t = 9.11$ ,  $df = 152$ ,  $P < 0.001$ ). This size difference was also evident in the overall body size. There was a significant positive linear relationship between longevity and body size for both male ( $t = 2.80$ ,  $df = 56$ ,  $P < 0.01$ ) and female ( $t = 3.89$ ,  $df = 94$ ,  $P < 0.001$ ) wasps (Fig. 1). Daily mortality data were used to construct survival curves for each sex (Fig. 2).

#### *Female Development*

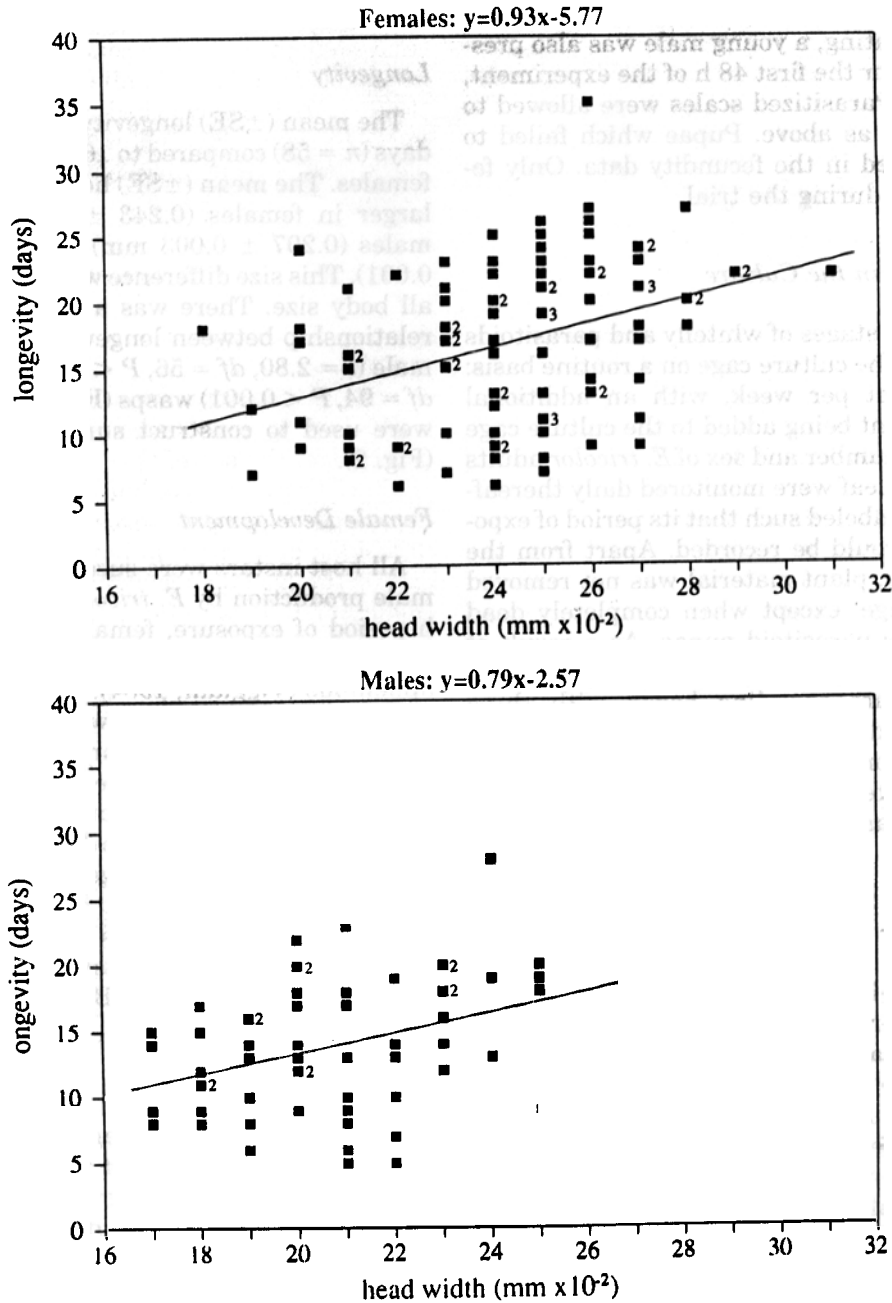
All host instars were successfully parasitized for female production by *E. tricolor*. On average, in the 24-h period of exposure, female *E. tricolor* laid approximately five eggs, which is within a range typical for aphelinids (Viggiani, 1984). Female development time was negatively correlated with the age of the host, being fastest in fourth instar nymphs (Table 1). These values are in close agreement with those of Avilla and Copland (1987) except that they observed fastest female development in third instar *T. vaporariorum* nymphs at 24°C. The range of development times for female *E. tricolor* was not overtly variable within or between replicates, as has been reported for another autoparasitoid species (Flanders, 1939; Broudryk and Douth, 1966; Gerling and Bar, 1971; Donaldson *et al.*, 1986).

