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Do host species influence the performance of *Encarsia formosa*, a parasitoid of *Bemisia tabaci* species complex?

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Abstract

The whitefly *Bemisia tabaci* (Gennadius) is a globally distributed species complex that includes several destructive pests of agriculture. In recent years, the high ability of *B. tabaci* to develop insecticide resistance indicates that using insecticides to control this pest has become unsustainable. Use of natural enemies as part of integrated management approaches is considered a key strategy for long term sustainable control. Here we investigated the effects of host species on the performance of a parasitoid. We tested this using *Encarsia formosa* Gahan (Hymenoptera Aphelinidae) and two members from *B. tabaci* species complex, MEAM1 and AsiaII7. The parasitoids were reared using MEAM1 or AsiaII7 hosts feeding on hibiscus. Those maintained on MEAM1 are referred to as M-*E. formosa* and those on AsiaII7 as A-*E. formosa*. Results showed that there were no significant differences between the pre-imaginal developmental times of M-*E. formosa* and A-*E. formosa* regardless of their whitefly hosts. However, M-*E. formosa* emergence rate after parasitism on MEAM1 was higher than that of A-*E. formosa* parasitizing MEAM1. On the contrary, A-*E. formosa* emergence rate after parasitism on AsiaII7 was higher than that observed for M-*E. formosa* parasitizing AsiaII7. In no-choice experiments, M-*E. formosa* females parasitized MEAM1 and AsiaII7 hosts in a similar rate but A-*E. formosa* parasitized less MEAM1 than AsiaII7 hosts. In choice experiments, M-*E. formosa* females parasitized more MEAM1 than AsiaII7 hosts and A-*E. formosa* parasitized AsiaII7 and MEAM1 hosts equally. These parasitism rates mirrored for the host checking and oviposition behavior of different *E. formosa* strains. Our results indicate that *B. tabaci* species does not influence parasitoid development period until adulthood, but that pre-imaginal experience is important for emergence rate, parasitism rate and behavior of *E. formosa* adults.

Key words: *Bemisia tabaci*, host quality, cryptic species, *Encarsia formosa*, host preference, biological control.

Introduction

The whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera Aleyrodidae) is a complex of at least 28 indistinguishable morphocryptic species (De Barro *et al.*, 2011; EFSA panel on plant health, 2013) that has a global distribution. It is a sucking insect pest that causes substantial damage to a wide range of crops through direct phloem feeding and loss of photosynthesis as a result of sooty mould growth (Berlinger, 1986). However, the most destructive damage results from the transmission of numerous plant viruses (Jones, 2003; Su *et al.*, 2013).

Insecticides play a key role for the control of whiteflies (Cuthbertson *et al.*, 2012). However, heavy reliance on chemical control could lead to the development of resistance in some species within the *B. tabaci* complex to most classes of insecticides (Basit *et al.*, 2013). Therefore, integrated pest management is seen as a more sustainable approach to control and, as part of this, biological control is an important element, with parasitoids being important contributors (Gerling *et al.*, 2001).

Numerous species of parasitic Hymenoptera, mainly from the genus *Encarsia* Forster and *Eretmocerus* Haldeman (Hymenoptera Aphelinidae), are known to parasitize *B. tabaci* (Mound and Halsey, 1978; De Barro *et al.*, 2000; Schmidt *et al.*, 2001; Gerling *et al.*, 2001; Schmidt and Polaszek, 2007; Li *et al.*, 2011) and have been subject to numerous studies. These studies can be grouped as: (1) oviposition choice and larval development (e.g. van Lenteren *et al.*, 1980; Drost *et al.*, 1999; Qiu *et al.*, 2007a; Yang and Wan, 2011); (2) tritrophic effects (e.g. Qiu *et al.*, 2005; Urbaneja *et al.*, 2007); (3) effects of temperature on life history traits (e.g. Qiu *et al.*, 2007b; Zandi-Sohani and Shishehbor, 2011); (4) parasitoid host feeding (Zang and Liu, 2008a); (5) interactions between natural enemies (Zang and Liu, 2008b; Lazreg *et al.*, 2009; Malo *et al.*, 2012); (6) lethal or sublethal effects of pesticides on parasitoids (e.g. Kumar *et al.*, 2008; Sugiyama *et al.*, 2011; Sohrabi *et al.*, 2013); (7) comparative studies of parasitoid performance (e.g. Drost *et al.*, 2000; De Barro and Coombs, 2009; Villanueva-Jimenez *et al.*, 2012). However, all these studies have focused on *B. tabaci* without considering it as a complex of multiple species.

The cryptic species of *B. tabaci* complex, as well as being reproductively incompatible, display a range of biological differences in terms of host plant utilization, ability to develop resistance to insecticides, plant virus transmission, tolerance to extreme temperatures and endosymbiont diversity (Ahmed *et al.*, 2010; Chu *et al.*, 2011; Qiu *et al.*, 2011; Rao *et al.*, 2012; Li *et al.*, 2012; Liu *et al.*, 2013; Yang *et al.*, 2013). This raises questions about the effects of host whitefly species on parasitoid performance.

