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ORIGINAL ARTICLE

Fitness of *Encarsia sophia* (Hymenoptera: Aphelinidae) parasitizing *Trialeurodes vaporariorum* and *Bemisia tabaci* (Hemiptera: Aleyrodidae)

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Abstract Fitness and efficacy of *Encarsia sophia* (Girault & Dodd) (Hymenoptera: Aphelinidae) as a biological control agent was compared on two species of whitefly (Hemiptera: Aleyrodidae) hosts, the relatively smaller sweetpotato whitefly, *Bemisia tabaci* (Gennadius) biotype 'B', and the larger greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood). Significant differences were observed on green bean (*Phaseolus vulgaris* L.) in the laboratory at 27 ± 2°C, $55\% \pm 5\%$ RH, and a photoperiod of 14 : 10 h (L : D). Adult parasitoids emerging from *T. vaporariorum* were larger than those emerging from *B. tabaci*, and almost all biological parameters of *E. sophia* parasitizing the larger host species were superior except for the developmental times of the parasitoids that were similar when parasitizing the two host species. Furthermore, parasitoids emerging from *T. vaporariorum* parasitized more of these hosts than did parasitoids emerging from *B. tabaci*. We conclude that *E. sophia* reared from larger hosts had better fitness than from smaller hosts. Those from either host also preferred the larger host for oviposition but were just as effective on smaller hosts. Therefore, larger hosts tended to produce better parasitoids than smaller hosts.

Key words biological control, body size, host size, oviposition, sweetpotato whitefly

Introduction

The sweetpotato whitefly, *Bemisia tabaci* (Gennadius) biotype 'B' (formerly known as silverleaf whitefly, *B. argentifolii* Bellows & Perring), and greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) are two key pests of vegetable, field and ornamental crops around the world (Mound & Halsey, 1978; Perring *et al*., 1993). Management of whitefly is challenging because of its intercrop movement, high reproduction, broad host range, resistance to insecticides and under-leaf habitat. Growers rely on the application of insecticides as the primary whitefly control strategy on field crops and vegetables. However, extensive use of chemical insecticides in food crops is of concern by the general public, policy makers and agricultural communities. Therefore, there is considerable interest in the development of biorational or biologically based strategies for management of these whiteflies that rely less on toxic chemical insecticides.

Many parasitoid species in the genera of *Encarsia* and *Eretmocerus* (Hymenoptera: Aphelinidae) are important natural enemies of the two whitefly species (Gerling, 1990; Polaszek *et al*., 1992). Over 170 species in the genus *Encarsia* have been described worldwide (Hayat, 1989). *Encarsia sophia* Girault & Dodd [= *E. transvena* (Timberlake)] is one of the most important parasitoid species parasitizing many whitefly species, including *B. tabaci* and *T. vaporariorum* (Kapadia & Puri, 1990; Gerling *et al*., 1998; Hunter & Kelly, 1998; Antony *et al*., 2003; Zang & Liu, 2008, 2009; Shi *et al*., 2009). Like most *Encarsia* species, *E. sophia* is solitary, arrhenotokous, heteronomous and autoparasitoid. Female eggs are laid internally in whitefly nymphs and develop as primary

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parasitoids, whereas males develop as hyperparasitoids, either on females of their own species or on other primary aphelinid parasitoids. It is found throughout the Old World and has been introduced in the New World (Heraty & Polaszek, 2000). It was originally released in California as part of the classical biological control program for the exotic biotype "B" of *B. tabaci* in the southern US and other parts of the world (De Barro, 1995; Gerling, 1996), and has become established in the field in several southern states of the US (Hoelmer & Goolsby, 2002).

