

PARASITOID NICHES OF *ENCARSIA FORMOSA* AND *ENCARSIA LYCOPERSICI* (HYMENOPTERA: APHELINIDAE) EXPLOITING *TRIALEURODES VAPORARIORUM* (HEMIPTERA: ALEYRODIDAE)

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ABSTRACT

Encarsia formosa Gahan (Hymenoptera: Aphelinidae) is an aphelinid endoparasitoid of the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae). *Encarsia lycopersici* (De Santis) is a parasitoid of the same host, but it is not known if both parasitoids occupy the same niche. In this study, the duration of development of the parasitoids, and the ability of both species to parasitize the 4 preimaginal instars of *T. vaporariorum* were determined. Results indicate that both *E. formosa* and *E. lycopersici* can parasitize all preimaginal instars of *T. vaporariorum*, and thus effectively occupy the same parasitoid niches, and they are part of the same parasitoid guild. However, variations in parasitism of the different preimaginal instars were observed. *Encarsia lycopersici* showed a higher parasitism rate on the first instar than on the third and fourth instars of *T. vaporariorum*. In contrast to *E. formosa*, which exhibited a lower parasitism rate on the first instar than on the fourth instar. In addition, *E. lycopersici* showed higher parasitism rate than *E. formosa* on the first instar of this host. This suggests that *E. lycopersici* may have a competitive advantage in exploiting the host, as it is the first to occupy it.

Key Words: greenhouse whitefly, stage-specific parasitism, preimaginal developmental time, biological control

RESUMEN

Encarsia formosa Gahan (Hymenoptera: Aphelinidae) es un afelinido endoparasitoide de la mosca blanca de los invernaderos *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae). *Encarsia lycopersici* (De Santis) es un parasitoide del mismo hospedero, pero no se conoce si ambos parasitoides ocupan el mismo nicho. En este estudio, la duración de desarrollo de los parasitoides y la capacidad de ambas especies de parasitar los cuatro estadios preimaginales de *T. vaporariorum* fueron determinadas. Los resultados indicaron que *E. formosa* y *E. lycopersici* pueden parasitar a *T. vaporariorum* en todos los estadios preimaginales, ocupan el mismo nicho y son parte del mismo gremio de parasitoides. Sin embargo, se observaron diferencias en la parasitación de los diferentes estadios preimaginales. *Encarsia lycopersici* mostró mayor parasitismo en el primer estadio que el tercero o cuarto estadio de *T. vaporariorum*, a diferencia de *E. formosa*, la cual exhibió menor parasitismo en el primer que en el cuarto estadio. Además, *E. lycopersici* mostró mayor parasitismo que *E. formosa* en el primer estadio del hospedero. Esto sugiere que *E. lycopersici* podría tener una ventaja competitiva en explotar el hospedero, porque es el primero en ocuparlo.

Palabras Claves: Moscas blancas, parasitismo por estadio, duración de desarrollo preimaginal, control biológico

The greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae), is one of the most important pests of vegetable, field and ornamental crops in the world (Vet et al. 1980; van Lenteren & Noldus 1990; Byrne & Bellows 1991; Park et al. 2004). It causes economic damage to crops by feeding on phloem sap and contaminating leaves and fruits with honeydew that facilitates sooty mold formation, and by transmitting plant viral diseases (van Lenteren & Noldus 1990; Byrne & Bellows 1991; Park et

al. 1998; Bi et al. 2002; Hodges & Evans 2005; Arnó et al. 2006). Management of *T. vaporariorum* in greenhouse-grown crops using *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) has been highly successful in many countries (van Lenteren & Woets 1988; Noldus & van Lenteren 1990; Kevan et al. 1991; Shipp et al. 1991; Hoddle et al. 1998) and is now being applied in Uruguay by inoculative releases.

Encarsia formosa will oviposit in all immature stages of *T. vaporariorum*, except in the egg and

the mobile first instar (crawler), but the third instar and the fourth-instar (which includes the "pupae") are the most susceptible and suitable stages for *E. formosa*. The rate of emergence of the parasitoid is highest from these stages (Nechols & Tauber 1977; Soto et al. 2002). Parasitoid development does not progress beyond its first instar until the host reaches the fourth instar (Nechols & Tauber 1977). The physiological mechanism that synchronizes development of *E. formosa*'s larva with that of its host is unknown, as are mechanisms by which the quiescent developing parasitoid larvae counter host defenses (Hoddle et al. 1998). These findings of Nechols & Tauber (1977) supersede those of Nell et al. (1976) who had stated that when first and second-instar larvae are parasitized, hosts and parasites die prematurely.

