

## Density-related sterility in *Eretmocerus mundus*

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### Abstract

While studying the reproductive capacity of *Eretmocerus mundus* Mercet (Hymenoptera: Aphelinidae) we found that varying numbers of females were sterile. Investigations showed that sterility occurred also in field populations, but at a very low rate. Laboratory sterility was significantly correlated with crowding of the parental females during oviposition. Whitefly hosts from which fertile or sterile females emerged did not differ in size, neither did the hind tibiae of fertile females differ in dimensions from those of sterile ones. Behavior of sterile females differed from that of the fertile ones in several parameters. They exhibited less leg drumming, used the ovipositor more frequently and for shorter durations, and changed more readily from probing to host stinging, and from a number of activities to walking. Altogether, their behavior appeared more restless and caused them to contact more hosts than fertile females. The possibility that the sterility is caused by crowding alone, or by the activity of microorganisms acting under crowded conditions, and the merits of the phenomenon for biological pest control are discussed.

### Introduction

*Eretmocerus mundus* Mercet (Hymenoptera: Aphelinidae) is a solitary parasitoid of the whitefly *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae). It is prevalent in the Mediterranean region (Gerling et al., 1980) and has recently been introduced into the US to assist in the biological control of *B. tabaci*. While appraising the possibilities for utilization of *E. mundus* for biological control in greenhouses, we were interested to assess the host-killing capacity and fecundity of our lab-reared parasitoids. During this study we discovered that some of the females were sterile, i.e. developed no eggs and produced no progeny. The search for the causes of the sterility led to a series of experiments that are reported here.

Sterility as such is nonadaptive, therefore it may either occur under particular circumstances that will render it adaptive, or as a malfunction. Adaptive cases of sterility are usually associated with sociality and dominance hierarchy (Tschinkel, 1985) where dominant females lay all or most of the eggs whereas the subordinate ones either lay few eggs or are completely sterile. Adaptive sterility also occurs as a temporary

phenomenon in insects that have a reproductive diapause. For example, in the milkweed bug *Oncopeltus fasciatus* (Dallas), a short photoperiod induces low levels of juvenile hormone in the blood, which brings about a reproductive diapause (i.e., temporary sterility) and subsequent migratory flights. Once the insects are exposed to longer photoperiods and to an abundant food supply, they mate and their ovaries develop (Eaton, 1985).

In the non-social, parasitic Hymenoptera, reports on sterility are limited to partial sterility. In most cases, females that normally are biparental lose their ability to produce males under certain conditions, and become parthenogenetic. This condition may be induced by environmental influence, particularly in association with parasitic microorganisms (Godfray, 1994; Zchori-Fein et al., 1995). Several of the better known cases involve parasitoids from the superfamily Chalcidoidea like trichogrammatids, pteromalids and aphelinids. Such sterility has not been reported in the genus *Eretmocerus*, but it was found in other aphelinids, most notably in species of *Aphytis* and *Encarsia* (Zchori-Fein et al., 1992, 1995).

Our studies differed from the above in that progeny of fertile females were totally sterile, and produced no progeny at all. This situation, which had not been previously reported in parasitic Hymenoptera, was investigated in our experiments. Given the fact that sterility can result from several causes, we had to choose on which factors to concentrate in our study. Because we worked under laboratory conditions and because we were interested in improving the prospect of rearing large numbers of parasitoids for biocontrol purposes, we chose to investigate the following: (1) Is sterility confined to the progeny of certain females while the progeny of others is free from it. A positive answer would have led us to investigate the differences between the two female types. (2) Is sterility associated with size differences of the hosts from which the females emerged. A positive answer would have led us to learn more about host sizes and the rearing conditions that led to them. (3) Is sterility associated with size differences in the affected vs. healthy females. This was done as there are numerous cases (Visser, 1994; Kazmer & Luck, 1995, and references therein) where a fitness-size relationship had been shown; (4) Did our rearing conditions, in particular the crowded situation to which parasitoids were often subjected, have a bearing on female sterility. The decision to study crowding was taken following the results of the first experiment and is discussed in more detail in the 'Results' section. Finally, the host killing capacity of the sterile vs. fertile females was examined and its implications for biological whitefly control are discussed.