#### *Male Development*

Because of the uniform age of primary hosts offered, it was not possible to detect any preference for a particular host instar for male development. All stages of the conspecific female parasitoids offered were successfully hyperparasitized by *E. tricolor*. Male development was consistently faster than female development, given equivalent host stages. As with females, parasitism of early host stages caused the male immature development time to be greatly extended (Table 2).

#### *Fecundity*

The mean ( $\pm$ SE) lifetime fecundity of *E. tricolor* females laying female eggs was 85.4 ( $\pm$ 13.85) at a mean rate of 7.3 ( $\pm$ 0.27) eggs per female per day. Total mean egg production peaked on Days 3 and 4 of the trial and remained high until Day 10, after which it declined. These values are in broad agreement with previous studies at lower temperatures.



**FIG. 1.** Regression of parasitoid size as measured by head width against longevity when maintained individually in tubes on a honey diet without hosts. Figures denote overlapping points. Sample sizes, 58 males, 96 females.

*Culture Sex Ratio Dynamics*

Sampling leaves at 2, 3, and 4 weeks following their introduction to the culture cage yielded a progressively more male biased sex ratio (Fig. 3). This was concurrent with an increasing percentage primary parasitism (means ±SE): 23 ± 3.4% at 2 weeks, 63 ± 6.1% at 3 weeks, 87 ± 4.1% at 4 weeks, and 95 ± 1.5% at 5 weeks.

Most plants were defoliated by 4 weeks of leaf sampling which accounts for the reduced sample at Week 5. When the samples from each week were pooled, clear patterns of emergence for each sex were evident. After 2 weeks of exposure, leaf samples displayed clear peaks of emergence for both sexes, females followed by males. In subsequent samples, the peak of female emergence showed a continual decline whereas the peak of male

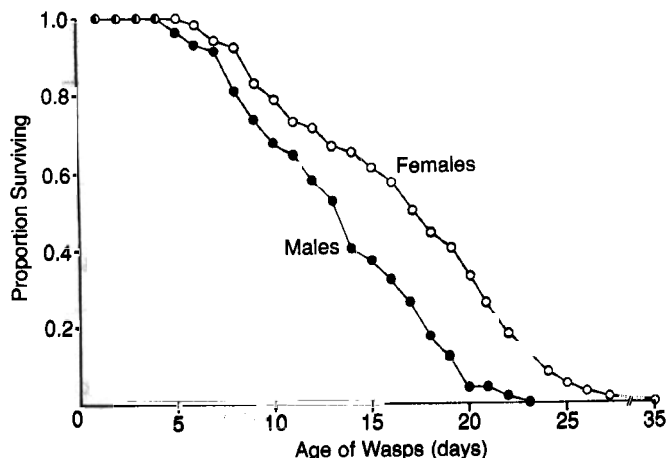


FIG. 2. Survival curves for each sex of *E. tricolor* when maintained on a honey diet without hosts (data from Fig. 1).

emergence became leptokurtotic; male emergence was extended in time. There was no evidence to suggest that the emergence data were biased by the fact that newly emergent females had an opportunity to hyperparasitize conspecifics in the interval (up to 24 h) between daily collections. If such activity had occurred, a distinct secondary peak of male emergence should have been observed some 14 days after peak female emergence: it was not.