Host quality is well known to influence parasitoid biological and behavioral traits such as fecundity, developmental time, emergence rate, secondary sex ratio, and size of the emerging adult wasps (Vinson and Iwantsch, 1980; Charnov, 1982; Godfray, 1994). Field experimental evidence suggests that differences of host quality do exist within the *B. tabaci* complex (De Barro and Coombs, 2009) or even within the same cryptic species of *B. tabaci* feeding on different host plants (Pessoa *et al*., 2016). For example, the mean parasitism by *Eretmocerus mundus* Mercet (Hymenoptera Aphelinidae) (Australian parthenogenetic strain) on the Australia (AUS) member of the *B. tabaci* complex averaged 12.05% whereas parasitism on Middle East-Asia Minor 1 biotype (MEAM1, formerly known as the B biotype *B. tabaci*) averaged 4.84%. Following the release of *Eretmocerus hayati* Zolnerowich et Rose (Hymenoptera Aphelinidae) as a biological control agent, field parasitism of MEAM1 4th instars increased to 29.04% (De Barro and Coombs, 2009), suggesting that *E. hayati* was better adapted to MEAM1 than *E. mundus*. Moreover, in the study of Pessoa *et al*. (2016), they investigated the tritrophical influence of transgenic Bt cotton on one parasitoid species of *B. tabaci*, *Encarsia desantisi* Viggiani (Hymenoptera Aphelinidae). Their results showed approximately 10% increase of adult emergence rate of *E. desantisi* when they developed from those *B. tabaci* hosts that fed on Bt cotton plants compared to those on non-Bt cotton; however, female parasitoid longevity decreased when their hosts fed on Bt cotton plants.

In current study we considered the relative ability of a parasitoid *Encarsia formosa* Gahan (Hymenoptera Aphelinidae) to use two different members of *B. tabaci* species complex, MEAM1 and AsiaII7. *E. formosa* is a solitary, thelytokous, primary and dominant endoparasitoid of *B. tabaci* in China (Li *et al*., 2011). *B. tabaci* MEAM1 first invaded China in the mid-1990s and has caused substantial damage to field and greenhouse crops across the country (Qiu *et al*., 2011). It belongs to the major clade that evolved in the Middle East/Africa/Asia Minor, whereas AsiaII7 is indigenous to the Asia region and is able to damage ornamental species such as variegated laurel, *Codiaeum variegatum* (L.)A.Juss and hibiscus, *Hibiscus rosa-sinensis* L. (Qiu *et al*., 2006; 2011; Boykin *et al*., 2013). The aim of this study was to determine whether parasitoid biology or behavior was influenced by the whitefly species used as its host.

Materials and methods

Plants and whiteflies

Hibiscus (*H. rosa-sinensis*) was used as the host plant for both MEAM1 and AsiaII7. The plants were grown in a greenhouse in plastic pots (12 cm diameter × 15 cm height) until they were 15-16 cm high. All the plants were free of pests at the beginning of experiments. Both whitefly species were collected in Guangzhou, China in 2006. MEAM1 insects were collected from eggplants (*Solanum melongena* L.) and AsiaII7 from variegated laurel (*C. variegatum*). Both whitefly species were reared on hibiscus in separate greenhouses at ambient temperatures and were tested regularly for species confirmation using mitochondrial cytochrome oxidase I (mtCOI) sequencing following Qiu *et al*. (2007c).

Parasitoid culture

E. formosa was collected from parasitized MEAM1 on tomato (*Lycopersicon esculentum* Mill.) plants at the Beijing Academy of Agriculture and Forestry Sciences in 2008 and maintained in culture on MEAM1 feeding on hibiscus. For the experiment, two separate parasitoid cultures were established, one with MEAM1 fed on hibiscus and the other with AsiaII7 also fed on hibiscus. Both parasitoid cultures were maintained on the different host species for 15 generations before experiments commenced. The *E. formosa* population maintained on MEAM1 is referred to as M-*E. formosa*, while the one maintained on AsiaII7 is referred to as A-*E. formosa*.

Development and emergence rate of *E. formosa* on MEAM1 and AsiaII7

One couple of either MEAM1 or AsiaII7 adults were released into one leaf cage (3.0 × 1.5 cm, d × h, with a 100 mesh/cm^2 cover at the top) on the underside surface of a hibiscus leaf. Both adults were removed after a 12 h oviposition period. For each leaf cage, eggs were left to hatch and the nymphs allowed to develop until they reached the 2nd-3rd instar stage. Approximately 40 nymphs at 2nd-3rd instar were kept for parasitization in each leaf cage.

Parasitoid pupae of *E. formosa* were collected and the adults left to emerge. The newly emerged wasps were incubated in a finger tube for one day with access to 10% honey. On the day after, a single female of M-*E. formosa* or A-*E. formosa* was introduced into the leaf cage containing 40 MEAM1 or AsiaII7 2nd-3rd instar nymphs and then left to oviposit for 12 h before being removed. After seven days the nymphs were examined with the aid of a stereomicroscope for the presence of a parasitoid larva; by this time the parasitoid larvae had reached the 3rd instar and were clearly visible through the nymph's cuticle. The following developmental periods of M-*E. formosa* and A-*E. formosa* using MEAM1 or AsiaII7 as hosts were recorded: (i) egg to 3rd instar, (ii) pupal stage and (iii) egg to adult. The emergence rate of parasitoid larvae from 3rd instar to adult was also recorded. There were four treatments: M-*E. formosa* parasitizing MEAM1, M-*E. formosa* parasitizing AsiaII7, A-*E. formosa* parasitizing MEAM1 and A-*E. formosa* parasitizing AsiaII7. Each set of treatments was repeated four times with five replicates per treatment. Each replicate consisted of one cage with approximately 40 nymphs of MEAM1 or AsiaII7 at 2nd-3rd instar.

Host checking and oviposition of *E. formosa*

When investigating the parasitism of *E. formosa* in the no-choice and choice experiments, the frequency of host checking and oviposition by M-*E. formosa* and A-*E. formosa* on MEAM1 and AsiaII7 was recorded over a 12 h period (from 8:00 to 20:00, the first 12 h of parasitization period of *E. formosa*), using a stereo camera connected to a computer. Host checking included the behavior of walking over the host, knocking with the antenna and inserting of their ovipositor inside the host momentarily. Oviposition was taken as when the female wasp inserted her ovipositor into *B. tabaci* nymphs lasting for several minutes, accompanied by the action of oviposition. Host checking and oviposition behaviors were measured as the time (min) spent by the parasitoids over the *B. tabaci* nymphs.