## Materials and methods

All of the *E. mundus* that we used originated from the field in Israel. The regular laboratory culture has been kept 6 or more months in the laboratory prior to the experiment. Rearing conditions were ca. 25 °C and 60% r.h. The hosts were *B. tabaci* growing on cotton plants (Acala SJ-2) that were either kept in sleeve cages or in individual 'bottle' cages (see below). The culture was maintained by putting 4–6 whitefly-infested plants into a cage and introducing ca. 10–40 *E. mundus* females once the hosts were in their third instar. After 15 days, when the new parasitoid generation was due to emerge, the leaves bearing the parasitized material were removed from the plants and placed in an 'emergence bottle'. Such bottles were prepared by removing the bottom of a clear plastic 2-liter soft-drink bottle, and fitting a removable cover over the opening. A hole

was cut in the side of the bottle and covered with cloth to facilitate air exchange. An empty scintillation vial was placed on top of the bottle, and all but the vial was covered with black paint or with paper. The parasitoids, which are attracted to light, concentrated in the vial and were collected once each day. They were used for the experiments or placed with new host plants.

For rearing and examining the oviposition of individual females, we used individual plant cages that were prepared like the emergence bottles but had no scintillation bottle on top and were not covered with black paint or paper. The plant, that had two true leaves which bore ca. 150 whitefly nymphs was placed in this cage and the parasitoid was introduced into it and kept there for as long as was called for.

Although *E. mundus* females are synovigenic, they emerge with numerous mature eggs which they may lay shortly thereafter. Therefore, it was possible to determine if a female was fertile by examining her ovarial condition already shortly after emergence. This was done by putting the female in a freezer for a few hours and then dissecting her in a droplet of water on a glass slide under a dissecting microscope. The ovaries were easily exposed and the number of ripe, or nearly ripe eggs was counted. We considered as ripe those eggs that separated from the ovary and floated freely in the water once the ovary was shaken lightly.

The experimental protocol was as follows: For determining whether sterility occurred only in the laboratory, we collected parasitized whitefly pupae from two locations: melon greenhouses in Ein Yahav, some 50 km south of the Dead Sea, in April and June of 1995, and an experimental cotton culture at the Eden Experimental farm, some 5 km south of Bet Shean, in March and in May of 1995. The material was reared out in emergence bottles in the lab and the ovarial condition of the females was examined.

The relationship between individual oviposition and progeny sterility was examined by placing one female per plant cage for three days. Thereafter, she was transferred to a new plant and the process was repeated for another three days. Ten days after the introduction of the female, the bottle containing the plant was covered with black paper and a scintillation vial was placed on top. The females that emerged and accumulated in the bottle were collected each day and dissected. As a control to this experiment we examined the females in the regular laboratory culture from which the experimental females had originally been taken, and that had been kept in the same environmental cabinet.

For estimating the killing of whiteflies by parasitoids, leaves bearing ca. 150 whitefly nymphs each were allowed to develop until the whiteflies reached maturity. Then we took advantage of the clear differences between whitefly nymphs which gave rise to whiteflies, those from which parasitoids emerged, and ones that died prior to emergence (Gerling, 1990), and sorted the nymphs accordingly.

In the second, crowding, experiment we kept the females on a plant continuously for ten days, and then the rearing container was turned into an emergence bottle by covering it and adding a scintillation vial on top. This experiment was conducted at three parasitoid densities: 1, 5, and 10–20 female parasitoids per bottle. Cultures from which only male parasitoids emerged were considered as resulting from oviposition by unfertilized females. Since it was not possible to determine if the progeny of such females were sterile, they were discarded.

