

ORIGINAL ARTICLE

Mating and host density affect host feeding and parasitism in two species of whitefly parasitoids

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Abstract The parasitoids in the genera of *Encarsia* and *Eretmocerus* (Hymenoptera: Aphelinidae) are important biological control agents of whiteflies, and some of them not only parasitize hosts but also kill them with strong host-feeding capacity. Two whitefly parasitoid species, *Encarsia sophia* and *Eretmocerus melanoscutus* were examined to determine if mating and host density affected their host feeding and parasitism. The whitefly host, *Bemisia tabaci*, was presented to these two wasp species in densities of 10, 20, 30, 40, 50 and 60 third-instar nymphs per clip cage. Mated whitefly parasitoid females fed on more hosts than unmated females under a range of host densities (under all six host densities for *En. sophia*; under the densities of 40 nymphs or more for *Er. melanoscutus*). Meanwhile, mated females parasitized more whitefly nymphs than unmated females under all host densities for both species. With increase of host density, mated or unmated *Er. melanoscutus* females killed more hosts by host feeding and parasitism. Mated *En. sophia* females killed more hosts by host feeding with increase of host density, whereas unmated females did not parasitize whitefly nymphs at all. Our results suggest that only mated female parasitoids with host-feeding behavior should be released in crop systems to increase their bio-control efficiency.

Key words *Bemisia tabaci*, biological control, *Encarsia sophia*, *Eretmocerus melanoscutus*

Introduction

Many species of insect parasitoids, almost all members of the Hymenoptera, not only oviposit in or on their hosts, but also feed on them (called host feeding) (Jervis & Kidd, 1986; Heimpel & Collier, 1996). Host feeding of parasitoid adults mainly involves consumption of host fluids

exuding from the ovipositor insertion site by the adult female parasitoids. This behavior has been observed in more than 140 species belonging to 17 families in Hymenoptera (Jervis & Kidd, 1986). Parasitoids obtain essential nutrients that increase their egg production and/or prolong longevity through host feeding (Collier, 1995; Giron *et al.*, 2004; Burger *et al.*, 2005). Parasitoid species with host-feeding habits kill hosts not only through parasitism, but also through host feeding, therefore they are promising agents for effective biological controls for pest insects in theory (Yamamura & Yano, 1988) and in practice (Jervis *et al.*, 1996).

Many studies have demonstrated that decisions by female parasitoids to feed upon hosts depend on environmental variables (Hansen & Jensen, 2002),

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physiological state of the parasitoids (Collier, 1995; Zang & Liu, 2009), and host availability (Videllet *et al.*, 1997; Rosenheim & Rosen, 1992). Clearly, the decision to host feeding depends on the internal state of the parasitoids. Therefore, a parasitoid's decision to either feed or oviposit may be influenced by mating status.

Bemisia tabaci (Gennadius), especially "biotype B", has been a devastating pest of ornamentals, vegetables and field crops worldwide (Perring *et al.*, 1993). Liu *et al.* (2007) found that the invasive *B. tabaci* biotype B can quickly displace the indigenous biotypes through asymmetric mating interactions. Recent studies on the systematics of *Bemisia tabaci* present convincing evidence that the whitefly is a species complex comprised of over 20 cryptic species, and the "biotype B" is in fact a whitefly species, not a biotype (Dinsdale *et al.*, 2010; Xu *et al.*, 2010; Wang *et al.*, 2010; De Barro *et al.*, 2011). Many attempts at controlling *B. tabaci* using parasitoids, especially species in the two genera *Encarsia* and *Eretmocerus* (Hymenoptera: Aphelinidae), have achieved success in protected environments as well as outdoors (Gerling *et al.*, 2001). Most whitefly parasitoid species are non-concurrent destructive host feeders (Zang & Liu, 2008; Shi *et al.*, 2009). *Encarsia sophia* (Girault & Dodd) [= *En. transvena* (Timberlake)] and *Eretmocerus melanoscutus* Zolnerowich & Rose, are among a large number of parasitoids reported to attack *B. tabaci* (Gerling *et al.*, 2001; Liu, 2007). The feeding capacities of female parasitoids of the two species have been evaluated by Zang & Liu (2008) who found that *En. sophia* and *Er. melanoscutus* exhibited stronger host-feeding capacity than *En. formosa*.

