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## Life History and Host Discrimination of *Encarsia deserti* (Hymenoptera: Aphelinidae), a Parasitoid of *Bemisia tabaci* (Homoptera: Aleyrodidae)

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**ABSTRACT** *Encarsia deserti* males and females develop at 25°C from egg to adult in 11–13 d, but females continue to emerge up to 18 d after pupation. Females live longer than males at 15 and 25°C. Mating occurs 2–48 h after emergence and no eggs producing males were laid by mated females. Females were primary parasitoids of the sweetpotato whitefly, whereas males were secondary, and developed as parasitoids of immature *E. deserti* females. Mated females laid  $63 \pm 4.16$  and  $57.8 \pm 4.24$  ( $\bar{x} \pm \text{SEM}$ ) eggs per female at constant 25°C and fluctuating 22–30°C, respectively. Mated females discriminated between parasitized and unparasitized hosts that were offered to them on a leaf patch, but unmated ones did not. Superparasitism occurred in all cases, but with unmated females up to 14 eggs were sometimes deposited per host. Mated females preferred to oviposit in third and early fourth instars, and unmated females preferred prepupae and young pupae of *E. deserti* females.

**KEY WORDS** *Encarsia deserti*, *Bemisia tabaci*, host discrimination, parasitoids, reproduction

THE SWEETPOTATO WHITEFLY, *Bemisia tabaci*, has many hosts (Mound & Halsey 1978), and damages crops in large parts of the world (Meyerdirk & Coudriet 1985). In our efforts to improve its control, we studied the biology and host associations of the parasitoids that attack it (Foltyn & Gerling 1985, Gerling 1986).

The parasitoid, *Encarsia deserti* Gerling and Rivnay, was introduced into Israel during 1982 from the southwestern United States, where it is a parasitoid of *B. tabaci*. It was grown in our laboratories, released in the field, and its biology and life history were studied. The present article describes some of these studies.

### Materials and Methods

Potted cotton plants ('Acala SJ2') served as hosts for *B. tabaci*, and were reared in controlled environmental chambers at  $25 \pm 1^\circ\text{C}$  and 55–60% RH except where noted otherwise. *E. deserti* individuals were originally obtained from Poston, Ariz., in 1982 (about 1,000 individuals), and reared under the same conditions as their hosts. All cultures were kept in wooden or plastic sleeve cages. For specific experiments, the parasitoids were confined either in "plant cages" or in "leaf cages." The first consisted of a transparent plastic cylinder (20 by 5 cm) that was placed over the infested plant and covered with a fine-mesh piece of cloth. The second was constructed from a clip-on vial (3 by 2 cm), the top of which was replaced by a 100-mesh

wire screen, or from a petri dish with a glass bottom and a plastic top, part of which was also replaced by a 100-mesh wire screen. Direct behavioral observations were conducted with similar petri dishes, but with a glass top. Virgin parasitoids were obtained by confining females in vials (3 by 2 cm) in which a piece of honey-soaked paper had been placed. The vials were watched daily and the females removed according to the requirements of the experiments. Mated females were obtained in similar vials, to which a newly emerged male had been added shortly before the females started to emerge. The presence of immature parasitoids within their hosts was confirmed by placing the whitefly nymph in question in a drop of 0.9% NaCl solution in water on a glass slide under a stereoscopic dissecting microscope, and tearing it apart with two fine needles.

Duration of development of females was studied at 25°C by confining within a plant cage eight mated females on each of three cotton plants that were infested with about 150 whitefly nymphs of instars 2–4. They were removed after 24 h and each day several randomly selected whiteflies were dissected until six parasitized individuals were found on each plant.

Male development was followed in a similar fashion by releasing two unmated females at 25°C on each of three plants, each of which bore 50–60 late larvae, prepupae, and young pupae of *E. deserti* females. Daily dissections were conducted until eight parasitized individuals per plant were found.

Longevity was determined by keeping parasitoids in small vials 0.5 by 3 cm each with a piece of honey-soaked paper, at the desired temperature and a photoperiod of 14:10 (L:D). Those held at

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15°C were removed to room temperature for 1 h every day to feed and digest their food. Ovipositing females were kept with a whitefly-bearing leaf for the first 12 d of the experiment because those were the days during which the females deposited most of their eggs. Eight experiments were conducted. They involved mated and unmated females, as well as males, at 15 and 25°C constant temperatures and at fluctuating temperatures of 22–30°C (10:14 h, respectively). For each set of experiments, median longevity was calculated together with its standard error ( $SE_{median} = SEM \times 1.2533$  [Sokal & Rohlf 1981]). Medians differing by 2 SE or more were considered significantly different.