Parasitization of *E. formosa* on MEAM1 and AsiaII7: no-choice and choice tests

A single hibiscus plant was chosen and two symmetrical, fully expanded leaves of similar size were selected. Each leaf was enclosed by a leaf cage and whiteflies were introduced and allowed to oviposit as described above. In no-choice experiments both leaves had the same whitefly species present. In the choice experiment one leaf had MEAM1 and the other had AsiaII7. When the nymphs had developed through 2nd-3rd instar, the excess of nymphs were removed, keeping 30 nymphs on each leaf. The whole plant was then enclosed in a plastic cylinder cage (15 × 30 cm, d × h, screened with 100 mesh/cm^2 mesh at the top). Adult parasitoids were obtained as before, and a single two day old M-*E. formosa* or A-*E. formosa* adult was introduced into the cage to oviposit for 24 h before being removed. Parasitism was checked 10 days after the wasp was released into the cage.

For no-choice experiments, the treatments were as follows, M-*E. formosa* parasitizing MEAM1, M-*E. formosa* parasitizing AsiaII7, A-*E. formosa* parasitizing MEAM1, A-*E. formosa* parasitizing AsiaII7 in each cylinder cage. For choice experiments, the treatments were as follows, M-*E. formosa* parasitizing both MEAM1/AsiaII7 hosts present in one cylinder cage, A-*E. formosa* parasitizing MEAM1/AsiaII7 hosts present in one cylinder cage. Each set of treatments was repeated four times with five replicates per treatment. Each cylinder cage containing MEAM1 hosts or AsiaII7 hosts in no-choice experiments was considered a replicate and each cylinder cage containing both hosts was considered as a replicate in choice experiments.

All the experiments were carried out in separate temperature-humidity controlled incubators (PQX-250, Jintan Experimental Instrument Co. Ltd., Jiangsu, China) at 26.0 ± 1 °C with 70-85% relative humidity, 14:10 (L:D) photoperiod; light intensity was approximately 3000 Lux.

Data analysis

The parasitism rate was calculated according to Qiu *et al.*, (2007b). There was no difference between the treatment blocks so these were pooled together. The percentage data were firstly arcsine-square-root-transformed. This data and the development time were then compared using two-way ANOVA analysis (parasitoid origin, whitefly species). Means were separated using the Student-Newman-Keuls Multiple range test at a significance level of α = 0.05 (SAS, 2012).

Results

Development and emergence rate of *E. formosa* on MEAM1 and AsiaII7

The developmental time of M-*E. formosa* and A-*E. formosa* are shown in figure1. There were no significant differences in developmental times (egg-3rd instar larvae, $F_{15,64} = 0.62$, $P = 0.844$; pupae, $F_{15,64} = 1.67$, $P = 0.080$ and egg-adult, $F_{15,64} = 0.52$, $P = 0.672$) regardless of the species of whitefly hosts used for pre-imaginal development.

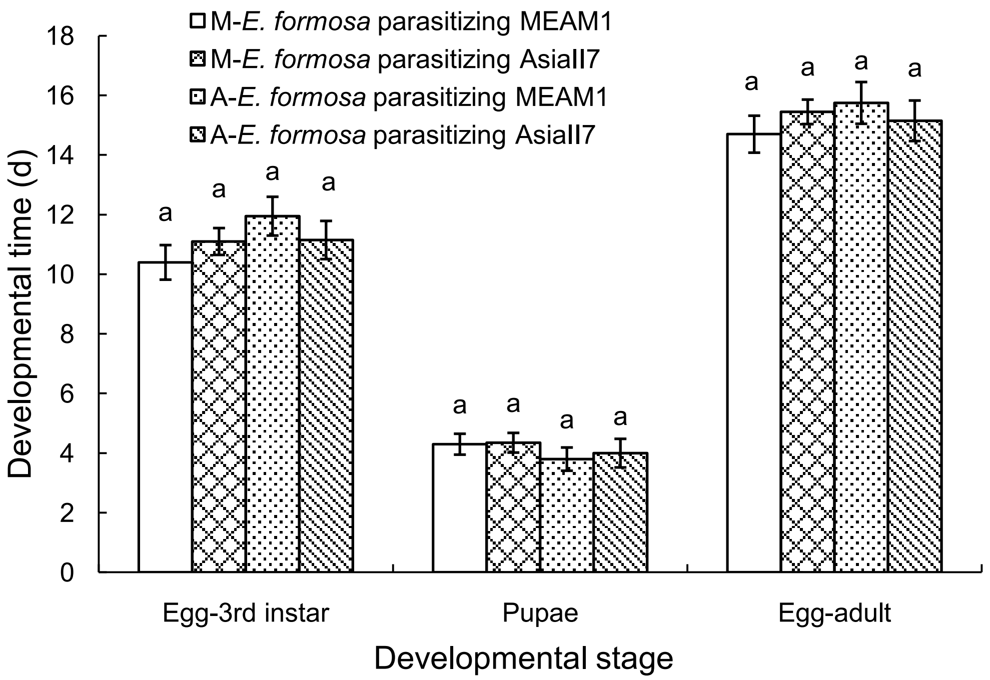

Figure 1. Mean developmental time (M ± SE, days) of *E. formosa* reared for 15 generations using MEAM1 or AsiaII7 hosts when parasitizing MEAM1 or AsiaII7. The same letter over the bars means there are no significant differences among the treatments in each developmental stage (Student-Newman-Keuls Multiple range test).