One of the most important relationships in parasitoid behavioral ecology is between size and fitness of adult females (Heinz, 1995; Hora *et al*., 1995). 'Parasitoid size-fitness' has been hypothesized to play a major role in host species selection in other parasitoid–host systems (van de Assem *et al*., 1989; King, 1994; Kazimirova, 1996). Size has been positively correlated with egg number, longevity and searching efficiency in parasitoids (Avilla & Copland, 1987; Visser, 1994; West *et al*., 1996). Earlier works have demonstrated that variation in host size influences life histories in *E. formosa* attacking *B. tabaci* and *T. vaporariorum* (van Alphen & Vet, 1986). Progeny from the smaller *B. tabaci* suffered increased juvenile mortality, reduced body size, fewer ovarioles and fewer eggs oviposited compared with progeny from the larger *T. vaporariorum* (Heinz, 1995). Hora *et al*. (1995) also found that *E. formosa* emerging from large pupae of *T. vaporariorum* were larger, had greater fecundity and lived longer than wasps emerging from smaller host pupae. However, this fitness advantage has not translated into preference behavior between small (male) or large (female) prepupae.

To maximize the potential of *E. sophia* for biological control of *B. tabaci* or *T. vaporariorum*, it is important to elucidate the fitness of *E. sophia* parasitizing both host whitefly species. In this study, we first determined the size of parasitized and unparasitized hosts, then determined developmental time in each of the two whitefly hosts, measured the body sizes of adult wasps emerged from each, and determined host preference and oviposition success in choice (single host species) and choice (two host species) tests. We used this information to compare the fitness of *E. sophia* parasitizing the two host species.

Materials and methods

Host plants

Green bean (*Phaseolus vulgaris* L., variety 'Ambra,' Harris Moran Seed Company, Modesto, CA, US) plants were used as the host for *B. tabaci* or *T. vaporariorum* in all experiments. The green bean seedlings were grown in 30-cm diameter plastic pots in potting medium (Metro-Mix 360, Sun Gro Horticulture, Terrell, TX, US) in a greenhouse until the two or three true-leaf stage. Individual leaves were used for all experiments. The leaves were excised and each leaf petiole was placed in a floral aquapic filled with a hydroponic solution (Aqua-Ponics International, Los Angeles, CA, US). These leaves readily rooted in a few days after they were propagated in the hydroponic solution. Once rooted, they would grow normally with excellent vigor for months.

Whitefly and parasitoid cultures

Two species of whitefly were used in this study, *B. tabaci* and *T. vaporariorum*. *B. tabaci* and *E. sophia* were originally collected on cabbage in the Texas AgriLife Research, Texas A&M University System at Weslaco, Texas, US. *T. vaporariorum* originated from poinsettia maintained in the greenhouse at the Department of Entomology, Michigan State University (East Lancing, MI, US). Before the whiteflies of both species were used in the experiments, they were cultured on green bean for two generations in an air-conditioned chamber at 27 ± 2°C, 55% ± 5% RH, and a photoperiod of 14 : 10 h (L : D).

Leaf clip-on cages (4.5-cm diameter) were used to confine whiteflies and parasitoids on host leaves. Approximately 50 adult whiteflies were released into each clip cage placed on the lower surface of excised green bean leaves. After 12 h, clip cages were removed, and all whitefly adults were removed using an aspirator. The leaves with whitefly eggs were placed in large wooden screen cages (60 × 60 × 60 cm). Based on our preliminary tests on development of *B. tabaci* and *T. vaporariorum* on green bean, *B. tabaci* were incubated for 13 days and *T. vaporariorum* for 15 days to obtain similarly developed third or early fourth instar nymphs for both species simultaneously, the preferred stages for *E. sophia* (Hunter & Kelly, 1998; Antony *et al*., 2003; Zang & Liu, 2008, 2009).

Males of *E. sophia* were reared separately by releasing virgin females on parasitized whitefly nymphs that had been exposed as third instars 4 days previous to mated female wasps. The hosts of the autoparasitoid would then have been third instar female larvae. Earlier work suggested that the *E. sophia* female prefers to oviposit unfertilized eggs in parasitized third or early fourth instar *B. tabaci* nymphs (Zang & Liu, 2008, 2009).