Preferential mating age was determined by observing the behavior of 10 females that were confined with males from emergence until mating. We also confined groups of males with virgin females of different ages in glass vials. Each group had ratios of between 1:3 and 4:10 males/females. Two hours after confinement, the females were placed singly on unparasitized host nymphs for oviposition. The ages of females that were examined and the numbers of groups for each age (in parentheses) were: 0–6 (5); 6–11 (6); 24–36 (7); and 48–96 (12) h. In addition, four groups of females that had previously been kept at 15°C for 10 d were confined with males and tested for mating.

Daily oviposition of fertilized females was examined individually. We confined each of 15 females with a male for 24 h after emergence, and then in a plant cage, upon a plant with 100–150 whitefly nymphs of instars 2–4. The experiment was run both at 25°C constant and at fluctuating temperatures (22–30°C, 10:14 h, respectively). Each 24 h the female was transferred to a new plant. The experiment was discontinued after 12 d because preliminary observations showed that although females oviposited for 18 d they laid most of their eggs (90% and over) during the first 12 d of their lives. The exposed hosts were kept for 2–9 d and then they were examined for parasitization. Timing of the oviposition peaks under the two temperature regimes was compared using the Kolmogorov-Smirnov test for two samples (Siegel 1956).

Oviposition preference was tested by observing the behavior of seven mated and six unmated females, each in a multiple-choice situation. For experiments with mated females, we isolated a female upon emergence with a male and a cotton leaf bearing a few hosts for 24–36 h. This permitted her to mate, to feed, and to gain some oviposition experience. Afterwards, each female was confined in a leaf cage on a cotton leaf bearing some 50 whiteflies of all instars, and observed until she left the leaf or became disinterested. All activities of the parasitoid were registered, the hosts that were touched by her were dissected, and the presence of parasitoid eggs was recorded.

The ability to discriminate between already

parasitized and still unparasitized hosts was tested by examining the dissection data obtained in the study of developmental duration and by direct observations.

Direct observations of the activity on a leaf were conducted with four mated and six unmated females. In each case the female was placed on a leaf with a suitable host population (24–43 third and early fourth instars for the mated females and 29–51 prepupae of *E. deserti* for unmated females). Each female was followed until she showed no more interest in the hosts or left the leaf patch. Observation was followed by dissections of all hosts with which the females had come into contact. Presence of discrimination by the females was determined by calculating the ratios of rejections of parasitized and unparasitized hosts and determining significance using a G test of independence (Sokal & Rohlf 1981).

## Results

Developmental duration from oviposition to the pupal stage was similar in both sexes and lasted about 8–9 d (Tables 1 and 2). Males started emerging on day 11 after oviposition and completed their emergence on day 13. The females also started to emerge on day 11 and showed a peak of emergence on days 11–14. However, their emergence continued for 15 more d, until day 28 after oviposition. The distribution of emergence from day 14 on amounted to one adult each on days 15, 18–21, 23, 27, and 29.

Longevity of both sexes was greater at lower temperatures (15°C) than higher ones (25°C constant or 22–30°C fluctuating temperature). Mated females lived much longer than unmated ones at 15°C. No difference was observed between longevity of females that were kept at fluctuating and constant temperature, but there is a tendency towards longer life of females not ovipositing versus ovipositing, in the same category (Table 3).

Because all the arrhenotokous species of *Encarsia* whose biology has been investigated have heteronomous sexual development, we examined the host relationships of *E. deserti* and found that only mated females oviposited in whitefly nymphs, whereas unmated ones laid in parasitized whiteflies and developed hyperparasitically. This fact made it desirable to ascertain the mating age of the females in order to use the females more efficiently for our cultures. We conducted preferential mating-age observations and experiments, which revealed that the male is unattracted to the female during her first 2 h after emergence. Thereafter he starts to react to the female by climbing on her back and establishing antennal contact lasting 3–5 min. If she is receptive, he moves back and genital contact is established. All of the females in the groups in the mating experiments, that had been confined with males for 11 h or less, oviposited; and therefore were consid-