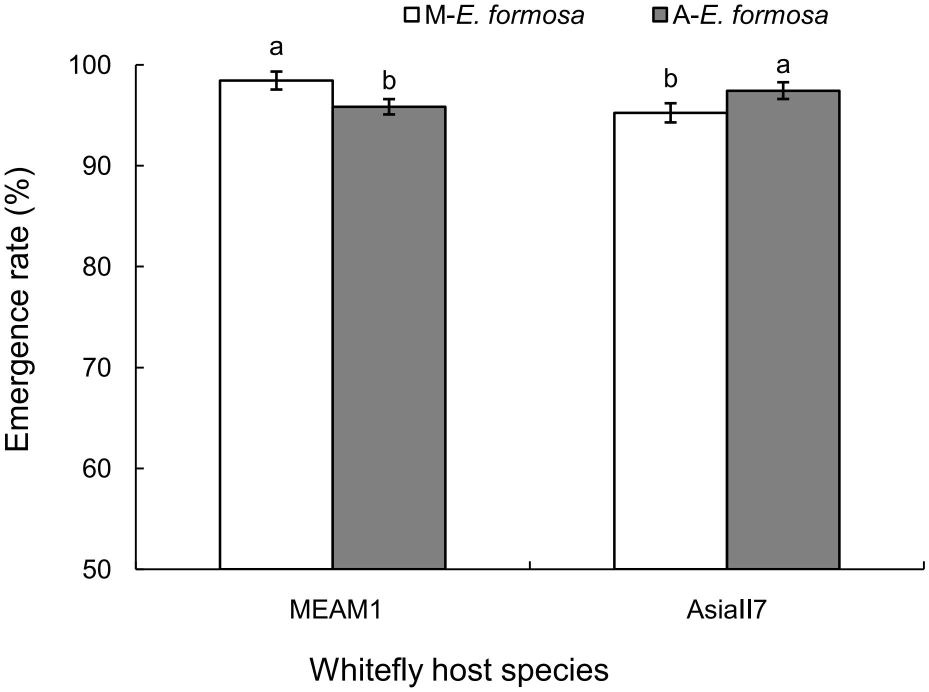

Figure 2. Emergence rate of *E. formosa* (M ± SE, %) reared for 15 generations using MEAM1 or AsiaII7 hosts when parasitizing MEAM1 or AsiaII7. The same letter over the bars means there are no significant differences among the treatments (Student-Newman-Keuls Multiple range test).

E. formosa emergence rate using different *B. tabaci* hosts

Emergence rate of *E. formosa* was always slightly but significantly higher when the host was the same species as the one from which the adult parasitoid had emerged than from the heterologous species host (figure 2, $F_{15,64}$ = 11.73, P = 0.003). The average emergence rate of M-*E. formosa* parasitizing MEAM1 was 98.45 ± 0.89%, but reduced to 95.25 ± 0.56% when the host was exchanged for AsiaII7. Similarly, the emergence rate of A-*E. formosa* reduced from 97.45 ± 0.83% when parasitizing AsiaII7 to 95.85 ± 0.55% when parasitizing MEAM1.

Host checking and oviposition frequencies of *E. formosa* on MEAM1 and AsiaII7: no-choice versus choice

When only MEAM1 nymphs were available, M-*E. formosa* exhibited significantly higher frequencies than A-*E. formosa* for both host checking (9.30 ± 0.52 vs. 7.10 ± 0.43 nymphs per parasitoid in the 12 h test period, respectively) and oviposition (6.95 ± 0.51 vs. 4.95 ± 0.34 nymphs per parasitoid, respectively). In contrast, when only AsiaII7 nymphs were available, no significant differences were found between M-*E. formosa* and A-*E. formosa* in the frequencies of host checking and oviposition (table 1). When both MEAM1 and AsiaII7 were available to M-*E. formosa*, a significantly higher frequency of host checking (8.95 ± 0.51 vs. 5.10 ± 0.34 nymphs per parasitoid) and oviposition (7.05 ± 0.47 vs. 3.10 ± 0.39 nymphs per parasitoid) was observed for MEAM1 relative to AsiaII7. Similarly, A-*E. formosa* showed significantly higher frequencies of host checking for AsiaII7 than for MEAM1 (8.10 ± 0.35 vs 6.05 ± 0.49 nymphs per parasitoid, respectively). However, oviposition frequencies were not significantly different between the MEAM1 and AsiaII7 hosts (table 2).

Table 1. Host checking and oviposition frequency of *E. formosa* (M ± SE, times) from either MEAM1 or AsiaII7 when parasitizing either MEAM1 or AsiaII7: no-choice experiments (12 h).

Host	Checking frequency*	Range	Oviposition frequency*	Range
M-*E. formosa* in MEAM1	9.30 ± 0.52 a	4-12	6.95 ± 0.51 a	1-9
M-*E. formosa* in AsiaII7	8.10 ± 0.71 ab	3-14	6.15 ± 0.58 ab	3-11
A-*E. formosa* in MEAM1	7.10 ± 0.43 b	2-10	4.95 ± 0.34 b	2-7
A-*E. formosa* in AsiaII7	7.95 ± 0.55 b	2-10	5.10 ± 0.61 b	2-8
$F_{15,64}$	4.81	-	3.85	-
P	0.0462	-	0.0467	-

*The same letter in one column means there are no significant differences among the treatments (Student-Newman-Keuls Multiple range test).

Table 2. Host checking and oviposition frequency of *Encarsia formosa* from either MEAM1 or AsiaII7 when parasitizing either MEAM1 or AsiaII7: choice experiments (12 h).

Host	Checking frequency*	Range	Oviposition frequency*	Range
M-*E. formosa* in MEAM1	8.95 ± 0.51 a	5-12	7.05 ± 0.47 a	3-10
M-*E. formosa* in AsiaII7	5.10 ± 0.34 c	3-8	3.10 ± 0.39 c	2-4
A-*E. formosa* in MEAM1	6.05 ± 0.49 b	3-10	4.75 ± 0.38 b	2-8
A-*E. formosa* in AsiaII7	8.10 ± 0.35 a	4-10	5.85 ± 0.76 ab	4-8
$F_{15,64}$	13.2	-	17.76	-
P	< 0.0001	-	< 0.0001	-

*The same letter in one column means there are no significant differences among the treatments (Student-Newman-Keuls Multiple range test).