Parasitoid fitness and/or physiological conditions may be associated both with the size of the host in which it developed and with the size of the ensuing parasitoid individual. Therefore, we also looked for a relationship of host and parasitoid size in relation to sterility. Morphometric measurements were taken by removing laboratory reared, whitefly pupae shortly before parasitoid emergence, and measuring their maximal width under a stereomicroscope. Parasitoids were measured by placing the female on her back in a drop of Hoyer's mounting medium exposing the hind tibia completely and measuring it using a Visopan Projection microscope and an electronic caliper.

Behavioral studies were conducted with females that were collected at the age of 0–24 h, released on whitefly-infested leaves for another 12 h, and then kept overnight in a vial supplied with honey. The next morning, each female was individually exposed to a whitefly-bearing leaf and her behavior was registered using 'The Observer' software (Noldus Information Technologies) and a hand-held computer. The events registered were: feeding (on honeydew or the leaf-surface), standing still, preening, drumming with the hind legs or with the antennae, host feeding, probing the host surface with the ovipositor either on top for host feeding or under the host (oviposition posture), and walking. Each host nymph attacked, either for feeding or for ovipositing was marked with a small color dot beside it. The observation lasted 90 min after which the wasps were placed in a freezer for later measurement of their hind tibia and dissection. The leaf was placed in an incubator for 10 days after which

the fate of each attacked host was registered and correlated with the respective activity and ovarial condition of the wasp (Table 1).

For statistical analysis the females were lumped into two groups, one with eggs and one without. Analysis consisted of comparing characteristics of fertile vs. sterile females using *t*-tests, or in the case of comparing frequencies  $\chi^2$  (tests of independence), as mentioned in the text. The comparisons given in Table 2 are the results of tests of independence conducted using the frequencies of steriles and fertiles for every transition. Measurements of whitefly pupae and parasitoid hind tibiae were compared using a *t*-test.

Correlation between parasitoid density and sterility was analyzed using Spearman's coefficient of rank correlation test (Sokal & Rohlf, 1981). Mortality data (Table 1) were compared following a correction for whitefly mortality without parasitoids using Abbot's formula as presented by Carey (1993). All numbers of progeny (e.g., Table 3) refer to female progeny only. Male progeny were not counted since they were not pertinent to the tested subject (female sterility).

## Results

Whitefly mortality without parasitoids amounted to 11.89% ( $n = 38$ , range 0–37.84%). Following exposure to sterile *E. mundus* there was an addition of 58% of the cases in which she fed on hosts and 44.3% mortality by females that were in oviposition posture. The corresponding additions to mortality with normal females was 84% for host feeding (Table 1) and 71.6% for oviposition posture (the latter taking into account both the mortality due to premature host mortality and to successful parasitoid development).

Measurements were taken from 12 whitefly pupae that yielded fertile females and from 26 pupae yielding sterile ones. No significant differences in pupal width were found ( $0.49 \pm 0.021$  mm, vs.  $0.48 \pm 0.012$  mm average  $\pm$  standard error) for pupae yielding healthy and sterile females respectively. Also hind tibia measurements were not significantly different ( $0.214 \pm 0.0039$  mm vs.  $0.220 \pm 0.0045$  mm) for 12 healthy and 26 sterile females, respectively.

Joint morphometric and behavioral studies were conducted with 15 wasps, of which 10 were sterile, and five had normal ovaries. The two groups did not differ in size (hind tibial lengths averages: 0.230 vs. 0.211 mm for fertile and sterile females, respectively). However, their behavior on the host patch

Table 1. Comparison of significantly different behaviors between sterile and fertile females of *E. mundus*