Encarsia sophia, a typical heteronomous hyperparasitoid, oviposits fertilized (female) eggs in whitefly nymphs and unfertilized (male) eggs externally on female immatures of their own or of other *Encarsia* and *Eretmocerus* species of whitefly nymphs (Giorgini & Baldanza, 2004). *Er. melanoscutus* is a solitary parasitoid ovipositing externally, under the nymphal host. This species is a biparental primary parasitoid, with both males and females developing in whitefly nymphs (Liu, 2007). Our previous work indicated that the effectiveness of bio-control on whiteflies by both species could be manipulated through improved host feeding and parasitizing capacity by food-deprivation for a certain period of time before they are released (Zang & Liu, 2009, 2010).

Mating affects the outcome of some fitness parameters such as lifetime fecundity, progeny production and sex ratio (Ridley, 1988). In addition, mating status of wasps might affect the biological characteristics which influence their control efficiency (Sousa & Spence, 2000; Pratisoli *et al.*, 2009). To our knowledge, effects of mating status

on host feeding in parasitoids have not been examined. In this study, we investigated the host feeding and parasitism between mated and unmated whitefly parasitoid species, *En. sophia* and *Er. melanoscutus* on their host, *B. tabaci*, under different host densities. The results will help explore the biological potential of natural enemies to improve their use in biological control programs.

Materials and methods

Insects and plants

Laboratory colonies of *En. sophia* and *Er. melanoscutus* were established from populations of parasitized B biotype of *B. tabaci* on melons and cabbage plants respectively, in a greenhouse in the Vegetable IPM Laboratory, Texas AgriLife Research, at Weslaco, TX, USA. Voucher specimens of these parasitoids and *B. tabaci* are deposited in the Insect Collection, Texas AgriLife Research, Texas A&M University System at Weslaco, TX, USA.

The parasitoids, *En. sophia* and *Er. melanoscutus*, were maintained in an air-conditioned insectary ($25 \pm 2^\circ\text{C}$, $55\% \pm 5\%$ RH, and a 14 : 10 h L : D regime) on *B. tabaci* maintained on potted cabbage in separate large cages (60 × 60 × 60 cm).

Cabbages (*Brassica oleracea* L. var. *capitata*, 'Golden Acre') were used as the host plant for *B. tabaci*. The cabbage plants growing with three fully extended true leaves were used in the experiments.

Host feeding and parasitism of mated and unmated whitefly parasitoids in relation to host densities

The cabbage leaves with nearly emerged parasitoids were placed in large Petri dishes (15.0 cm diameter and 1.5 cm depth), and were monitored every few minutes. The parasitoids were collected with an aspirator as soon as they emerged. Then, one virgin female or a pair of male and female adults of *En. sophia* (or *Er. melanoscutus*) was placed into a clear glass tube (10.0 cm length and 1.2 cm diameter) with one end closed and another end ventilated with a polyethylene screen. Honey was supplied by depositing 10 droplets of 20% honey solution onto a piece of parafilm (1.0 cm × 1.0 cm) that was affixed to the walls of each glass tube. All glass tubes with parasitoids were placed on the bottom of large Petri dishes (15.0 cm in diameter) with wet filter paper. After 24 h, one mated or unmated *En. sophia* (or *Er. melanoscutus*) female was introduced on a cabbage leaf with different densities of third-instar whitefly nymphs enclosed by a clip-on cage for 24 h.

The following procedures were used to obtain the desired stage of hosts. Thirty female and male adults of *B. tabaci* B biotype were introduced onto the lower surface of a cabbage leaf on a potted plant with a clip cage (4.0 cm diameter) for oviposition for 12 h. The nymphs were then monitored daily until they developed into third instars. The density of whitefly nymphs included 10, 20, 30, 40, 50 and 60 third-instar nymphs in an area covered by a clip cage ($\approx 12.6 \text{ cm}^2$). All experiments were conducted in an air-conditioned insectary at $28 \pm 2^\circ\text{C}$, $75\% \pm 5\%$ RH, and a photoperiod of 14 : 10 h L : D. Host mortality by host feeding and parasitism was examined under a stereoscopic microscope 6 days after parasitoid removal. A total of 25 females for each treatment were initially used, and the data from 18–22 replicates were used because a few females were missing during the experiment.