Parasitization of *E. formosa* on MEAM1 and AsiaII7: no-choice versus choice

In no-choice experiments, when only MEAM1 or AsiaII7 nymphs were available, the parasitism by M-*E. formosa* was slightly higher on MEAM1 than on AsiaII7; however, when only one of the two whitefly host nymphs were available, the parasitism by A-*E. formosa* on AsiaII7 nymphs were significantly higher than that observed on MEAM1 nymphs (figure 3A). In choice experiments, when both MEAM1 and AsiaII7 hosts were available together, M-*E. formosa*, showed higher parasitism on MEAM1 than on AsiaII7 (figure 3B). However, when both MEAM1 and AsiaII7 were available to A-*E. formosa* there was no significant difference in parasitization (figure 3B).

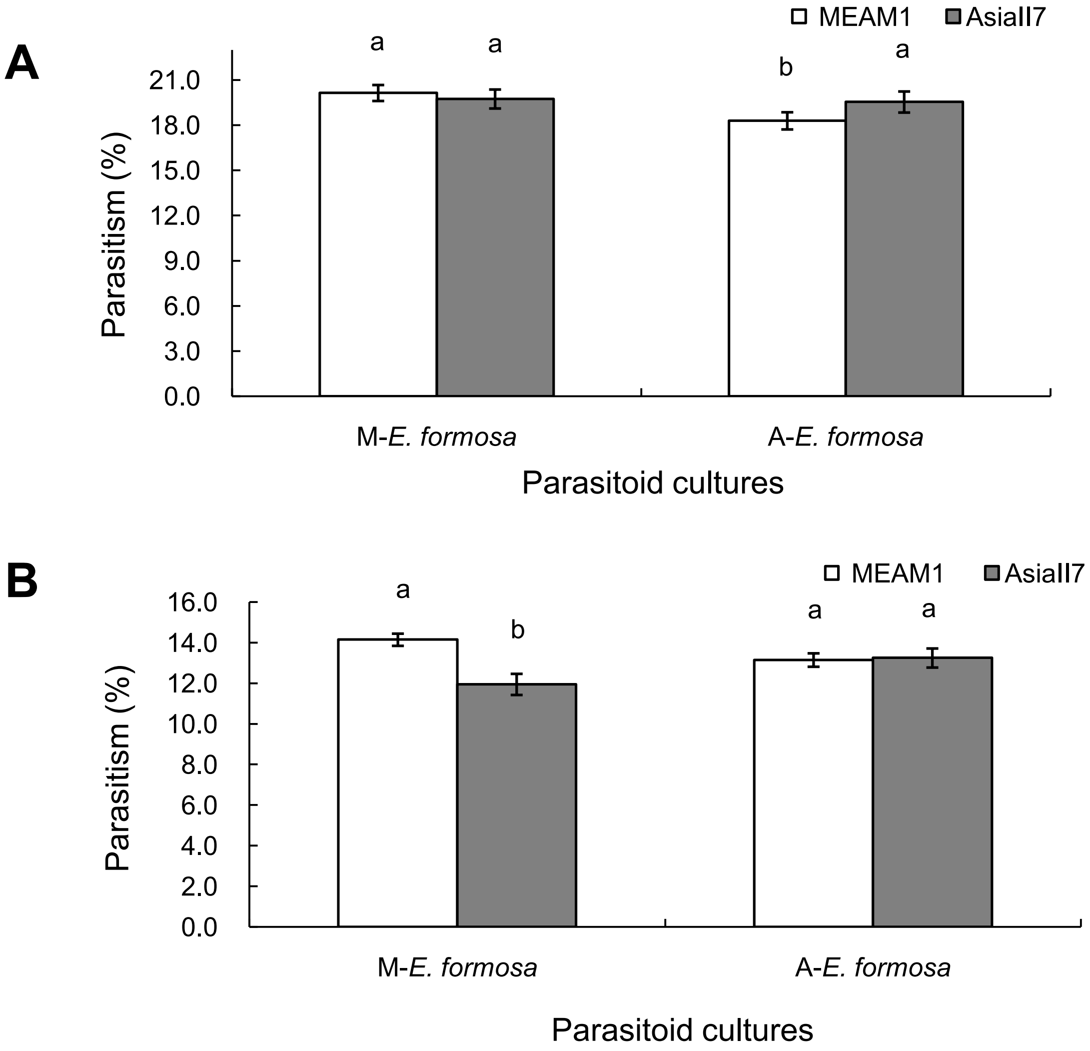

Figure 3. Parasitism of *E. formosa* (M ± SE, %) reared for 15 generations using MEAM1 or AsiaII7 hosts when parasitizing either MEAM1 or AsiaII7 in no-choice tests (A) and choice tests (B). The same letter over the bars means there are no significant differences among the treatments (Student-Newman-Keuls Multiple range test).

Discussion

Use of parasitoids in biological control has become a key factor of integrated pest management strategies. Foraging behavior of a certain parasitoid may be variable within and among different host populations at the genotypic or the phenotypic level. However, investigations into the relationship between host usage and offspring performance in different host species are limited (Ode *et al.*, 2005).