In 2003, *Encarsia lycopersici* (De Santis) was first detected in organic greenhouses in Uruguay, later reaching high levels of parasitism of *T. vaporariorum*. *Encarsia lycopersici* has also been recorded in Chile (Estay & Bruna 2002), Brazil (Evans & Angulo 1996, De Oliveira et al. 2003) and Argentina (Castresana & Paz 2007). *Encarsia lycopersici* is a little studied species, and it is unknown if *E. lycopersici* and *E. formosa* employ similar strategies for exploiting their common host and, following Root (1967), whether they occupy the same parasitoid niche to form a parasitoid guild (Hawkins & MacMahon 1989).

Parasitoid guilds are defined by which host stage is attacked, the mode of parasitism (ectoparasitoid or endoparasitoid) and the form of parasitoid development after host attack (continuous throughout life stages or protracted at the first instar stage until the host reaches a certain stadium). The time when the host stage is attacked is primarily defined by the stadium (egg, larval, pupal, or adult), and within the larval stadium by early, mid and late instars (Mills 1992). Parasitoid guilds result from interspecific competition, which is a major factor in determining the trophic niche width of sympatric species at both ecological and evolutionary levels (MacArthur 1972; Godfray 1994).

To assess whether these 2 parasitoids occupy the same niche, this study determined the duration of preimaginal development, and the ability of *E. formosa* and *E. lycopersici* to parasitize each of the 4 nymphal instars of *T. vaporariorum*. Differences in host exploitation by the 2 parasitoids could indicate favorable outcomes of interspecific competition for 1 of the 2 species, and could have consequences for their coexistence, as well as for the biological control of *T. vaporariorum* in greenhouses if both species were to be released together. In addition it is important to ascertain whether the naturally occurring *E. lycopersici* might reduce the effectiveness of *E. formosa* releases.

MATERIALS AND METHODS

Insect and Plant Colonies

Trialeurodes vaporariorum and *E. formosa* colonies collected from the horticultural region in southern Uruguay (Department of Canelones) (S 34° 29' W 56° 02') have been kept at the Entomology Unit of the Faculty of Agronomy since 2001 (Montevideo, Uruguay). Individuals from these colonies were maintained in closed greenhouses at 22-26 °C, 65 ± 10% RH and natural photoperiod, according to the protocol described by Scopes & Biggerstaff (1971). *Encarsia lycopersici* was collected in the same region as *E. formosa*, and raised specifically for this study. New individuals were added regularly to reinforce the colonies. Based on previous studies carried out by the Entomology Unit (Pascal et al. 2003) the tobacco plant (*Nicotiana tabacum* L.; Solanales: Solanaceae) was chosen as a host for *T. vaporariorum*. The initial tobacco plants (Virginia, cv. 'K-326') were grown from seeds obtained from commercial producers in northern Uruguay.

Production of Specific Nymphal Instars of *T. vaporariorum* for Tests

Groups of 4 tobacco plants were placed in metal cages (45 cm L × 45 cm W × 75 cm H), covered by fine muslin to prevent development of high humidity. The plants were exposed to 100 *T. vaporariorum* adults for 24 h in a room kept at a temperature of 22-26 °C, 65 ± 10% RH and natural photoperiod. After this 24 h period adult whiteflies were removed from the plants using a hand vacuum, and the plants were transferred to another room at 25 ± 1 °C and kept under the same environmental conditions until each one of the 4 nymphal instars of the greenhouse whitefly was reached.

Parasitism of *E. formosa* and *E. lycopersici* on Different *T. vaporariorum* Instars

To assess the ability of *E. formosa* to parasitize different *T. vaporariorum* instars, 1-d old parasitoid females were placed individually in 20 plastic cages (3 cm Ø × 2 cm H), called 'clip cages' according to Liu & Stansly (1996). The cages were placed on tobacco leaves over patches containing at least 40 nymphs of *T. vaporariorum*, a number that exceeds the daily parasitism ability of the parasitoid. A drop of honey was placed on the leaf section covered by each clip cage to feed the parasitoid. This process was conducted with each of the 4 nymphal instars of *T. vaporariorum*. After 24 h, the clip cage was removed and the parasitoid was recorded as being alive, dead or missing. A circle was drawn on the leaf to indicate where the clip cage had been placed.