Activity	Fertile	Sterile	Significance	Criterion measured
Stinging (oviposition posture)	6	17.6	*P < 0.05	average events per hour
Stinging (host feeding)	1.07	2.47	*P < 0.005	average events per hour
Feeding on stung hosts	87.5%	48.39%	***P < 0.005	percent of total events
	<i>n</i> = 8	<i>n</i> = 31		
Killing hosts while in oviposition posture	**29.5%	**44.3%	***P < 0.05	total number of events
	<i>n</i> = 44	<i>n</i> = 111		
Killing hosts during host feeding	**84%	**58%	***P < 0.0001	total number of events
	<i>n</i> = 7	<i>n</i> = 16		
Stinging (oviposition posture)	109.52	41.76	*P < 0.0001	average duration, seconds/host
Drumming with hind legs	334.36	39.61	*P < 0.001	average duration, seconds/observation
Drumming with antennae	331.06	662.95	*P < 0.05	average duration, seconds/observation

\* *t*-test.

\*\* Following Abbott's correction to account for natural mortality.

\*\*\*  $\chi^2$ -test.Table 2. Comparison of transition frequencies between activities of fertile vs. sterile females of *E. mundus*

Activity (from to)	Parasitoid female*	Significance
Walking – standing	fertile	P < 0.001
Walking – feeding on leaf	fertile	P < 0.001
Probing – host feeding	fertile	P < 0.005
Stinging for host feeding – preening	fertile	P < 0.05
Ovip. posture – hind leg drumming	fertile	P < 0.001
Hind leg drumming – preening	fertile	P < 0.001
Preening – hind leg drumming	fertile	P < 0.001
Walking – drumming with antennae	sterile	P < 0.001
Probing – stinging for host feeding	sterile	P < 0.05
Preening – Probing	sterile	P < 0.001
Oviposition posture – walking	sterile	P < 0.001
Hind leg drumming – walking	sterile	P < 0.001
Preening – walking	sterile	P < 0.001

\* The parasitoid in this column exhibits prevalence of the transition in question.

Table 3. The number and fertility of female progeny of *Eretmocerus mundus* females in relation to the degree of crowding to which they were subjected during oviposition

Degree of crowding	One mother		Five mothers		Ten mothers	
	Total number of progeny	% sterile daughters	Total number of progeny	% sterile daughters	Total number of progeny	% sterile daughters
1	5	0	1	0	3	66.7
2	5	0	11	90.9	8	87.5
3	15	6.67	30	3.3	3	100
4	6	0	15	53.3	36	86.11
5	5	0	45	2.08	4	100
average progeny/ female	7.2		4.08		1.08	

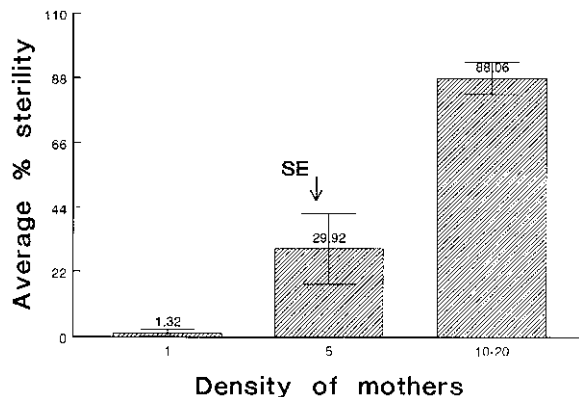


Figure 1. Density-related sterility in *E. mundus* females.

differed. Fertile females exhibited less frequent stinging attempts and antennal drummings, but each activity lasted longer than that of sterile ones. They also fed and killed more stung hosts through host-feeding (Table 1). Fertile females also performed more leg drumming, mostly as part of a cycle involving the movement from leg drumming to preening and vice versa. They also moved more often from probing activity to feeding on the wounds of stung hosts. Sterile females showed higher frequency of moving from other activities (oviposition posture, hind leg drumming and preening) to walking, from probing to host stinging for host feeding, and to probing from walking and preening (Table 2).

The field collected material from Ein Yahav yielded altogether three sterile females (one female out of the 35 collected in April and two out of the 23 collected in June), whereas that from Eden yielded none out of the 35 collected females. Thus, it was established that sterility occurred also in field populations.