#### Oviposition Behavior

There were clear differences in the times required to parasitize primary and secondary hosts. The mean ( $\pm$ SE) drilling and oviposition time for third instar nymphs ( $210 \pm 43.1$  s,  $n = 16$ ) was not significantly different from the time required to parasitize fourth instar nymphs ( $277 \pm 78.3$  s,  $n = 24$ ) ( $t = 0.75$ ,  $df = 38$ , NS). The mean oviposition time required for laying male eggs in conspecific pupae, however, was significantly greater than that for fourth instar nymphs ( $669 \pm 84.1$  s,  $n = 14$ ) ( $t = 3.41$ ,  $df = 36$ ,  $P < 0.001$ ). The dissection results from this and other studies (Wil-

liams, 1991) revealed that the frequency of egg encapsulation in primary or secondary hosts was consistently very low (1–2%). When offered a choice of whitefly instars, there was a marked preference of ovipositing females to exploit late instar nymphs for oviposition (Table 3). All instars were used almost equally for host feeding.

#### DISCUSSION

A detailed study of the biology of *E. tricolor* confirmed the autoparasitic nature of development. As in other parasitic Hymenoptera with haplo-diploid sex determination, virgin females can lay haploid male eggs and can control the sex of their offspring after mating.

There was a positive linear relationship between size and longevity for both sexes. Comparable longevity values in a similar system have been reported for *E. cibiciensis* (male, 9.3 days; female, 17.4 days), *E. adrianae* (male, 17.1 days; female, 23.5 days), and *E. deserti* (male, 18.3 days; female, 22.6 days) parasitizing *Bemisia tabaci* (Lopez-Avila, 1988). van Lenteren *et al.* (1987) investigated the effect of such diets and host plants (cucumber, tomato, and tobacco) on the longevity and fecundity of *E. formosa*. They found no correlation, between parasitoid size and longevity in this species.

Both female and male eggs were able to develop in all stages of primary and secondary hosts respectively, although a strong preference to exploit late instar whitefly nymphs for female production was detected in line with other studies (Artigues *et al.*, 1992b). Development times were extended when males or females were laid in early host stages. When a female egg was deposited in a first, second, or third instar nymph, Avilla and Copland (1987) reported that hatching occurred in the following instar. There are three advantages to a female parasitoid choosing to oviposit in larger hosts. First, she can assess the host resource exactly with regard to size, quality, and suitability at the moment of oviposition. Second, eggs laid in early instar hosts will suffer the same age-related mortality risks as the

TABLE 1

Instar Acceptability and Development Times for Female *E. Tricolor* in *A. proletella* Nymphs

Whitefly instar	Replicates	Mean number of eggs developed/rep ( $\pm$ SE)	First pupae seen (days postoviposition)	Mean development time $\pm$ SE (days)	Range of development times (days)
1	10	4.9 $\pm$ 0.69	12	22.3 $\pm$ 0.34	18–28
2	10	5.6 $\pm$ 0.56	11	19.6 $\pm$ 0.20	17–24
3	10	6.6 $\pm$ 1.08	10	19.1 $\pm$ 0.24	16–24
4	13	5.5 $\pm$ 0.68	9	18.7 $\pm$ 0.25	14–24



TABLE 2

Instar Acceptability and Development Times for Male *E. tricolor* Laid in Conspecific Female Hosts

	Age of female host		
	2-3 days	6-7 days	10-11 days
Number of successful replicates	6	5	6
Number of males emerging	41	27	36
Mean development time $\pm$ SE (days)	19.87 $\pm$ 0.22	16.48 $\pm$ 0.26	14.28 $\pm$ 0.14
Range of development times (days)	18-22	15-20	12-16

host (e.g., predation, disease, etc.). Third, shorter development times in late instar hosts reduce the period for which the offspring is susceptible to hyperparasitism. The increase in development time of male *E. tricolor* laid in young female hosts suggests that the male larva waits until the female larva has grown sufficiently before hyperparasitic development proceeds. This has also been observed in *Encarsia perniciosi* (Chumakova and Goryunova, 1963) and many indirect autoparasitoids which lay male eggs in unparasitized primary hosts in anticipation of future primary parasitism (Cendana, 1937; Flanders, 1936, 1959, 1969; Walter, 1983). Avilla and Copland (1987), however, failed to detect any significant differences in male development times in different conspecific host stages.