Our results showed that while at times subtle, *E. formosa* showed significant differences between whitefly species for host checking, oviposition and emergence rate. *E. formosa* reared on MEAM1 tended to outperform those reared on AsiaII7. In addition, pre-imaginal experience had a generally positive influence on the choice of whitefly host species for oviposition. The differences may be attributed to the learning and memory of *E. formosa* progeny. Learning and memory have been shown in a number of insects, especially in members of the Hymenoptera (Eisenhardt, 2006; Smid *et al.*, 2007; Hoedjes *et al.*, 2011; Schurmann *et al.*, 2012). Brotodjojo and Walter (2006) investigated the behavior of a generalist egg parasitoid *Trichogramma pretiosum* Riley (Hymenoptera Trichogrammatidae) when parasitizing two different field hosts, *Helicoverpa armigera* (Hubner) (Lepidoptera Noctuidae) and *Spodoptera litura* (F.) (Lepidoptera Noctuidae). The results revealed that those *T. pretiosum* progeny that developed from *H. armigera* eggs and from *S. litura* eggs varied significantly in their lifespan and fecundity. As in the study of Brotodjojo and Walter (2006), our current work also indicates that the host used for parasitoid development influences subsequent host preference and performance of adult parasitoids.

It is well known that the performance of parasitoids which accept a number of host species is influenced by their host species. Ode *et al.* (2005) measured the behavioral and developmental differences in the parasitic wasp, *Aphidius colemani* Viereck (Hymenoptera Braconidae) across four aphid hosts. They tested the effect of the parental host species in which the parasitoids developed on the number of hosts attacked, the proportion of each host species accepted for oviposition and the survival of progeny. Their results revealed that the parental hosts had a marked influence on the progeny body size, but not on the other host-use parameters. Ghimire and Phillips (2014) similarly observed that the reproductive performance of the gregarious ectoparasitoid, *Habrobracon hebetor* (Say) (Hymenoptera Braconidae) was strongly influenced by species of Lepidoptera host. While Ghimire and Phillips (2014) explored parasitoid performance across species belonging to several different genera, Pomari *et al.* (2012) considered biological characteristics of *Telenomus remus* Nixon (Hymenoptera Platygastridae) developed from eggs of different *Spodoptera* Guenee species. Again, they found that performance varied across the different, but more closely related, host species.

In the context of *B. tabaci*, the misplaced belief that it was a single species may have led to wrong conclusions on whether parasitoid performance was influenced by the host. Our results indicate that whitefly species does influence performance of parasitoids and that it is not rational to assume equivalent performance by a parasitoid species across a phytophagous species complex. As such, our findings confirm to what we would expect from studies involving other host-parasitoid systems.

In addition, our findings indicate that, to ensure the achievement of biological control, when more than one pest species is simultaneously targeted (such as different whitefly or aphid species that share the same natural enemies in one ecosystem), the mass rearing of parasitoid or predators should select a pest host that is very specific to the target pest.

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References

AHMED M. Z., REN S. X., XUE X., LI X. X., JIN G. H., QIU B. L., 2010.- Prevalence of endosymbionts in *Bemisia tabaci* populations and their in vivo sensitivity to antibiotics.- *Current Microbiology*, 61: 322-328.

BASIT M., SAEED S., AHMAD M., SAYYED A. H., 2013.- Can resistance in *Bemisia tabaci* (Homoptera: Aleyrodidae) be overcome with mixtures of neonicotinoids and insect growth regulators?- *Crop Protection*, 44: 135-141.

BERLINGER M. J., 1986.- Host plant resistance to *Bemisia tabaci*.- *Agriculture, Ecosystems & Environment*, 17: 69-82.

BOYKIN L. M., BELL C. D., EVANS G., SMALL I, DE BARRO P. J., 2013.- Is agriculture driving the diversification of the *Bemisia tabaci* species complex (Hemiptera: Sternorrhyncha: Aleyrodidae)?: Dating, diversification and biogeographic evidence revealed.- *BMC Evolutionary Biology*, 13: 228.

BROTODJOJO R. R. R., WALTER G. H., 2006.- Oviposition and reproductive performance of a generalist parasitoid (*Trichogramma pretiosum*) exposed to host species that differ in their physical characteristics.- *Biological Control*, 39: 300-312.

CHARNOV E. L., 1982.- *The theory of sex allocation*.- Princeton University Press, Princeton, NJ, USA.

CHU D., GAO C. S., DE BARRO P., ZHANG Y. J., WAN F. H., KHAN I .A., 2011.- Further insights into the strange role of bacterial endosymbionts in whitefly, *Bemisia tabaci*: Comparison of secondary symbionts from biotypes B and Q in China.- *Bulletin of Entomological Research*, 101: 477-486.

CUTHBERTSON A. G. S., BUXTON J. H., BLACKBURN L. F., MATHERS J. J., ROBINSON K., POWELL M. E., FLEMING D. A., BELL H. A., 2012.- Eradicating *Bemisia tabaci* Q on poinsettia plants in the UK.- *Crop Protection*, 42: 42-48.

DE BARRO P. J., COOMBS M. T., 2009.- Post-release evaluation of *Eretmocerus hayati* Zolnerowich and Rose in Australia.- *Bulletin of Entomological Research*, 99: 193-206.

De Barro P. J., Driver F., Naumann I. D., Schmidt S., Clarke G. M., Curran J., 2000.- Descriptions of three species of *Eretmocerus haldeman* (Hymenoptera: Aphelinidae) parasitising *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) and *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae) in Australia based on morphological and molecular data.- *Australian Journal of Entomology*, 39: 259-269.

De Barro P. J., Liu S. S., Boykin L. M., Dinsdale A. B., 2011.- *Bemisia tabaci*: A statement of species status.- *Annual Review of Entomology*, 56: 1-19.

Drost Y. C., Qiu Y. T., Posthuma-Doodeman C. J. A. M., van Lenteren J. C., 1999.- Life-history and oviposition behaviour of *Amitus bennetti*, a parasitoid of *Bemisia argentifolii*.- *Entomologia Experimentalis et Applicata*, 90: 183-189.

Drost Y. C., Qiu Y. T., Posthuma-Doodeman C. J. A. M., van Lenteren J. C., 2000.- Comparison of searching strategies of five parasitoid species of *Bemisia argentifolii* Bellows and Perring (Hom., Aleyrodidae).- *Journal of Applied Entomology*, 124: 105-112.