**Table 1.** Numbers of *E. deserti* female developing at 25°C

	Time (d)														Remarks	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15-29	
Egg	18	18	12													In host blood
Larva I		6	13	2												Elongate and caudate
Larva II			5	13	1											Closed respiratory system seen
Larva III				3	12	4	3									Host mycetomes dislodged
Prepupa					5	6	5									Open spiracles seen
Pupa						8	10	43 <sup>a</sup>	43 <sup>a</sup>	30 <sup>a</sup>	19 <sup>a</sup>	16 <sup>a</sup>	9 <sup>a</sup>	1 <sup>a</sup>		Meconia cast
Adults emerged										13	11	3	7	8		1 dead pupa remained
Total	18	18	18	18	18	18	18	18	18 <sup>a</sup>							
Total progeny, n = 187																

<sup>a</sup> Until the day 8 the numbers represent 18 parasitized hosts that were dissected daily. Thereafter, the numbers represent actual emergence of the remaining 43 parasitized hosts.

ered to have been fertilized. Of the older females, 70% (24 out of 35) from the 24- to 36-h age group laid eggs, but only 7 females of the 82 that were over 48 h old laid eggs. Only two eggs were laid by the 37 females that had been kept at 15°C for 10 d prior to confinement with males. These results indicated that the principal period of attraction for males by females of *E. deserti* is from hour 2 of life on, and lasts for about 36–48 h.

The results of the tests for daily oviposition (Fig. 1) showed a peak during the first 7 d. No significant differences were observed between the two temperature regimes, but a trend towards higher oviposition was observed under fluctuating temperatures (total,  $\bar{x} \pm \text{SEM}$  per female, 945, 63  $\pm$  SE; 868, 57.8  $\pm$  4.74; for fluctuating and constant temperatures, respectively). There was also a statistically nonsignificant trend towards earlier peak oviposition under fluctuating temperatures. The peak number of eggs per female under constant temperature was obtained from two females on day 3 and by 13 females on days 4–6 after emergence. Peak oviposition under fluctuating temperatures was obtained by seven females on days 1–3 and by six females on day 4 after emergence. The daily oviposition rates did not differ (9–16 versus 5–16 eggs per day per female, fluctuating and constant temperatures, respectively).

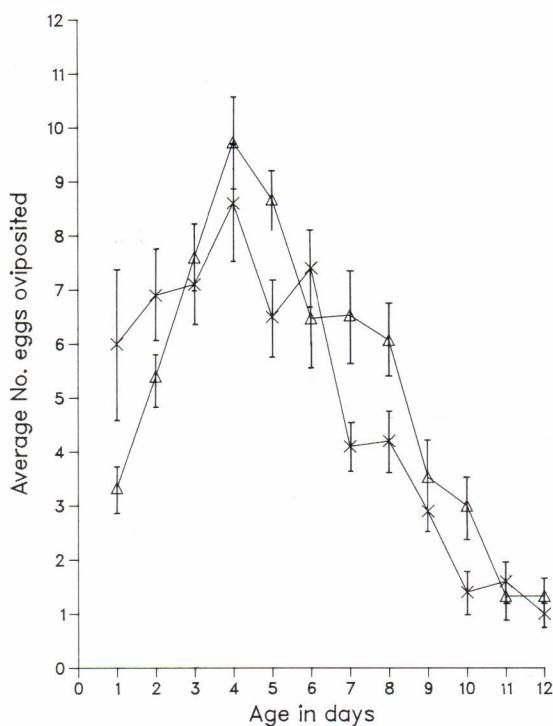
The behavior of the female while on a host-infested leaf was observed and found to contain similar behavioral elements to those described by van Lenteren et al. (1976) for *E. formosa*. The four leading elements were antennal drumming, drilling, host-feeding (feeding of the parasitoid on host body fluids) and preening. The first is practiced after examination of the host, while encountering hosts, and while examining them. After examining the host nymph, an act that may include walking on it and occasionally turning 180°, the female may start drilling with the ovipositor. Her wings and antennae are pressed to her body and the ovipositor is extruded. At times the female may retract the ovipositor while moving about on the host. Once drilling has commenced, she may perform short drilling bouts of up to about 6 s, or longer ones from 90–200 s each. At times, after a short drilling bout, the female resumes drumming for a short time and then commences to feed on the oviposition wound. Drilling is always terminated with preening. Preening may also take place between two sessions of antennal drumming.