There are no data on the frequency of superparasitism in this study, although the frequency of egg encapsulation was very low both host types. *E. tricolor* females avoid primary superparasitism except under conditions of low host availability (Artigues *et al.*, 1992b). The proportion and species of secondary hosts available appear to influence the frequency of primary superparasitism. Primary superparasitism was overtly reduced when *E. formosa* rather than conspecific secondary hosts were offered for male production (Artigues *et al.*, 1992a). This is also reflected in a marked preference to oviposit in nonconspecific hosts rather than conspecifics as has been demonstrated in *E. tricolor* (Avilla *et al.*, 1991; Williams, 1991) and which is discussed later.

Female *E. tricolor* showed rates of egg production in agreement with other studies (e.g., Artigues *et al.*, 1987, 1992a). Like many aphelinid species (Jervis and Kidd, 1986), adult *E. tricolor* are synovigenic and emerge with very few mature oocytes, typically 0.8-2.6. Females must host-feed before full egg maturation can occur. No relationship between the number of mature oocytes at emergence and parasitoid size or subsequent fecundity has been found in *E. tricolor* (Avilla and Copland, 1988), although a strongly positive correlation has been reported for fecundity in *E. formosa* (van Lenteren *et al.*, 1987).

The extra effort required to drill through the parasit-

oid pupal case meant that laying male eggs took about three times longer than laying female eggs. This represents a greater investment in male over female offspring and would be expected to cause a shift in the sex ratio in favor of females (Fisher, 1930). However, such differences are probably of minor importance compared to the time necessary to search for, locate, and assess each type of host. Consequently, inequalities in oviposition times for each sex are unlikely to be significant factors in selecting for biased sex ratios in *E. tricolor*. In this respect, egg limitation and the relative availability of male and female hosts are likely to be far more influential (Godfray and Waage, 1991).

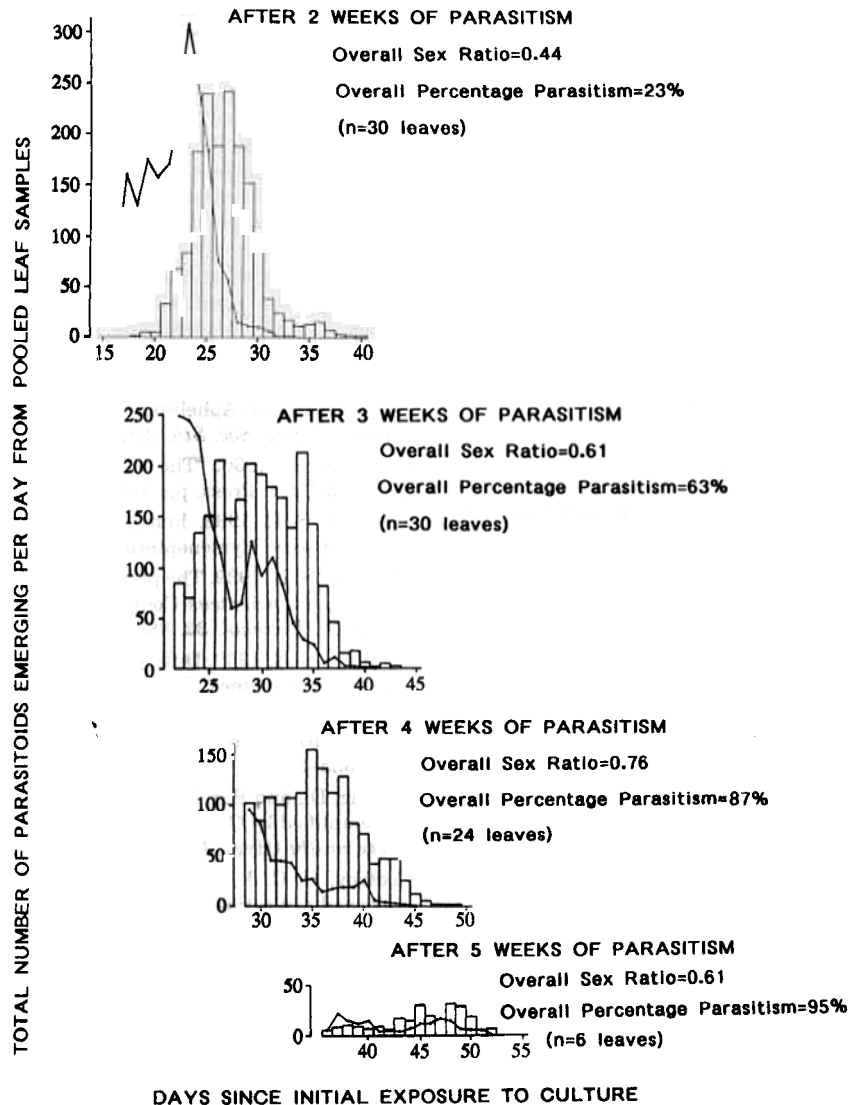
The sex ratio in the culture cage was strongly influenced by the period of exposure of any particular plant. The sex ratio of *E. tricolor* emerging from leaves shifted from female-biased after 2 weeks exposure to a strong male bias subsequently. This again reflects the unusual reproductive strategy of these aphelinids and the intimate relationship between sex ratio and the availability of male and female hosts. It also draws attention to the importance of maintaining abundant material for female production within cultures of these parasitoids. Failure to do so will rapidly drive the sex ratio to a strong male bias resulting in a decreased yield of parasitoid material from the culture (especially females) and possibly an eventual failure of the culture completely.