Size of parasitized and unparasitized whiteflies

Whitefly eggs were obtained as described above and allowed to develop to third or fourth instar, and then *E.*

sophia were released. As soon as the whitefly pupae developed to red or black-eye stage, an indication of the presence of a pharate whitefly or parasitoid adult, the maximum width and the length of the whitefly pupae were measured to determine the influence of parasitization on size of both *B. tabaci* and *T. vaporariorum*. An ocular micrometer on a compound microscope was used for the measurement. Thirty parasitized and unparasitized pupae of each whitefly species were measured.

Development, longevity and body size of E. sophia *parasitizing* B. tabaci *and* T. vaporariorum

Five females and one male of *E. sophia* emerging within 24 h of each other were confined for a 6-h mating period in a leaf clip-on cage. The females were then introduced in a leaf clip-on cage on a green bean leaf infested with approximately 50 *B. tabaci* or *T. vaporariorum* nymphs for 24 h. The parasitoid adults were aspirated out, the leaf clip-on cage removed, and the leaf was held undisturbed in a screen cage (60 × 60 × 60 cm). The nymphs were examined daily beginning 4 days after exposure to the parasitoids. The development of the parasitoids was monitored daily until adults emerged or died inside the whitefly host. A total of 60 parasitoids were thus observed for each host whitefly species.

Longevity of starved *E. sophia* Female wasps were collected as they emerged from either *B. tabaci* or *T. vaporariorum* and placed in 10 mL glass vials without food. The longevity of 50 parasitoid adults from each host species were observed in 12 h intervals until all died.

Adult size measurement Emerged adults females (< 24 h) were collected in 10 mL glass vials and placed at −20°C for 2 h. The wasps were then placed in 75% NaOH solution for 12 h. Head width at the widest point and body length from the frons to the tip of the abdomen of 30 *E. sophia* adult females from each whitefly host were measured using an ocular micrometer on a stereomicroscope. The left hind leg was removed from each adult under a microscope using a sharp dissecting knife, and the length a hind tibia from each was measured as reported by Roskam *et al.* (1996) who found a positive correlation between flight capacity and body size and a positive relationship between head width and hind tibia length of *E. formosa* as an indication of body size and reproduction capacity.

Oviposition preference and suitability of whitefly species based on original host

The experimental unit consisted of two symmetrical bean leaves bearing one of the two whitefly species (no-choice test) or with each bearing a different whitefly species (choice test). We found earlier that the development time from egg to late third and early fourth instar nymphs of *T. vaporariorum* was approximately 3 days longer than that of the *B. tabaci* (C. Luo & T.-X. Liu, unpubl. data). Therefore, the eggs of the two whitefly species were obtained 3 days apart. First, approximately 50 whitefly adults were released into a leaf clip-on cage placed on one set of leaves. After 12 h, all whiteflies were aspirated out and the leaf clip-on cages were removed and incubated for 3 days in insect-proof cages and incubated for 3 days. Subsequently, the process was repeated but with *B. tabaci* and all whitefly nymphs were then allowed to develop for 12 days to late third and early fourth instar. Approximately 50 nymphs for each whitefly species were used on each leaf, and the remaining ones were carefully removed using an insect pin without damaging the leaf surface. A mated female *E. sophia* reared from one or the other whitefly host was then introduced for 24 h into a cage containing the two whitefly-infested leaves. Whitefly nymphs were examined daily. Those that were parasitized gradually turned black and were marked on the adjacent leaf surface with an Indian ink pen. Daily observations continued until wasps emerged or died in their hosts. Each treatment had 20 replicates in the no-choice test, and 15 replicates in the choice test.

Statistical analysis

Development time, measurements of whitefly and parasitized pupal size and head width, body length and tibia length of parasitoid adults, longevity of parasitoid adults emerged, and nymphs parasitized from *B. tabaci* and *T. vaporariorum*, were analyzed using one-way analysis of variance (ANOVA), and means were separated using the least significant difference (LSD) test after a significant F-test at $P > 0.05$ (SAS Institute, 2008). Survival rates were transformed to the arcsine square root (arcsine [percent mortality/100]^2) to stabilize error variances (Gomez & Gomez, 1984) before being subjected to ANOVA and untransformed means were reported. A choice index was calculated as: $C = A/(A + B)$; where A was *T. vaporariorum* and B was *B. tabaci* when the index for *T. vaporariorum* was calculated, and vice versa when the index for *B. tabaci* was calculated.

