



The suitability of biotypes Q and B of *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) at different nymphal instars as hosts for *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae)

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ABSTRACT

Encarsia formosa Gahan (Hymenoptera: Aphelinidae) is a solitary endoparasitoid that is commercially reared and released for augmentative biological control of whiteflies infesting greenhouse crops. In most areas in China, the invasive and destructive whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) biotype Q has replaced *B. tabaci* biotype B and has become dominant between the two. A better understanding of the suitability of different nymphal instars of *B. tabaci* biotypes Q and B as hosts for *E. formosa* is needed to improve the use of this parasitoid for biological control. Parasitism of the four nymphal instars of *B. tabaci* biotypes Q and B by the commercial strain of *E. formosa* mass reared on *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae) was assessed in the laboratory. The results indicated that *E. formosa* parasitized and successfully developed on all instars of both biotypes but performed best on the 3rd instar of *B. tabaci* biotype B and on the 2nd, 3rd, and 4th instars of *B. tabaci* biotype Q. The host-feeding rate of the adult parasitoid was generally higher on nymphal instars of *B. tabaci* biotype Q than on the corresponding nymphal instars of biotype B and was significantly higher on the 2nd and 3rd instars. For both whitefly biotypes, the parasitoid's immature developmental period was the longest on the 1st instar, intermediate on the 2nd and 3rd instars, and the shortest on the 4th instar. The parasitoid emergence rate was significantly lower on the 1st instar than on the other three instars and did not significantly differ between *B. tabaci* biotype B and biotype Q. Offspring longevity was greater on the 3rd and 4th instars than on the 1st instar and did not significantly differ between the two *B. tabaci* biotypes. The results indicate that commercially-produced *E. formosa* can parasitize all instars of *B. tabaci* biotypes B and Q, making this parasitoid a promising tool for the management of the two biotypes of *B. tabaci* present in China.

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INTRODUCTION

The sweetpotato whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae), is a serious pest of many important vegetable, field, and ornamental crops in the tropics and subtropics. *Bemisia tabaci* not only directly damages plants by feeding and by secreting honeydew (which supports sooty mould), but also damages plants by transmitting more than 100 begomoviruses that greatly reduce crop yields (De Barro *et al.*, 2011). Recent studies suggest that *B. tabaci* is a species complex containing more than 30 morphologically indistinguishable cryptic species (De Barro *et al.*, 2011; Boykin *et al.*, 2013; Lee *et al.*, 2013). The two most invasive and destructive species are the Middle East-Asia Minor I species and the Mediterranean species, formerly referred to as biotype B and Q, respectively (De Barro *et al.*, 2011; Pan *et al.*, 2012). Here, we refer to them as biotypes. Biotype B was first recorded in China in the early 1990s, and its subsequent spread resulted in severe crop damage and losses throughout China (Luo *et al.*, 2002). Biotype Q was first detected in Yunnan, China in 2003 (Chu *et al.*, 2006). Studies indicate that biotype Q has quickly replaced biotype B and has become the dominant *B. tabaci* biotype in many regions of China (Chu *et al.*, 2010; Teng, Wan & Chu, 2010; Pan *et al.*, 2011). Biotype Q is currently considered a more serious pest than biotype B because of its greater virus transmission efficiency (Pan *et al.*, 2012; Liu *et al.*, 2013) and higher insecticide resistance (Rauch & Nauen, 2003; Luo *et al.*, 2010; Xie *et al.*, 2014).

Biological control is an attractive alternative for the sustainable management of *B. tabaci* populations. *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) is a uniparental (thelytokous) hymenopteran parasitoid (Agekyan, 1982) that has been used commercially for the augmentative biological control of whiteflies infesting greenhouse crops, including *B. tabaci* and the greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae) (Hoddle, Van Driesche & Sanderson, 1998; Gerling, Alomar & Arno, 2001; Grille *et al.*, 2012; Liu, Stansly & Gerling, 2015). Although studies have demonstrated that *E. formosa* can effectively parasitize whiteflies (Hu, Gelman & Blackburn, 2002; Zhang *et al.*, 2003; Takahashi, Filho & Lourencao, 2008; Zang & Liu, 2008; Wang *et al.*, 2015), some factors including the parasitoid strain (Zhang *et al.*, 2003), the host instar (Zhang *et al.*, 2003; Urbaneja & Stansly, 2004; Wang *et al.*, 2015), and the species on which the parasitoid was reared (Johanna, Rott & Silvia, 2007; Dai *et al.*, 2014; Wang *et al.*, 2015) might substantially affect the fitness of *E. formosa*.