Encarsia lycopersici is a biparental species unlike *E. formosa*, which is uniparental. Thus, a group of *T. vaporariorum* pupae parasitized by *E. lycopersici* was maintained at $25 \pm 1^\circ\text{C}$ until adult parasitoids emerged. After emergence, the *E. lycopersici* adults were left together for 24 h to allow for fertilization of the females. Following this, the parasitoids were placed individually in clip cages and the same steps as described above for *E. formosa* were followed.

Because it was not possible to determine the gender of the *E. lycopersici* individuals before placing them in clip cages (gender-specific morphological features are visible only under magnification), their genders were determined under an optical microscope after they had been exposed to hosts for 24 h in the clip cages. The parasitoids were then mounted on slides in Hoyer's solution and observations of genitalia and antennae were made based on descriptions in De Santis (1957). Clip cage experimental results from male *E. lycopersici* individuals were discarded. On average 40 repetitions were necessary in order to obtain results from 20 females.

Duration of Parasitoid Preimaginal Development at 25 °C

When the greenhouse whitefly nymphs began to turn black (indicating parasitoid development) the circled area on each leaf was excised and placed in a plastic container (6.5 $\varnothing$ $\times$ 2.5 cm H), and the insects continued their development in a growth chamber at $25 \pm 1^\circ\text{C}$. The parasitoid pupae were counted and then observed daily to determine the date of parasitoid emergence. The developmental time of the emerged parasitoids was used in statistical analyzes for each of the four nymphal instars of *T. vaporariorum*.

Statistical Analysis

A randomized experimental design was used and treatments were organized in a factorial arrangement with 2 factors: instar of the greenhouse whitefly (4 levels) and parasitoid species (2 levels). The 2 parasitoid characteristics under study were analyzed: preimaginal development of the parasitoid at different host instars and ability to parasitize different host instars.

A general linear model was used to analyze preimaginal duration (expressed in d). Variance components were estimated using the restricted maximum likelihood method (REML) for the 2 parasitoid factors and their interaction, using the number of individuals as the covariant variable. A Tukey Multiple Range Test, adjusted by Kramer (1956) was performed to compare all pairs of treatments (species and instars).

To analyze the ability of each species to parasitize hosts, the numbers of parasitized "pupae"

were analyzed. A generalized linear model was used assuming a Poisson distribution with an over-dispersion parameter and a logarithmic link function. The average number of parasitized pupae was calculated. All tests in the generalized linear model are likelihood ratio tests, thus a chi-square statistic was used (or an F statistic approximation, which is the ratio of 2 chi-square distributions). Replicates in which the female failed to parasitize any hosts were discarded. Because the clip cages were repetitions in a completely randomized design (not part of the variations), statistical analysis was performed using a set of observations that differed depending on the parasitoids that actually emerged (for calculating the duration of development) or the nymphal stages that were parasitized (for parasitic ability). Analyses were conducted using the procedures GLM and GENMOD from SAS/STAT (2007), respectively.

RESULTS

Parasitism of *E. formosa* and *E. lycopersici* on Different *T. vaporariorum* Instars

The analysis of parasitic ability for both parasitoids in relation to the instars of *T. vaporariorum* was not significant for parasitoid species level or host instar, although there was significant species-instar interaction. This means that the two parasitoid species do not behave in the same manner because even though they both attack the 4 nymphal instars of the host, they do so to different degrees (Table 1). Parasitism by *E. formosa* was significantly higher only when the fourth instar of the host was exposed to the parasitoid compared with the first instar of the host ($\chi^2 = 5.26$; $df = 1$; $P = 0.0218$), but no difference in ability to parasitize was evident between the second instar and third instar compared with the first and fourth instars (Table 2). *Encarsia lycopersici* showed lower parasitism in the more advanced instars of *T. vaporariorum*. Parasitism at the first instar differed from that recorded at the third ($\chi^2 = 8.18$; $df = 1$; $P = 0.0042$) and fourth ($\chi^2 = 6.47$; $df = 1$; $P = 0.0110$), whereas among the remaining instars no differences were observed. Parasitism between the 2 parasitoid species at each instar of

TABLE 1. ANALYSIS OF PARASITISM OF *E. FORMOSA* AND *E. LYCOPERSICI* ON DIFFERENT INSTARS OF *T. VAPORARIORUM* (GENERALIZED LINEAR MODEL).