In the laboratory, thirty one individually cultured females yielded 596 female progeny (average, 19.22 range 1–56). Most of them (487 individuals) had between 10 and 25 eggs in their ovaries upon emergence, whereas 108 females had between 1–9 eggs. All had clearly visible, developed, ovaries. One progeny female had no eggs. The control laboratory culture, in which several females had been kept in the same cage, had 17.39% sterile females in the parental generation (4 out of 23), and 40% in the  $F_1$  generation (4 out of 10). In both cases, the sterile individuals had no eggs and no trace of an ovarial structure or spermatheca could be discerned.

Since the control and experimental setups differed in the density of the parasitoids per cage, we ran a second experiment in which we tested the effects

of group confinement, or crowding upon ovipositing *E. mundus*. The results (Table 3 and Figure 1) show considerable variation in the number of progeny that the females produced. The solitary females had 5–15 female progeny per individual, those with 5 females per bottle cage, averaged <1–9 progeny per female, and those with 10 females per bottle cage averaged ca. <1–3.6 progeny per female (Table 3). The trend towards the increase of sterility in  $F_1$  with crowding of ovipositing females was significant ( $P < 0.001$ ,  $n = 15$ ,  $r_s = 0.809$ ).

## Discussion

Judging from the known biology of *E. mundus*, which is a solitary (non-social) short-lived non-migratory insect, we could not find an adaptive advantage to the sterility of the females, consequently, we assumed that it is a malfunction created by unusual circumstances. The females of *E. mundus* produced normal progeny when kept in solitary confinement with hosts, sterility of progeny increased with the degree of crowding. This reaction was significant in spite of the great variability in the number of progeny produced. Therefore, the appearance of sterile females should be explained in relation to the change from solitary to crowded conditions during oviposition.

The mode by which sterility of *Eretmocerus* progeny comes about under crowded conditions has not been studied. At this stage, we can only hypothesize that unfavorable factors may act on the parents and/or progeny and cause sterility. Such factors could be pathogenic agents or the direct effects of crowding on host quality.

The involvement of pathogenic microorganisms in reproductive disorders of parasitic Hymenoptera has so far been reported only for inducing partial sterility, i.e., even though a female had been infected, she was not devoid of all eggs and was still able to produce some eggs or progeny, either male or female (Luck et al., 1992). However, this does not preclude the possibility that certain infections do render the females sterile. Such infections, which in nature are only sporadic and therefore do not have a decisive effect on the fitness of the *E. mundus* population, could be greatly enhanced under the crowded laboratory conditions. These could act in a density dependent manner due to their mode of transmission, e.g., through the faeces of the parasitoids (Luck et al., 1992).

The possibility that such microorganisms are transmitted through faecal infection may also be correlated with the fitness value that the wasps' behavioral changes confer upon the microorganisms. Once sterile, females use the ovipositor more frequently and for shorter durations both for host feeding and for insertion under the host for apparent oviposition (Table 1). They also changed more readily from probing to host stinging, and from oviposition posture, from hind leg drumming, and from preening to walking (Table 2). These changes point to their more 'restless' behavior during which they may contact more hosts than the normal females and thus spread the infectious organisms more effectively.

The second alternative involves changes in host quality due to host feeding and/or superparasitism. Gerling (1966) showed that both occurred readily in *E. near californicus*. It expressed itself in premature host death (and therefore the death of the parasitoids developing therein), or in the success of one larva to survive and the death of the other, supernumerary larvae. Superparasitism was also observed with *E. mundus* (e.g., Gerling et al., 1990).