Another concern regarding the fitness of *E. formosa* and its use for augmentative biological control of *B. tabaci* is that many studies of this host-parasitoid interaction have used *E. formosa* reared on biotypes B or Q (Zhang *et al.*, 2003; Dai *et al.*, 2014; Liu *et al.*, 2014), despite the fact that commercial *E. formosa* is mass reared on *T. vaporariorum* (Natskova, 1987; Cheng *et al.*, 1989). Some reports suggest that the progeny of *E. formosa* distinguish its hosts after preimaginal conditioning. Dai *et al.* (2014) found that *E. formosa* parasitized more whitefly nymphs if it attacked the same host species on which it had been reared. Also, the host-feeding and oviposition potential of *E. formosa* reared on *T. vaporariorum* were significantly higher on the castor whitefly, *Trialeurodes ricini* (Misra) (Hemiptera: Aleyrodidae), than on *B. tabaci* B biotype (Wang *et al.*, 2015). Therefore, some

doubts arise about the efficacy of *E. formosa* mass reared on *T. vaporariorum* for controlling *B. tabaci* biotype B or Q.

The main objective of this study was to evaluate the suitability of different nymphal instars of *B. tabaci* biotypes B and Q as hosts for *E. formosa* mass reared on *T. vaporariorum*. We used laboratory assays to evaluate the following parameters concerning *E. formosa* fitness: parasitism rate; host-feeding rate; the immature developmental period; emergence rate; and longevity of progeny.

MATERIALS AND METHODS

Whitefly and parasitoid cultures

The biotype B population used in this study was originally collected from an infested cabbage (*Brassica oleracea*) field in Beijing, China in 2004, and the biotype Q (Q1 genotype) population was originally collected from poinsettia (*Euphorbia pulcherrima*) plants in Beijing, China in 2009. Biotypes were confirmed by random amplified polymorphic DNA polymerase chain reaction (RAPD-PCR) (Luo *et al.*, 2002; Rao *et al.*, 2011) and the genotype of biotype Q was identified as Q1 using the PCR-RFLP analysis of the *COI* (mitochondrial cytochrome oxidase I) amplicons (Parrella, Scassillo & Giorgini, 2012). Both biotype populations were maintained on tomato plants in a greenhouse at 26 ± 1 °C with $70 \pm 5\%$ relative humidity (RH) and 16 h of photophase. The greenhouse was located at the Institute of Vegetables and Flowers, Chinese Academy of Agricultural Sciences, Beijing, China.

The strain of *Encarsia formosa* used in this study was obtained from the Beneficial Insects Research Center, Shandong Academy of Agricultural Sciences. The parasitoid had been maintained on a population of *T. vaporariorum* reared on tobacco plants for more than 10 years.

Infested experimental plants

Potted tomato plants (*Lycopersicon esculentum* Mill, variety “No. 9 Zhongza”) with 6 to 8 fully expanded leaves were used as host plants for biotypes B and Q. These plants were grown in a greenhouse under the same conditions described for the whiteflies. Twenty newly emerged adults (10 females and 10 males) of *B. tabaci* biotype B or Q were placed on the abaxial surface of one leaflet of a tomato plant. The 20 whitefly adults were contained in a leaf clip-cage (2.5 cm diameter, one clip cage per plant). After 24 h, the adults were removed, and all plants containing whiteflies eggs were maintained in a climate chamber at 27 ± 1 °C with $70 \pm 5\%$ RH and 14 h of photophase. The eggs were examined daily with a stereoscopic microscope (SZ2-ILST, OLYMPUS) until they developed into 1st, 2nd, 3rd, or 4th instar nymphs. The number of nymphs was then adjusted to 30 per clip cage for the experiment. This required approximately 160 tomato plants, each with one clip cage.

Parasitism and adult host-feeding rates on different instars and biotypes of *Bemisia tabaci*

Caged tomato leaflets infested with 30 nymphs (biotype Q or B at 1st, 2nd, 3rd, or 4th instar) were obtained as described in the previous section. Subsequently, one newly emerged *E. formosa* female (24 h old) was introduced into each clip-cage and then removed after

24 h. The percentages of nymphs that were parasitized or fed by *E. formosa* adults were determined at 8–10 d after the *E. formosa* females were removed from the clip-cages. Nymphs were recorded as parasitized when the parasitoid brown pupae were visible inside the body of the nymphs and the nymphs were recorded as fed by *E. formosa* adults if their bodies were desiccated and flat under stereoscopic microscope. Each combination of biotype and nymphal instar was represented by approximately 20 replicate cages.