Recently, two autoparasitoid species have been shown to suffer sex ratio disorders such as reported for

TABLE 3

Ovipositional Preferences When a Choice of Whitefly Instars Was Offered to Inexperienced *E. tricolor* Females

	Whitefly instar			
	First	Second	Third	Fourth
Total number encountered	95	35	80	--
Number parasitized	0	0	16	24
Number drilled but rejected	0	1	23	33
Number used for host feeding	3	5	5	7



**FIG. 3.** Daily emergence of male (bars) and female (lines) *E. tricolor* from leaves exposed to parasitism in the culture cage for 2–5 weeks. Data on parasitoids emerging from leaf samples were pooled at each time point to give total sample sizes of 3677 parasitoids after 2 weeks of parasitism, 4132 after 3 weeks, 1965 after 4 weeks, and 398 after 5 weeks.

several other parasitoids, most notably the pteromalid *Nasonia vitripennis* (e.g., Skinner, 1982; Werren *et al.*, 1986; Nur *et al.*, 1988). Affected *E. pergandiella* diploid (female) eggs will develop as semifunctional haploid males following loss of the paternal genome from the egg. Consequently, in this species, males can develop and emerge from primary as well as secondary hosts (Hunter *et al.*, 1993). In the normally thelytokous *E. formosa*, large numbers of males have been produced following antibiotic treatment suggesting a cytoplasmically inherited microorganism as the causative agent (Zchori-Fein *et al.*, 1992). How common such afflictions are among heteronomous aphelinids is unknown, although examination of *E. tricolor* has revealed no evi-

dence of sex ratio disorders in this species (M. S. Hunter, personal communication).

Of additional relevance to the biocontrol of whiteflies is that *E. tricolor* has been reported to show a marked preference to exploit non-conspecifics over conspecifics for the production of males. This was not apparently due to size or developmental effects of males emerging from another species, but may be a mechanism by which female *E. tricolor* avoid hyperparasitizing their own progeny (Avilla *et al.*, 1991; Williams, 1991). Clearly, the possibility that autoparasitoids may have a highly negative impact on conventional species already parasitizing a particular whitefly pest should be considered. The result of such hyperparasitic attack on

alternative endoparasitoid populations should be carefully assessed before introduction of the autoparasitoid; host-parasitoid-autoparasitoid population models could be of great predictive value in this respect.

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