EFSA Panel on Plant Health, 2013.- Scientific opinion on the risks of plant health posed by *Bemisia tabaci* species complex and viruses it transmits for the EU territory.- *EFSA Journal*, 11 (4): 3126.

Eisenhardt D., 2006.- Learning and memory formation in the honeybee (*Apis mellifera*) and its dependency on the cAMP-protein kinase A pathway.- *Animal Biology*, 56: 259-278.

Gerling D., Alomar Ò., Arnò J., 2001.- Biological control of *Bemisia tabaci* using predators and parasitoids.- *Crop Protection*, 20: 779-799.

Ghimire M. N., Phillips T. W., 2014.- Oviposition and reproductive performance of *Habrobracon hebetor* (Hymenoptera: Braconidae) on six different pyralid host species.- *Annals of the Entomological Society of America*, 107: 809-817.

Godfray H. C. J., 1994.- *Parasitoids: behavioral and evolutionary ecology*.- Princeton University Press, NJ, USA.

Hoedjes K. M., Kruidhof H. M., Huigens M. E., Dicke M., Vet L. E. M., Smid H. M., 2011.- Natural variation in learning rate and memory dynamics in parasitoid wasps: opportunities for converging ecology and neuroscience.- *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 278: 889-897.

Jones D. R., 2003.- Plant viruses transmitted by whiteflies.- *European Journal of Plant Pathology*, 109: 195-219.

Kumar P., Whitten M., Thoeming G., Borgemeister C., Poehling H. M., 2008.- Effects of bio-pesticides on *Eretmocerus warrae* (Hym., Aphelinidae), a parasitoid of *Bemisia tabaci* (Hom., Aleyrodidae).- *Journal of Applied Entomology*, 132: 605-613.

Lazreg F., Huang Z., Ali S., Ren S., 2009.- Effect of *Lecanicillium muscarium* on *Eretmocerus* sp nr. *furuhashii* (Hymenoptera: Aphelinidae), a parasitoid of *Bemisia tabaci* (Hemiptera: Aleyrodidae).- *Journal of Pest Science*, 82: 27-32.

Li S. J., Xue X., Ahmed M. Z., Ren S. X., Du Y. Z., Wu J. H., Cuthbertson A. G. S., Qiu B. L., 2011.- Host plants and natural enemies of *Bemisia tabaci* (Hemiptera: Aleyrodidae) in China.- *Insect Science*, 18: 101-120.

Li X. C., Degain B. A., Harpold V. S., Marcon P. G., Nichols R. L., Fournier A. J., Naranjo S. E., Palumbo J. C., Ellsworth P. C., 2012.- Baseline susceptibilities of B- and Q-biotype *Bemisia tabaci* to anthranilic diamides in Arizona.- *Pest Management Science*, 68: 83-91.

Liu B. M., Preisser E. L., Chu D., Pan H. P., Xie W., Wang S. L., Wu Q. J., Zhou X. G., Zhang Y. J., 2013.- Multiple forms of vector manipulation by a plant-infecting virus: *Bemisia tabaci* and tomato yellow leaf curl virus.- *Journal of Virology*, 87: 4929-4937.

Malo S., Amo J., Gabarra R., 2012.- Intraguild interactions between the predator *Macrolophus pygmaeus* and the parasitoid *Eretmocerus mundus*, natural enemies of *Bemisia tabaci*.- *Biocontrol Science and Technology*, 22: 1059-1073.

Mound L. A., Halsey S. H., 1978.- *Whitefly of the World*.- British Museum, John Wiley & Sons, UK.

Ode P. J., Hopper K. R., Coll M., 2005.- Oviposition vs. offspring fitness in *Aphidius colemani* parasitizing different aphid species.- *Entomologia Experimentalis et Applicata*, 115: 303-310.

Pomari A. F., Bueno A. D. F., De Freitas Bueno R. C. O., Júnior A. O. M., 2012.- Biological characteristics and thermal requirements of the biological control agent *Telenomus remus* (Hymenoptera: Platygastridae) reared on eggs of different species of the genus *Spodoptera* (Lepidoptera: Noctuidae).- *Annals of the Entomological Society of America*, 105: 73-81.

Pessoa R., Rossi G. D., Busoli A. C., 2016.- Transgenic cotton-fed *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) affects the parasitoid *Encarsia desantisi* Viggiani (Hymenoptera: Aphelinidae) development.- *Neotropical Entomology*, 45: 102-106.

Qiu B. L., De Barro P. J., Ren S. X., 2005.- Development, survivorship and reproduction of *Eretmocerus* sp. nr *furuhashii* (Hymenoptera: Aphelinidae) parasitizing *Bemisia tabaci* (Hemiptera: Aleyrodidae) on glabrous and non-glabrous host plants.- *Bulletin of Entomological Research*, 95: 313-319.

Qiu B. L., Ren S. X., Wen S. Y., Mandour N. S., 2006.- Population differentiation of three biotypes of *Bemisia tabaci* (Hemiptera: Aleyrodidae) in China by DNA polymorphism.- *Journal South China Agricultural University*, 30: 1-6.

Qiu B. L., De Barro P. J., He Y. R., Ren S. X., 2007a.- Suitability of *Bemisia tabaci* (Hemiptera: Aleyrodidae) instars for the parasitization by *Encarsia bimaculata* and *Eretmocerus* sp nr. *furuhashii* (Hymenoptera: Aphelinidae) on glabrous and hirsute host plants.- *Biocontrol Science and Technology*, 17: 823-839.

Qiu B. L., De Barro P. J., Ren S. X., Xu C. X., 2007b.- Effect of temperature on the life history of *Eretmocerus* sp nr. *furuhashii*, a parasitoid of *Bemisia tabaci*.- *BioControl*, 52: 733-746.