Source	df	χ^2	Pr > χ^2
Species	1	0.08	0.7813 ns
Instar	3	0.99	0.8032 ns
Species * Instar	3	14.75	0.0020 **

** Indicates interaction was significant at 0.01 level.

TABLE 2. AVERAGE NUMBER $\pm$ SE OF WHITEFLY NYMPHS PARASITIZED BY *ENCARSIA FORMOSA* AND *E. LYCOPERSICI* DURING THE FIRST 24 h AFTER THEIR EMERGENCE, ACCORDING TO THE INSTAR OF *TRIALEURODES VAPORARIORUM* EXPOSED TO PARASITISM.

<i>Encarsia</i> species	1 st instar		2 nd instar		3 rd instar		4 th instar	
	N*	Number parasitized	N*	Number parasitized	N*	Number parasitized	N*	Number parasitized
<i>E. formosa</i>	97	4.0 $\pm$ 0.6 b	101	5.1 $\pm$ 0.7 ab	107	5.4 $\pm$ 0.7 ab	123	6.2 $\pm$ 0.7 a
<i>E. lycopersici</i>	144	7.2 $\pm$ 0.8 a	107	5.4 $\pm$ 0.7 ab	85	4.2 $\pm$ 0.6 b	91	4.5 $\pm$ 0.6 b

Means followed horizontally by the same letter are not significantly different ($P < 0.05$) in the χ^2 approximation to the Likelihood Ratio Test.

*Cumulative number of whitefly nymphs involved in the trials.

T. vaporariorum differed only in the first instar, with higher parasitism by *E. lycopersici* than *E. formosa* ($\chi^2 = 10.65$; $df = 1$; $P = 0.0011$). However, *E. lycopersici* showed a decrease and *E. formosa* an increase in parasitism when presented with preimaginal instars of *T. vaporariorum* from first to fourth instar. Without taking into account the instar of the parasitized host *E. formosa* and *E. lycopersici* parasitized an average of 5.1 and 5.2 individuals in the first 24 h, respectively.

Encarsia formosa showed no differences in its preimaginal development time when parasitizing in the first, second or third instar of *T. vaporariorum* ($P < 0.05$). However, the preimaginal developmental time at the fourth instar was significantly shorter than at the first instar ($T-K, DBM = 4.9925$; $P = 0.005$) and second instar ($T-K, DBM = 4.0375$; $P = 0.0041$), though not significantly different from the third instar ($T-K, DBM = 3.2601$; $P = 0.0713$) (Table 3).

Duration of Parasitoid Preimaginal Development at 25 °C

Preimaginal development time of the parasitoids varied by species and by the instar at which parasitism occurred ($F = 20.24$; $df = 8, 14$; $P < 0.0001$). *Encarsia lycopersici* showed a longer preimaginal development period than *E. formosa* (23.3 and 19.1 d respectively) ($T-K, Difference Between Means (DBM) = -4.1737$; $P < 0.0001$) when the instar of *T. vaporariorum* at which the host was parasitized was not considered. The preimaginal development time of *E. lycopersici* was longer than that of *E. formosa* when parasitism took place in the first instar ($T-K, DBM = -3.8726$; $P = 0.0071$), second instar ($T-K, DBM = -3.9775$; $P = 0.0046$) and fourth instar ($T-K, DBM = -6.0450$; $P < 0.0001$) of *T. vaporariorum* but not in the third instar, where no difference between the species was evident ($T-K, DBM = -2.7998$; $P = 0.1833$).

DISCUSSION

The reduced duration of preimaginal development of *E. formosa* when it parasitized the later instars of *T. vaporariorum* agrees with the results reported by Nechols & Tauber (1977). These researchers found that when *T. vaporariorum* is parasitized by *E. formosa* early in its development, the parasitoid eggs hatch but larval development is suppressed until the host reaches the fourth instar, thus prolonging the duration of development. Such behavior could not be verified in *E. lycopersici* as the development period was not significantly reduced when it parasitized the more advanced instars of *T. vaporariorum*. Except in the third instar, the duration of development was longer in *E. lycopersici* than in *E. formosa*. In parasitoids, increased development time, though it may contribute to larger size, can lead to an increased risk of mortality associated

TABLE 3. PREIMAGINAL DEVELOPMENT TIME (MEAN $\pm$ STANDARD ERROR) OF *ENCARSIA FORMOSA* AND *E. LYCOPERSICI* AT 25 °C FOR EACH OF THE INSTARS OF *TRIALEURODES VAPORARIORUM* IN WHICH THE PARASITISM OCCURRED.