Results

Size of parasitized and unparasitized whiteflies

All unparasitized nymphal stages of *T. vaporariorum* were larger than those of *B. tabaci* (length: $F = 49.97$;

Table 1 Length and width of unparasitized nymphal stages and parasitized fourth instars ("pupae") of *B. tabaci* and *T. vaporariorum* on green bean by *E. sophia*.

Instars	Size in mm ± SE ($n = 30$)†			
	B. tabaci		*T. vaporariorum*	
	Length	Width	Length	Width
First instar	0.26 ± 0.04 a	0.16 ± 0.13 A	0.28 ± 0.09 a	0.17 ± 0.15 A
Second instar	0.37 ± 0.19 b	0.24 ± 0.17 B	0.43 ± 0.17 a	0.34 ± 0.12 A
Third instar	0.45 ± 0.23 b	0.39 ± 0.22 B	0.61 ± 0.11 a	0.40 ± 0.15 A
Fourth instar‡	0.74 ± 0.14 b*	0.52 ± 0.31 B*	0.78 ± 0.14 a*	0.46 ± 0.13 A*
Fourth instar – parasitized‡	0.63 ± 0.46 b*	0.40 ± 0.28 B*	0.71 ± 0.30 a*	0.43 ± 0.12 A*

†Mean lengths followed by the same lowercase letters or widths followed by the same uppercase letters between the two whitefly species are not significantly different at $P = 0.05$ (LSD, SAS Institute, 2008).
‡Mean lengths or widths of unparasitized and parasitized fourth instars followed by an '*' in the same whitefly species are significantly different at $P = 0.05$ (LSD, SAS Institute, 2008).

df = 1,58; $P = 0.0001$; width: $F = 78.90$; df = 1,58; $P = 0.0001$) except first instars (length: $F = 0.35$; df = 1,58; $P = 0.4857$; width: $F = 0.08$; df = 1,58; $P = 0.8762$) (Table 1).

Parasitized "pupae" of both whitefly species were significantly smaller (in length and width) than their unparasitized counterparts (*T. vaporariorum*: length, $F = 131.43$; df = 1,58; $P = 0.0001$; width, $F = 5.20$; df = 1,58; $P = 0.0262$. *B. tabaci*: length, $F = 128.12$; df = 1,58; $P = 0.0001$; width, $F = 202.12$; df = 1,58; $P = 0.0001$) (Table 1). Additionally, parasitized "pupae" of *T. vaporariorum* were significantly larger than those of *B. tabaci* (length: $F = 48.46$; df = 1,58; $P = 0.0001$; width: $F = 29.71$; df = 1,58; $P = 0.0001$).

Development, longevity and size of E. sophia *parasitizing* B. tabaci *and* T. vaporariorum

Development Developmental times of *E. sophia* eggs and larvae (from oviposition to pupation) and pupae (from pupation to adult emergence) were not significantly different between the two host whitefly species (eggs and larvae: $F = 2.55$; df = 1,118; $P = 0.1127$; pupae: $F = 2.68$; df = 1,118; $P = 0.1042$) (Table 2). The overall developmental times of *E. sophia* from oviposition to adult emergence were not significantly different when parasitizing the two whitefly species ($F = 1.50$; df = 1,118; $P = 0.2232$).

Longevity The adults of *E. sophia* emerged from *T. vaporariorum* survived significantly longer without supplemental food (2.3 ± 0.5 days) than those emerged from *B. tabaci* (1.8 ± 0.4 days) ($F = 41.49$; df = 1,58; $P = 0.0001$) (Table 2).

Body size The adults of *E. sophia* emerged from *T. vaporariorum* were significantly larger than those emerged from *B. tabaci* (body length: $F = 25.35$; df = 1,58; $P < 0.0001$; head width: $F = 75.91$; df = 1,58; $P < 0.0001$, Table 3). Similarly, the hind tibia of *E. sophia* adult females emerged from *T. vaporariorum* were significantly longer than those emerged from *B. tabaci* ($F = 74.82$; df = 1,58; $P < 0.0001$).