Qiu B. L., Coats S. A., Ren S. X., Idris A. M., Xu C. X., Brown J. K., 2007c.- Phylogenetic relationships of *Bemisia tabaci* (Homoptera: Aleyrodidae) populations from China and India, based on mtCOI DNA sequencing and host plants comparison.- *Progress in Natural Science*, 17: 645-654.

Qiu B. L., Dang F., Li S. J., Ahmed M. Z., Jin F. L., Ren S. X., Cuthbertson A. G. S., 2011.- Comparison of biological parameters between the invasive B biotype and a new defined Cv biotype of *Bemisia tabaci* (Hemiptera: Aleyrodidae) in China.- *Journal of Pest Science*, 84: 419-427.

Rao Q., Xu Y. H., Luo C., Zhang H. Y., Jones C. M., Devine G. J., Gorman K., Denholm I., 2012.- Characterisation of neonicotinoid and pymetrozine resistance in strains of *Bemisia tabaci* (Hemiptera: Aleyrodidae) from China.- *Journal of Integrative Agriculture*, 11: 321-326.

SAS, 2012.- *JMP 10.0*.- SAS Institute Inc., Cary, NC, USA.

Schmidt S., Polaszek A., 2007.- The Australian species of *Encarsia* Förster (Hymenoptera, Chalcidoidea: Aphelinidae), parasitoids of whiteflies (Hemiptera, Sternorrhyncha, Aleyrodidae) and armoured scale insects (Hemiptera, Coccoidea: Diaspididae).- *Journal of Natural History*, 41: 33-36.

Schmidt S., Naumann I. D., De Barro P., 2001.- *Encarsia* species (Hymenoptera: Aphelinidae) of Australia and the Pacific Islands attacking *Bemisia tabaci* and *Trialeudores vaporariorum* (Hemiptera: Aleyrodidae), a pictorial key and description of four new species.- *Bulletin of Entomological Research*, 91: 369-387.

SCHURMANN D., SOMMER C., SCHINKO A. P. B., GRESCHISTA M., SMID H. M., STEIDLE J. L. M., 2012.- Demonstration of long-term memory in the parasitic wasp *Nasonia vitripennis*.- *Entomologia Experimentalis et Applicata*, 143: 199-206.

SMID H. M., WANG G. H., BUKOVINSZKY T., STEIDLE J. L. M., BLEEKER M. A. K., VAN LOON J. J. A., VET L. E. M., 2007.- Species-specific acquisition and consolidation of long-term memory in parasitic wasps.- *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 274: 1539-1546.

SOHRABI F., SHISHEHBOR P., SABER M., MOSADDEGH M. S., 2013.- Lethal and sublethal effects of imidacloprid and buprofezin on the sweetpotato whitefly parasitoid *Eretmocerus mundus* (Hymenoptera: Aphelinidae).- *Crop Protection*, 45: 98-103.

SU Q., PAN H. P., LIU B. M., CHU D., XIE W., WU Q. J., WANG S. L., XU B. Y., ZHANG Y. J., 2013.- Insect symbiont facilitates vector acquisition, retention, and transmission of plant virus.- *Scientific Reports*, 3: 1367.

SUGIYAMA K., KATAYAMA H., SAITO T., 2011.- Effect of insecticides on the mortalities of three whitefly parasitoid species, *Eretmocerus mundus*, *Eretmocerus eremicus* and *Encarsia formosa* (Hymenoptera: Aphelinidae).- *Applied Entomology and Zoology*, 46: 311-317.

URBANEJA A., SÁNCHEZ E., STANSLY P. A., 2007.- Life history of *Eretmocerus mundus*, a parasitoid of *Bemisia tabaci*, on tomato and sweet pepper.- *BioControl*, 52: 25-39.

VAN LENTEREN J. C., NELL H. W., SEVENSTER VAN DER LELIE L. A., 1980.- The parasite-host relationship between *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae): IV. Oviposition behaviour of the parasite, with aspects of host selection, host discrimination and host feeding.- *Zeitschrift für Angewandte Entomologie*, 89: 442-454.

VILLANUEVA-JIMENEZ J. A., SCHELLHORN N. A., DE BARRO P. J., 2012.- Comparison between two species of *Eretmocerus* (Hymenoptera: Aphelinidae): reproductive performance is one explanation for more effective control in the field.- *Biological Control*, 63: 333-338.

VINSON S. B., IWANTSCH G. F., 1980.- Host suitability for insect parasitoids.- *Annual Review of Entomology*, 25: 397-419.

YANG N. W., WAN F. H., 2011.- Host suitability of different instars of *Bemisia tabaci* biotype B for the parasitoid *Eretmocerus hayati*.- *Biological Control*, 59: 313-317.

YANG X., XIE W., WANG S. L., WU Q. J., PAN H. P., LI R. M., YANG N. N., LIU B. M., XU B. Y., ZHOU M., ZHANG Y. J., 2013.- Two cytochrome P450 genes are involved in imidacloprid resistance in field populations of the whitefly, *Bemisia tabaci*, in China.- *Pesticide Biochemistry and Physiology*, 107: 343-350.

ZANDI-SOHANI N., SHISHEHBOR P., 2011.- Temperature effects on the development and fecundity of *Encarsia acaudaleyrodis* (Hymenoptera: Aphelinidae), a parasitoid of *Bemisia tabaci* (Homoptera: Aleyrodidae) on cucumber.- *BioControl*, 56: 257-263.

ZANG L. S., LIU T. X., 2008a.- Host-feeding of three parasitoid species on *Bemisia tabaci* biotype B and implications for whitefly biological control.- *Entomologia Experimentalis et Applicata*, 127: 55-63.

ZANG L. S., LIU T. X., 2008b.- Intraguild interactions between *Bemisia tabaci* predator, *Delphastus catalinae*, and parasitoid, *Encarsia sophia*, and their impacts on whitefly suppression.- *Journal of Insect Science*, 8: 53.

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