Data analyses

Host mortality by host-feeding or parasitism on third instar whitefly nymphs by mated or unmated *En. sophia* or *Er. melanoscutus* at different host densities was analyzed using one-way analysis of variance (ANOVA) and means were separated using Tukey's test at $P < 0.05$. Paired *t*-test was used in the analyses of host mortality caused by host feeding or parasitism between mated and unmated *En. sophia* or *Er. melanoscutus* at various host densities. The host mortality caused by parasitism and host feeding in relation to host density was fitted to the Holling's disk equation (type II model) (Holling, 1959): $N_a = aTN/(1 + aThN)$, where N_a is the number of whiteflies killed by host feeding or parasitism, N is host density, T is the exposure time and T_h is the handling time per host. The trends of host feeding or parasitism via host density in mated or unmated parasitoids were presented through nonlinear regression analysis. All statistical analyses were

done using the statistical software package DPS (Tang & Feng, 2002).

Results

Host feeding and parasitism between mated and unmated *En. sophia*

Mated *En. sophia* females fed on more hosts than unmated females under each of the host densities ($t = 2.39$ – 3.91 ; $\text{df} = 37$ – 39 ; $P = 0.0004$ – 0.0221). There were significant differences in the numbers of host feeding by unmated ($F_{5,110} = 8.54$; $P < 0.0001$) or mated ($F_{5,116} = 11.7$; $P < 0.0001$) *En. sophia* at different host densities. Number of hosts killed through host feeding by unmated or mated parasitoids increased with increase of host density when less than 40 hosts were offered. Mated parasitoids exhibited a tendency to parasitize more hosts with increase of host density ($F_{5,116} = 10.35$; $P < 0.0001$). Unmated parasitoid females did not parasitize any host (Table 1). Generally, mated *En. sophia* females killed more hosts by host feeding and parasitism than unmated females.

Host feeding and parasitism between mated and unmated *Er. melanoscutus*

With increase of host density, unmated or mated *Er. melanoscutus* females killed more hosts by host feeding (unmated: $F_{5,115} = 6.36$; $P < 0.0001$; mated: $F_{5,114} = 21.26$; $P < 0.0001$). Similarly, parasitism significantly increased with increase of host density whether for unmated *Er. melanoscutus* females ($F_{5,115} = 11.87$; $P < 0.0001$) or mated females ($F_{5,114} = 106.44$; $P < 0.0001$). Mated parasitoids parasitized more hosts than unmated ones under each of the host densities ($t = 2.78$ – 3.30 ; $\text{df} = 38$ – 39 ; $P = 0.0027$ – 0.0100).

Table 1 Host feeding and parasitism of mated and unmated *En. sophia* in relation to host densities.

Host density	No. of host feeding		No. of parasitism	
	Unmated	Mated	Unmated	Mated
10	3.1 \pm 0.2 c A	4.2 \pm 0.2 c B	0	4.0 \pm 0.4 c
20	4.1 \pm 0.3 b A	5.6 \pm 0.3 b B	0	6.6 \pm 0.4 b
30	4.9 \pm 0.3 ab A	5.8 \pm 0.3 b B	0	6.5 \pm 0.5 b
40	4.9 \pm 0.4 a A	6.7 \pm 0.4 a B	0	7.6 \pm 0.4 ab
50	5.3 \pm 0.3 a A	6.4 \pm 0.4 ab B	0	7.2 \pm 0.4 ab
60	5.5 \pm 0.4 a A	7.0 \pm 0.3 a B	0	8.4 \pm 0.7 a

Means in a column followed by the same lower case letter do not differ significantly ($P > 0.05$) by Tukey's test, and means in a row followed by the same upper case letter do not differ significantly ($P > 0.05$) by paired *t*-test.

Table 2 Host feeding and parasitism of mated and unmated *Er. melanoscutus* in relation to host densities.