Immature developmental period, emergence rate, and longevity of *Encarsia formosa* on different instars and biotypes of *Bemisia tabaci*

Leaves in clip-cages with parasitoid pupae were obtained as described in the previous sections and were then detached from the plants. The leaf petioles were wrapped in cotton wool, which was then saturated with distilled water; the petioles and cotton wool were placed in plastic Petri dishes (diameter 8.5 cm, height 1.5 cm, one leaf per dish). A filter paper disk saturated with distilled water was also placed beneath each leaf. The pupae in the Petri dishes were examined daily with a stereoscopic microscope until adult parasitoids emerged. Immature developmental period (time from oviposition through adult emergence) and the number of parasitoids emerged were recorded. Upon emergence, the parasitoid adults were individually collected and maintained in 1-mL plastic tubes without food supply; these parasitoid adults were checked daily until they died, at which time their longevity was recorded.

Data analysis

Data were first checked for normality and were transformed when necessary to meet the assumption of normal distribution. Proportional data including parasitism rate of *E. formosa*, host-feeding rate of *E. formosa* adults, and emergence rate of *E. formosa* were arcsine-square root transformed before analyses. Two-way ANOVAs were used to assess the effects of *B. tabaci* biotype and instar on the following parameters: parasitism rate of *E. formosa*, host-feeding rate of *E. formosa* adults, immature developmental period of *E. formosa*, emergence rate of *E. formosa* adults from pupae, and longevity of *E. formosa* adults. Results were plotted with Sigmaplot version 12.0. Tukey's test was used to separate treatment means when a main effect or interaction was significant. Statistical analyses were performed with SPSS (version 19.0, Chicago, IL, USA) (Jiao *et al.*, 2013; Liu *et al.*, 2014; Zhang *et al.*, 2016).

RESULTS

Parasitism rate of *Encarsia formosa* as affected by *Bemisia tabaci* biotype and instar

The parasitism rate of *E. formosa* was significantly affected by host instar ($F_{3,151} = 22.43$, $P < 0.0001$) but not by host biotype ($F_{1,151} = 1.65$, $P = 0.200$). The interaction between host biotype and host instar was not significant ($F_{3,151} = 2.50$, $P = 0.061$). *Encarsia formosa* parasitized all instars of biotypes B and Q. For biotype B, the parasitism rate was highest on the 3rd instar (31.74%), intermediate on the 2nd instar (21.65%) and 4th instar (22.73%), and lowest on the 1st instar (11.54%). As for biotype Q, the parasitism rate did not