In some cases we saw the female reexamine, redrill, and even reoviposit in the same host several times, i.e., the female that had finished drilling left the host, then took a walk on the leaf during which she might examine other hosts, and

**Table 2.** Numbers of *E. deserti* males developing at 25°C

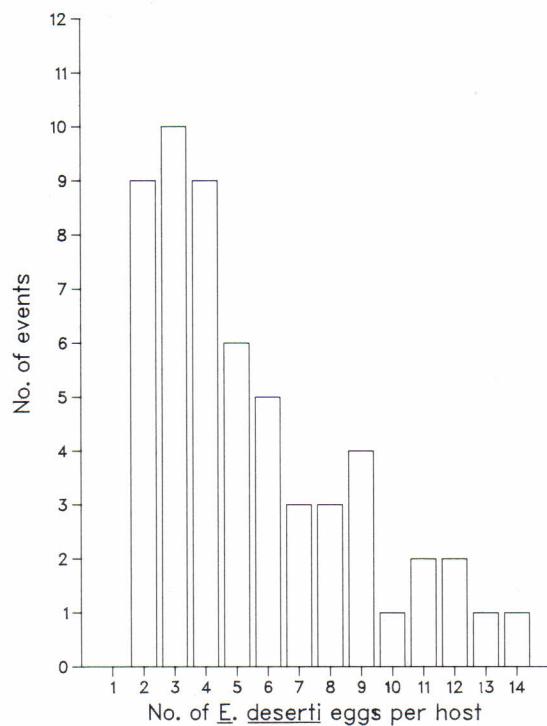
	Time (d)													Remarks	
	1	2	3	4	5	6	7	8	9	10	11	12	13		
Egg	24	24	12												Deposited in <i>E. deserti</i> body fluids
Larva I			12	9											Feeds internally
Larva II				15	20	7									Feeds internally upon molt
Larva III					4	17	8								Leaves host and feeds externally
Prepupa						4									Spiracles open
Pupa							12 <sup>a</sup>	37 <sup>a</sup>	37 <sup>a</sup>	37 <sup>a</sup>	22 <sup>a</sup>	4 <sup>a</sup>	1 <sup>a</sup>		Meconia cast
Adults emerged										15	18	3			1 dead pupa remained
Totals	24	24	24	24	24	24	24	24 <sup>a</sup>							
Total progeny, n = 205															

<sup>a</sup> Until day 7, the numbers represent 24 parasitized hosts that were dissected daily. Thereafter, the numbers represent actual emergence of the remaining 37 pupae.



**Fig. 1.** Average daily oviposition of 15 *E. deserti* females during the first 12 d of their lives under two temperature regimes. Vertical lines mark  $\pm 1$  SEM.  $\Delta$ , 25°C.  $\times$ , 22–30°C.

came back to the original host for another bout. On one occasion, this behavior was repeated by a mated female for six consecutive times and three eggs were laid. Four unmated females, out of the six that were observed, showed similar behavior, returning to the same host two to four times each. The seven mated females that were observed in the host-stage preference tests had 222 encounters with whiteflies ( $\bar{x} \pm \text{SEM} = 31.7 \pm 2.79$ ; range, 26–48). All of the females oviposited mainly on third and early fourth instars (Table 4). Oviposition also occurred in the second instar, in which only two of the seven females laid eggs, and in the



**Fig. 2.** Frequency distribution of the supernumerary eggs deposited by unmated *E. deserti* females during 24 h confinement.

prepupa of the whitefly, in which six females laid. Host-feeding was performed by all seven females. Two females fed five times on hosts, one fed three times, two fed twice, and two once. Feeding was performed on all but early fourth and prepupal stages, with most occurring on the second instar (Table 4).

The six unmated females that were observed in the host preference tests had 146 encounters ( $\bar{x} \pm \text{SEM} = 24.3 \pm 2.4$ ; range, 13–38). Host-feeding occurred only on stages that were unacceptable for oviposition, i.e., first instars and unparasitized whitefly nymphs (Table 5). We also noted that all instances of host feeding followed short (up to 60

**Table 3.** Results of the longevity studies conducted with *E. deserti*

Conditions <sup>a</sup>	Females						Males		
	Unmated			Mated			<i>n</i>	Med $\pm$ SE <sub>median</sub>	Max
	<i>n</i>	Med $\pm$ SE <sub>median</sub> <sup>c</sup>	Max	<i>n</i> <sup>d</sup>	Med $\pm$ SE <sub>median</sub>	Max			
15°C NO	59	57 $\pm$ 2.07	79	36	84 $\pm$ 0.96	90	30	40 $\pm$ 1.54	57
25°C NO	—	—	25a	25	25 $\pm$ 2.3	40	28c	16 $\pm$ 1.56	28
25°C OV	—	—	15abc	17	17 $\pm$ 2.3	33	—	—	—
22–30°C OV	—	—	15bc	14	14 $\pm$ 1.24	21	—	—	—
22–30°C NO	—	—	18ac	20	20 $\pm$ 1.76	26	—	—	—

<sup>a</sup> NO, not ovipositing; OV, ovipositing.