Host density	No. of host feeding		No. of parasitism	
	Unmated	Mated	Unmated	Mated
10	0.9 ± 0.2 c A	1.4 ± 0.2 d A	5.6 ± 0.9 e A	8.2 ± 0.4 f B
20	2.0 ± 0.2 b A	1.7 ± 0.2 cd A	12.9 ± 1.4 d A	17.2 ± 0.5 e B
30	1.8 ± 0.2 b A	2.4 ± 0.3 c A	16.4 ± 2.3 cd A	23.8 ± 0.7 d B
40	2.0 ± 0.3 b A	3.5 ± 0.5 b B	20.0 ± 2.5 bc A	29.1 ± 1.2 c B
50	2.6 ± 0.4 ab A	4.5 ± 0.4 a B	24.2 ± 2.7 ab A	33.4 ± 1.5 b B
60	3.2 ± 0.4 a A	4.9 ± 0.3 a B	27.1 ± 3.1 a A	37.5 ± 1.4 a B

Means in a column followed by the same lower case letter do not differ significantly ($P > 0.05$) by Tukey's test, and means in a row followed by the same upper case letter do not differ significantly ($P > 0.05$) by paired t -test.

Moreover, the mated parasitoids fed on more hosts than unmated ones when more than 30 hosts were offered ($t = 2.76\text{--}3.71$; $df = 38$; $P = 0.0007\text{--}0.0096$) (Table 2). Generally, mated *Er. melanoscutus* killed more hosts by host feeding and parasitism than unmated females.

The results of regression analyses showed significant trends in increases of host feeding via host density for mated or unmated whitefly parasitoids (mated *En. sophia*: $r^2 = 0.9480$, $df = 1,4$, $P = 0.0010$; unmated *En. sophia*: $r^2 = 0.9838$, $df = 1,4$, $P = 0.0001$; mated *Er. melanoscutus*: $r^2 = 0.9649$, $df = 1,4$, $P = 0.0005$; unmated *Er. melanoscutus*: $r^2 = 0.8367$, $df = 1,4$, $P = 0.0106$) (Fig. 1). Whether for mated or unmated wasps, *En. sophia* fed on more whitefly nymphs than *Er. melanoscutus* in the same exposure time. Moreover, mated females clearly fed on more whiteflies than unmated females in both parasitoid species (Fig. 1). Similarly, there were significant trends in increase of parasitism via host den-

sity for the two parasitoid species (mated *En. sophia*: $r^2 = 0.9016$, $df = 1,4$, $P = 0.0038$; mated *Er. melanoscutus*: $r^2 = 0.9974$, $df = 1,4$, $P = 0.0000$; unmated *Er. melanoscutus*: $r^2 = 0.9932$, $df = 1,4$, $P = 0.0000$) (Fig. 2).

Discussion

Host-feeding by females of hymenopteran parasitoids has been recognized as an asset in biological pest suppression since the mid-1980s (Jervis & Kidd, 1986). Some parasitoid species exhibit strong host-feeding capacity, for example, *Metaphycus helvolus* (Compere) (DeBach, 1943), *Trichogramma turkestanica* Meyer (Hansen & Jensen, 2002) and *En. sophia* (Zang & Liu, 2008), and the effectiveness of their host feeding to control insect pests is similar to or more than that of their parasitism. Many

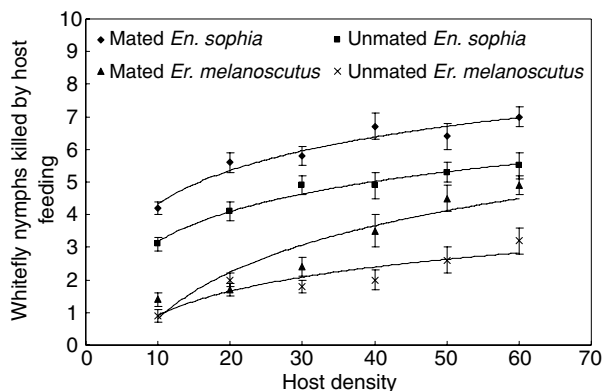


Fig. 1 Number of whitefly nymphs fed on by mated or unmated *En. sophia* and *Er. melanoscutus* on different numbers of host. Curves are given by the Holling disk equation (type II model). Vertical bars are standard errors.