Host quality effects on parasitoids have been studied in several instances (see Godfray, 1994, for a review), most notably with species of the genus *Trichogramma*. Experiments with these parasitoids were facilitated by the fact that many *Trichogramma* species readily oviposit in the laboratory in eggs that vary in size and taxonomic affiliation. Additionally, the fact that these parasitoids are idiobionts, i.e. at parasitoid oviposition, the host already contains the total food supply that will be available for complete immature parasitoid development, made it possible to estimate the amount of available nutrients, which is an important component of host quality. Thus, Flanders (1935) showed that *T. evanescens* developed much larger individuals that were fivefold as prolific when developing on eggs of *Astigmene acreae* Drury, than when developing on *Sitotroga cerealella* (Olivier). Salt (1941) reared the same species of parasitoids on the eggs of the unnatural neuropteran host *Sialis lutaria* L. rather than on eggs of Lepidoptera, and found the resulting progeny 'structurally normal but feeble and barren'. He has also shown that differences in host quality may affect the size of antennae and wings, fecundity, developmental period, vigor, and behavior. These examples demonstrate that the ability of the parasitoids to reach maturity and even to develop a morphologically normal appearance, may not exclude the possib-

ility that physiological changes might have occurred due to inadequate nutrition during larval development.

The study of nutritional effects on sterility is most advanced in the honeybees where definite effects of food quality and of hormonal titers on ovarian development has been demonstrated. However, in spite of the intensive studies, the pathway by which the nutritional condition brings about the necessary hormonal changes is still unclear (Hertfelder, 1990). In the genus *Eretmocerus* penetration of the larva into the host induces substantial changes in epidermal growth (Gerling et al., 1991) that are presumably associated with changes in hormonal titers. Moreover, the nutrition of the first and second larval instars of the parasitoid is mediated through a vital, host-originating capsule (Gerling et al., 1990). Consequently, once several young parasitoid larvae are developing within one whitefly nymph, which is capable of supporting only one parasitoid, we may expect both nutritional and hormonal abnormalities. These may manifest themselves in the absence of required proteins (Beckage, 1993), and/or hormonal titers, and may influence ovarian development in the developing parasitoid.

The fact that a few sterile females were found in the field suggests that sterility in *E. mundus* is not a laboratory product, although the crowded conditions in our cages enhanced it. In our experiments the parasitoid females were confined to the same leaves for 10 days and therefore were forced to repeatedly search and attack the same hosts (van Lenteren, 1981). Under normal field conditions, parasitoid females are free to leave and search for other host-bearing leaves whenever they decide that the present patch is not productive anymore (Shimron et al., 1991). Thus, not more than 2-3 adult *E. mundus* are usually found on a leaf (Forer, 1985). An exception to this occurs when whitefly density reaches hundreds of nymphs per leaf. If many of these are parasitized, and more than one whitefly generation develops on the same leaf, numerous parasitoids may search the leaf on which they emerged, and crowded conditions may develop. Such a situation, that often occurs on melons, may explain the appearance of sterile females in the samples taken from Ein Yahav. The samples taken from the Eden farm were collected from moderately infested cotton leaves, in which whitefly and parasitoid crowding did not occur.

All of our experiments were conducted in the laboratory. Therefore, we can calculate the rates at which each host killing event takes place and compare the killing potentials of sterile vs. fertile females. Sterile females attain an average of 17.6 oviposition postures

per hour, out of which 44.3% cause host mortality i.e. 8 hosts killed per hour. They also attain 2.4 host feeding postures during which they kill 58% or 1.4 whiteflies, totaling 9.4 hosts killed per hour. Fertile females have 6 ovipositions per hour out of which 71.6% cause mortality, i.e., 4.3 hosts. They also attain 1.07 host feeding postures killing 84% of the hosts, or, 0.9 hosts, totaling 5.2 whiteflies per hour. Therefore, sterility caused by crowding of *E. mundus* results in a net decrease in fecundity of the population and an increase in their host killing capacity. Such a feature could be beneficial in inundative biological control where laboratory-reared individuals would kill the whiteflies in a greenhouse or any limited space. Once the parasitoids would reproduce in the release sites, their population density would decrease greatly as would also the proportion of sterile females.

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