<sup>b</sup> Med, days at which median survival was observed.

<sup>c</sup> SE<sub>median</sub> = SEM  $\times$  1.2533. Differences were considered significant when they amounted to two SE<sub>median</sub> or more.

<sup>d</sup> Values followed by the same letter were not significantly different.

**Table 4.** Results of host-instar oviposition preference tests, with seven mated females of *E. deserti*

Instar of <i>B. tabaci</i>	No. encounters		Drilling		Oviposition <sup>a</sup>		Host feeding	
	$\bar{x} \pm \text{SEM}$	Range						
1st	5.9 ± 0.51	4-8	0.7 ± 0.16	0-1	0	0	0	0.7 ± 0.16
2nd	4.9 ± 0.96	3-10	2.1 ± 0.40	0-4	0.4 ± 0.30	0-2	1.6 ± 0.53	0-4
3rd	6.7 ± 0.64	5-10	4.6 ± 0.53	2-6	3.7 ± 0.47	2-6	0.3 ± 0.18	0-1
4th early	4.9 ± 0.74	3-9	3.7 ± 0.52	2-6	3.3 ± 0.47	1-5	0	0
4th prepupa	4.4 ± 0.69	3-7	1.3 ± 0.29	0-2	1.1 ± 0.26	0-2	0	0
4th pupa	5.0 ± 0.52	3-7	0.1 ± 0.14	0-1	0	0	0.14 ± 0.14	0-1

<sup>a</sup> As indicated by the presence of an egg upon dissection.

s) drilling bouts. Eggs were laid principally in mature larvae and immature pupae of *E. deserti* females.

Examination of the data obtained from dissecting 108 parasitized hosts in the study of developmental duration of mated females revealed 11 cases (10.2%) of superparasitism, each involving two *E. deserti* within a whitefly nymph. These data pertain only to the dissection conducted during the first 6 d after oviposition, because superparasitism could not be detected in older individuals. Superparasitism by unmated females could be detected throughout the immature development, during which we found 144 parasitized hosts, of which 50 (35%) were superparasitized, each containing between 2 and 14 parasite progeny amounting to 308 supernumeraries (Fig. 2).

Direct observations of the activity on a leaf were conducted with four mated and six unmated females. The former females were given a total of 130 hosts with which they had 106 encounters that resulted in 46 rejections and 60 acceptances. Nineteen rejections were after antennal contact only, 13 were after short drilling bouts and 14 were after long drilling bouts. Of the 60 accepted hosts, 53 were first ovipositions and 7 were cases of superparasitism, constituting 28% of all (25) encounters with already-parasitized hosts. Fifty-eight ovipositions, including all those resulting in superparasitism, were performed during long ovipositor insertions.

The unmated females were given 224 hosts, of which they encountered 184, accepted 102, and rejected 82. The rejections included 37 after an-

tennal contact only, 32 after short drilling bouts, and 13 after long drilling bouts. Of the 102 accepted hosts, 82 were first ovipositions and 20 were cases of superparasitism, which were 40% of all (50) encounters with parasitized hosts. Ninety ovipositions, including 18 of those resulting in superparasitism, were performed during long ovipositor insertions. The ratio of rejections to encounters of unparasitized hosts was 28/81 for mated and 52/134 for unmated females. The ratio for rejections of already parasitized hosts was 18/25 and 20/25 for mated and unmated females, respectively. Statistical examinations (*G* test of independence) showed that mated females discriminated between parasitized and unparasitized hosts (*G* = 5.49; *df* = 1; *P* < 0.05), whereas unmated ones did not.