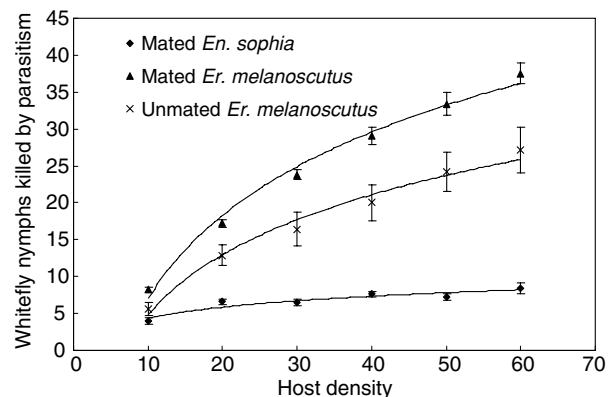


Fig. 2 Number of whitefly nymphs parasitized by mated or unmated *En. sophia* and *Er. melanoscutus* on different numbers of host. Curves are given by the Holling disk equation (type II model). Vertical bars are standard errors.

factors affect the host-feeding behavior of parasitoids, such as environmental variables (Hansen & Jensen, 2002), egg load (Collier, 1995), host stage and host density (Videllet *et al.*, 1997; Rosenheim & Rosen, 1992). Recently we found that food-deprivation durations of whitefly parasitoids prior to release also affected host-feeding capacity (Zang & Liu, 2009, 2010). Our present study showed that mated female *En. sophia* obviously fed on more whitefly nymphs than unmated ones under a range of host densities (Table 1). The mated *Er. melanoscutus* also fed on significantly more hosts than unmated ones when more than 30 hosts were offered (Table 2). In addition, regardless of mated or unmated females, both species exhibited a tendency to increase host feeding with increase of host density within a certain range of host densities (Fig. 1). These results demonstrated that mating status of these parasitoids influenced host feeding.

Many studies demonstrate that mating status affects biological characteristics of parasitoids. For example, unmated females of *Lydella jalisco* Woodley, *Er. eremicus* Rose & Zolnerowich, *Laelius pedatus* (Say) and *Tiphodytes gerriphagus* Marchal, had longer lifespans and flew for longer periods, took longer time to lay their clutches, and conducted fewer of probes on a host compared to corresponding mated ones (Lauziere *et al.*, 2001; Bellamy & Byrne, 2001; Mayhew & Heitmans, 2000; Sousa & Spence, 2000). Moreover, mated females of *Trichogramma pretiosum* Riley and *Pseudaphycus maculipennis* (Mercet) parasitized more hosts than unmated females (Pratissoli *et al.*, 2009). Our current study also showed that mated *Er. melanoscutus* parasitized more hosts than unmated ones under a range of host densities (Table 2). As for unmated *En. sophia*, no whitefly nymphs were parasitized at all in the experiment (Table 1). Host feeding is another critical biological characteristic of parasitoids which influences their control efficiency (Jervis & Kidd, 1986; Shi *et al.*, 2009). To our knowledge, we are the first to report that mated parasitoid females could feed on more hosts than unmated ones.

Our data also show that mated *Er. melanoscutus* parasitized more whitefly nymphs than mated *En. sophia* in 24 h under the same host density (e.g. 37.5 vs. 8.4 nymphs at the density of 60 hosts). In contrast, the mated *En. sophia* fed on more whitefly nymphs than mated *Er. melanoscutus* under the same experimental conditions (e.g. 7.0 vs. 4.9 nymphs at the density of 60 hosts) (Tables 1 and 2). The results accorded with our previous study (Zang & Liu, 2008). Although *Er. melanoscutus* exhibited better bio-control efficacy on *B. tabaci* with high parasitism than *En. sophia* in the experiment, there was no significant difference in parasitism throughout their lifespan. However, *En. sophia* killed more whitefly nymphs through host

feeding than *Er. melanoscutus*, thus the total whitefly mortality (parasitism and host feeding) caused by the former was significantly more than by the latter (Zang & Liu, 2008). Our previous work indicated food deprivation for 6 h prior to releasing whitefly parasitoids not only caused more host mortality through host feeding, but also improved their parasitism and longevity (Zang & Liu, 2009, 2010). More hosts fed on by mated parasitoids are likely to improve their parasitism and longevity compared to unmated ones, and this speculation warrants investigation in the future.

In using a biological control strategy, when pest populations exceed the economic threshold, mass-reared parasitoids may be argumentatively released. It is very important to find ways to manipulate the parasitoids so that they may quickly destroy as many hosts as possible through destructive host feeding and parasitism. The present study suggests the mated female parasitoids with host-feeding behavior will be recommended to release in crop systems for increasing their bio-control efficiency.

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