Table 2 Developmental time in days of *E. sophia* parasitizing *B. tabaci* and *T. vaporariorum* and longevity of starved adults emerged from two whitefly species.

Parasitoid hosts	Egg to black pupae Days ± SE†	Pupa to adult emergence Days ± SE†	Adult longevity†
T. vaporariorum	6.4 ± 0.6	5.0 ± 0.2	2.3 ± 0.5 A
B. tabaci	6.5 ± 0.7	5.0 ± 0.3	1.8 ± 0.4 B

†Means followed by the same letter or no letter are not significantly different ($P > 0.05$, LSD, SAS Institute, 2008).

Table 3 Head width, body length and hind tibia length for *E. sophia* emerging from *B. tabaci* and *T. vaporariorum*.

Host	Measurement, mm ± SE†		
	Head width	Body length	Hind tibia length tibia
T. vaporariorum	0.26 ± 0.10 a	38.64 ± 0.34 a	10.18 ± 0.10 a
B. tabaci	0.22 ± 0.24 b	36.31 ± 0.32 b	8.83 ± 0.12 b

†Means in same column followed by same letter are not significantly different ($P > 0.05$, LSD, SAS Institute, 2008).

Suitability and ovipositional preference for whitefly species based on original host

There were no differences in parasitism rates between the two whitefly species in the no-choice tests, regardless of host origin of the ovipositing females. *E. sophia* females that were originally reared from *T. vaporariorum* parasitized similar numbers of *T. vaporariorum* nymphs and *B. tabaci* nymphs ($F = 0.52$; df = 1,58; $P = 0.67$) (Table 4). Almost all parasitoid immatures successfully survived to adults, 98.2% from *T. vaporariorum* and 99.0% from *B. tabaci*. Similarly, *E. sophia* females that were originally reared from *B. tabaci* also parasitized similar numbers of *T. vaporariorum* nymphs and *B. tabaci* nymphs ($F = 0.75$; df = 1,58; $P = 0.000\,1$) (Table 4). Again, almost all parasitoid immatures successfully survived to adults, 98.7% from *T. vaporariorum* and 99.0% from *B. tabaci*. In contrast, all females preferred *T. vaporariorum* for oviposition regardless of which whitefly host they originated from (Table 5). Similarly, the *E. sophia* that were originally reared from *B. tabaci* also parasitized more *T. vaporariorum* than *B. tabaci* ($F = 22.00$; df = 1,58; $P = 0.000\,1$). *E. sophia* reared from *T. vaporariorum* had a 71.0% chance to choose *T. vaporariorum* to lay eggs and only 29% chance to choose *B. tabaci*. Similarly, *E. sophia* reared from *B. tabaci* had a 66% chance to choose *T. vaporariorum* to lay eggs and only 32% chance to choose *B. tabaci*. Again, 96.8%–98.3% of parasitoid immatures successfully developed to adults regardless of host.

Discussion

Several authors determined the sizes of various developmental stages of *T. vaporariorum* and *B. tabaci* on various host plants (Liu & Oetting, 1993; Ghahhari & Hatami, 2001). Our data clearly show that all corresponding stages of *T. vaporariorum* with the exception of the first instar are larger than the corresponding stage of *B. tabaci* on green bean (Table 1). Blackburn *et al*. (2002) found that *E. formosa*, a cogenor of *E. sophia*, would not molt to its final instar until its host, *T. vaporariorum*, reached maximum size. We found that although the *E. sophia* parasitized nymphs of *B. tabaci* or *T. vaporariorum*, they were able to continue development and the resulting whitefly "pupae" were significantly smaller than their unparasitized counterparts (Table 1). For *B. tabaci* this difference amounted to 17.5% and 30.0% for length and width, respectively, compared to 9.9% and 7.0%, respectively, for *T. vaporariorum*.