## Discussion

To date, detailed developmental studies exist on two species of *Encarsia* parasitic on *B. tabaci*. They are *Encarsia formosa* (mainly when growing on the greenhouse whitefly) as reviewed by Vet et al. (1980), and *Encarsia lutea* (Foltyn 1984). Both species have a developmental duration of about 15 d at 25°C. The male/female relationship has hardly been studied in *E. formosa*, because males are very rare in this species, but the data do not show protandry (Vet et al. 1980). The same holds true for *E. lutea*, which is arrhenotokous (Foltyn 1984).

*E. deserti* is the parasitoid of *B. tabaci* with the shortest developmental duration known to date. It, too, has no protandry, but all of the males emerge shortly following pupation, whereas the pupal pe-

**Table 5.** Results of host-instar oviposition preference tests with six unmated females of *E. deserti*

Instar of host <sup>a</sup>	No. encounters		Drilling		Oviposition <sup>b</sup>		Host feeding	
	$\bar{x} \pm \text{SEM}$	Range						
1st	3.0 ± 0.82	0-5	0.3 ± 0.21	0-1	0	0	0	0.3 ± 0.21
2nd	2.7 ± 0.67	1-5	1.5 ± 0.43	0-3	0.2 ± 0.17	0-1	0	0
3rd	3.5 ± 0.76	1-6	2.0 ± 0.63	0-4	1.3 ± 0.42	0-2	0	0
Prepupa	4.0 ± 1.10	2-9	3.8 ± 0.96	2-8	3.7 ± 0.61	2-6	0	0
Young pupa	6.3 ± 1.48	2-11	6.0 ± 1.13	0-3	5.7 ± 1.09	2-9	0	0
Mature pupa	2.1 ± 0.48	1-4	1.3 ± 0.49	0-3	0.3 ± 0.21	0-1	0	0
Unparasitized host	2.6 ± 0.42	1-4	1.3 ± 0.17	1-2	0	0	0	1.3 ± 0.3
								0-2

<sup>a</sup> Host was an immature *E. deserti* within a fourth instar or a pupa *B. tabaci*, except for the "unparasitized host," which was a third-instar *B. tabaci*.

<sup>b</sup> As indicated by the presence of an egg upon dissection.

riod of the females is so drawn out that virgin females emerging on days 11–13 after oviposition are able to lay male-producing eggs in some of the pupae of their sisters, allowing the males, which emerge 11–13 d later, to have a chance of finding their newly emerged sisters with which to mate. Thus, this mechanism for delayed female emergence may provide increased chances for development of both sexes, especially in isolated populations.

Host-feeding occurred during short drilling bouts, whereas ovipositions usually took place during long ones. No other difference was observed in the stance of the female or in the mode of ovipositor insertion. The female parasitoid, mated or unmated, did not feed upon the preferred stages for oviposition. A distinction is thus made between predation (host-feeding) and parasitization with respect to host acceptance.

Host relationships of *E. deserti* resemble those of *E. formosa* (van Lenteren et al. 1976), *E. lutea* (Foltyn 1984), and *Eretmocerus mundus* (Foltyn & Gerling 1985), in that the female rejects her hosts after antennal contact or after ovipositor probes. However, the role of probing by the ovipositor for rejection was larger in *E. deserti* (55–60% of the rejections) than in *Eretmocerus mundus* (2–5% of the rejections) (Foltyn & Gerling 1985). Numbers of females that were tested for host discrimination were small, yet a few characteristics of *E. deserti* can be learned from our experiments. Mated females showed similar percentages of superparasitism in the dissection data and the direct observations (10.2 and 11.6%, respectively). Only one superparasitized host with three eggs was found; the rest had two eggs in each. Observation tests showed that the mated females discriminated between parasitized and unparasitized hosts, because their rate of rejection for the first was significantly higher than for the second. However, there probably are additional parameters associated with host selection, because the female was seen repeatedly returning to already parasitized hosts. Similar observations on the behavior of *E. formosa* (van Lenteren et al. 1976), where a "host that was rejected several times may be accepted for oviposition at a later encounter," were also left without adequate explanations.

Progeny of unmated females were distributed in a different fashion. The dissections that followed 24 h of activity by two females, each upon 50–60 hosts, resulted in 20% superparasitism, but up to 14 supernumeraries per host, whereas the direct observations of a female upon a whitefly-infested leaf patch showed 35% superparasitism with only two eggs per host. In addition, no discrimination between parasitized and unparasitized

hosts could be shown. This lack of discrimination is probably a function of low probability that the female would reencounter the same host under field conditions; a situation that may be associated with the short period in her lifetime during which she is capable of depositing male-producing eggs.

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