Parasitoid Species	Instar parasitized	Number of whiteflies parasitized	Preimaginal time (in days)
<i>Encarsia formosa</i>	1	94	21.0 $\pm$ 0.10 a
	2	82	20.1 $\pm$ 0.11 a
	3	104	19.3 $\pm$ 0.09 ab
	4	92	16.0 $\pm$ 0.10 b
<i>Encarsia lycopersici</i>	1	128	24.9 $\pm$ 0.08 a
	2	88	24.0 $\pm$ 0.11 a
	3	76	22.1 $\pm$ 0.11 a
	4	80	22.1 $\pm$ 0.12 a

Means followed by the same letter are not significantly different ($P < 0.05$) in the Tukey-Kramer test.

with the possible death of its host (Pennacchio & Strand 2006).

The preimaginal development time of *E. formosa* observed in this study was similar to the time reported by Qiu et al. (2004) using parasitoids originating in Beltsville (USA) (19.8 d). The preimaginal development time of *E. formosa* when parasitizing the first instar of *T. vaporariorum* was similar to that obtained by Hu et al. (2002) (21.2 d) but different from the observed when *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) was the host (18.1 d). This difference can be explained by variations in the size and development rate of the host and the environmental conditions (Hu et al. 2003). Soto (1997) reported a preimaginal development time of 16.6 d when the host was parasitized at instar 3 and 18.6 d when it took place at instar 4.

The parasitism when *E. formosa* was exposed to different instars of the host in this study differ from those reported by Nell et al. (1976), Nechols & Tauber (1977) and Soto et al. (2002) who found that the third, fourth and prepupal stages of *T. vaporariorum* had higher parasitism by *E. formosa*. The number of individuals parasitized by *E. formosa* in the first 24 h was similar to that obtained by Qiu et al. (2004) for *E. formosa* (Beltsville strain) reared on *B. tabaci* on *Poinsettia* (5.25 individuals) and less than *E. formosa* (Dutch strain) reared on *T. vaporariorum* on tobacco (6.75 individuals). In the case of *E. lycopersici* there is no literature available for comparison.

The results indicate that *E. formosa* and *E. lycopersici* are able to parasitize and develop successfully on all preimaginal instars of *T. vaporariorum*. The two species occupy the same parasitoid niche when exploiting this host and are therefore part of the same parasitoid guild; however, they show different levels of success in parasitizing the different instars of the host. *Encarsia lycopersici* showed higher parasitism on the first instar than on the third and fourth instars of *T. vaporariorum*, in contrast to *E. formosa*, which exhibited lower parasitism on the first instar than on the fourth instar. In addition, *E. lycopersici* showed higher parasitism than *E. formosa* on the first instar of this host. This could affect the competitive relationship between the two species given that, when two parasitoids attack successive host stages, the early-acting species often has a competitive advantage (Briggs 1993; Wang et al. 2003), which could respond to an evolutionary gradient of parasitoids toward early colonization of their hosts (Pennacchio and Strand 2006). No studies have addresses competition between these two species for a single host. However, the available evidence suggests that *E. lycopersici* may have a competitive advantage in exploiting the host, as it is the first to occupy it. In contrast to *E. formosa*, which is widely distributed and mass reared for whitefly control around the world, *E. lycopersici* is

a rare species mostly restricted to some countries of South America. Many ecological reasons may influence the distribution of these species in the world; however, in greenhouses in which *E. lycopersici* and *E. formosa* appear at the same time, the first is more abundant than the latter (Grille, G. pers. obsv.).

In summary, the outcome of competitive interactions between two species depends on the species' relative abilities to consume shared resources (which are species specific) as well as the relative proportions of different resource types in the environment (Schoener 1974; Chase & Belovsky 1994). Given this relationship, it is easy to see how the outcomes of competitive dynamics can vary predictably as the relative proportions of resource types in the environment vary and how they may account for some of the temporal and spatial variation observed in competitive systems (Chase 1996).

The knowledge gained about the success of *E. formosa* and *E. lycopersici* in exploiting *T. vaporariorum*, invites reflection on the competitive relationships of species within parasitoid guilds, and their potential influence on biological control when different species are present in the same ecosystem. Future studies in the field involving these species should be conducted, which could confirm the characteristics and effects of their interactions.

ACKNOWLEDGMENTS

A special thank you to Nick J. Mills (Department of Environmental Science, Policy and Management, University of California Berkeley) for responding to our questions about the niche occupied by the 2 species of *Encarsia* studied. We also thank Patrice Bolland supervised by Bernard Pintureau (UMR INRA/INSA de Lyon, France) who mounted and photographed the *E. lycopersici* individuals to facilitate identification of the sexes.

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