Our results show that the developmental time of *E. sophia* was not significantly different between the two whitefly hosts (Table 2). However, the parasitoids emerging from the larger *T. vaporariorum* were significantly larger than from the smaller *B. tabaci* (Table 3). Our results were in agreement with those reported by Hora *et al*. (1995) who found that when *E. formosa* parasitized from large prepupae of *T. vaporariorum*, the resulting offspring were larger, and had greater fecundity and longevity than those initiated from smaller prepupae.

Table 4 Numbers of whitefly nymphs parasitized by *E. sophia* originally reared on *T. vaporariorum* or *B. tabaci* in no-choice tests.

Original hosts	Offered hosts	Nymphs parasitized/female Mean ± SE†	Adult emerged
T. vaporariorum	*T. vaporariorum*	16.5 ± 7.7 a	98.2%
T. vaporariorum	*B. tabaci*	14.5 ± 6.3 a	99.0%
B. tabaci	*T. vaporariorum*	17.7 ± 7.1 a	98.7%
B. tabaci	*B. tabaci*	15.5 ± 8.1 a	99.0%

†Means in same subcolumn between the two introduced hosts followed by same letter are not significantly different ($P > 0.05$, LSD, SAS Institute, 2008).

Table 5 Numbers of whitefly nymphs parasitized by *E. sophia* originally reared on *T. vaporariorum* or *B. tabaci* in choice tests.

Original hosts	Offered hosts	Nymphs parasitized/female Mean ± SE†	Emerged rate (%)	Choice index (C_I), %
T. vaporariorum	*T. vaporariorum*	9.3 ± 5.2 a	96.8	71.0
	B. tabaci	3.8 ± 3.9 b	97.3	29.0
B. tabaci	*T. vaporariorum*	8.9 ± 3.5 a	97.7	62.2
	B. tabaci	5.4 ± 3.6 b	98.3	37.8

†Means in same subcolumn between the two hosts followed by same letter are not significantly different ($P > 0.05$, *t*-test, SAS Institute, 2008).

In *E. formosa*, Hora *et al*. (1995) found that the fitness advantage of the large parasitoids emerged from large hosts did not result in preference for larger prepupae. In contrast, we found that the parasitoids originally from either of two host species preferred the larger host in choice tests (Table 5) even though there were no differences among hosts in no-choice tests (Table 4).

Many studies also show that adult size is a major factor affecting the reproductive success, that is fitness of parasitoid wasps (Visser, 1994). Bethke *et al.* (1991) reported that the hind tibial length in *E. formosa* could change based on the length of a new host species. They found that the hind tibial length decreased when switched from *T. vaporariorum* on tobacco to smaller *B. tabaci* on poinsettias, and did not increase again on this host for up to 18 generations. Vianen & van Lenteren (1986) also found that individuals of *E. formosa* reared on the large host *Aleyrodes proletella* L. were larger than those reared on the smaller *T. vaporariorum*. Similarly, Greenberg *et al*. (2002) found that the length of adult *Eretmocerus mundus* Mercet and *Er. eremicus* Rose & Zolnerowich was greater when reared from *T. vaporariorum* than from *B. tabaci* (0.614 *vs*. 0.505 and 0.635 *vs*. 0.510 mm, respectively).

We did not find any difference in parasitoid emergence success between whitefly hosts. Similar results have been reported by Bethke *et al*. (1991) who found that emergence rates of *E. formosa* were not different for any host association examined, but there was a significant increase in the fecundity of *E. formosa* after 18 generations on *B. tabaci* as a host on poinsettia when switched from *T. vaporariorum* as a host on tobacco.

In conclusion, in our no-choice test we found that the developmental times of *E. sophia* were not different in *T. vaporariorum* and *B. tabaci*. However, *E. sophia* adult females emerged from the larger *T. vaporariorum* were significantly larger than those emerged from the smaller hosts. *E. sophia* reared from either host species produced more offspring from the larger hosts than from the smaller hosts in the choice tests, but produced similar numbers of offspring in the no-choice test. The information in this study will help to provide a better understanding of the relationships between *E. sophia* fitness, mass-rearing host selection and improving the effectiveness and predictability of augmentative biological control as a pest control technology using mass-reared parasitoids.

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