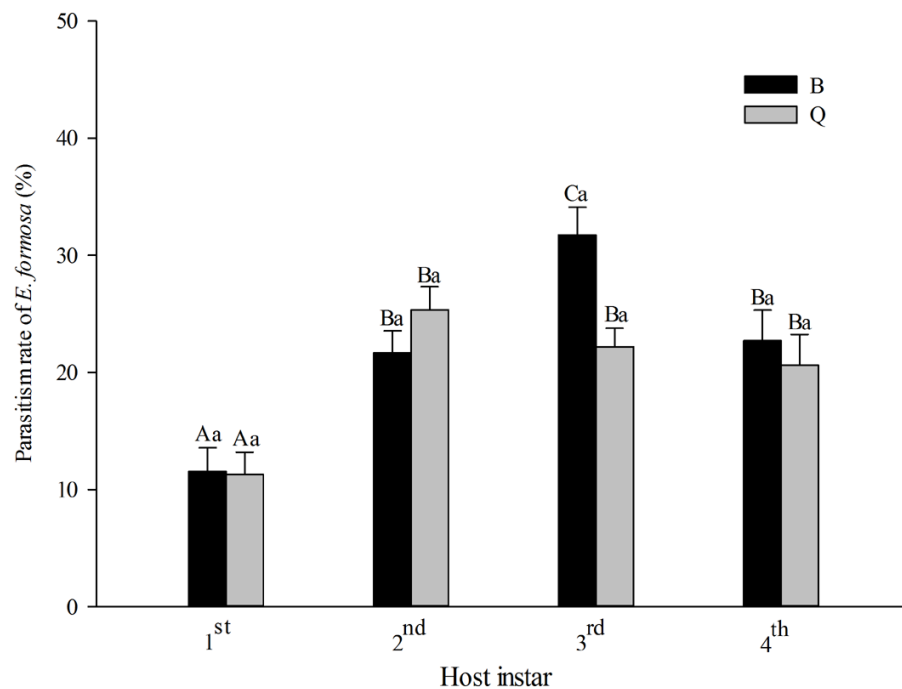


Figure 1 Parasitism rate of *Encarsia formosa* as affected by host biotype (*Bemisia tabaci* biotype Q or B) and instar (1st, 2nd, 3rd, or 4th). Values are means \pm SE. Means with different uppercase letters are significantly different within each biotype. Means with different lowercase letters are significantly different within each instar. Tukey test, $p < 0.05$.

significantly differ among the 2nd, 3rd and 4th instars and was significantly lower on the 1st instar (Fig. 1).

Host-feeding rate of *Encarsia formosa* adults as affected by *Bemisia tabaci* biotype and instar

The host-feeding rate of *E. formosa* adults was significantly affected by host biotype ($F_{1,128} = 12.96$, $P < 0.001$) and host instar ($F_{3,128} = 4.41$, $P = 0.005$) but was not significantly affected by the interaction between host biotype and host instar ($F_{3,128} = 1.69$, $P = 0.173$). For biotype B, the host-feeding rate of *E. formosa* adults was highest on the 1st instar (7.04%), intermediate on the 2nd instar (4.75%) and 3rd instar (4.44%), and lowest on the 4th instar (4.01%). For biotype Q, the host-feeding rate did not significantly differ among the four host instars. The host-feeding rate of the parasitoid tended to be higher on all instars of biotype Q than on biotype B, but the difference was significant only for the 2nd and 3rd instars (Fig. 2).

Immature developmental period of *Encarsia formosa* as affected by *Bemisia tabaci* biotype and instar

The immature developmental period of *E. formosa* was significantly affected by the host biotype ($F_{1,150} = 77.67$, $P < 0.0001$) and host instar ($F_{3,150} = 76.78$, $P < 0.0001$). There was interaction between host biotype and host instar ($F_{3,150} = 11.60$, $P < 0.0001$). For both biotypes of *B. tabaci*, immature developmental period was longer on 1st instar nymphs

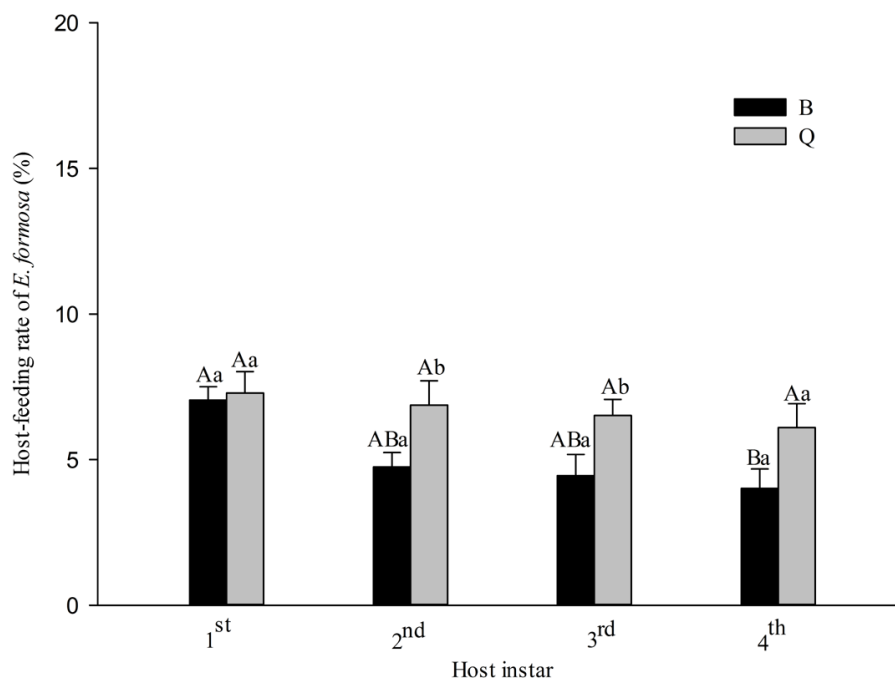


Figure 2 Host-feeding rate of *Encarsia formosa* as affected by host biotype (*Bemisia tabaci* biotype Q or B) and instar (1st, 2nd, 3rd, or 4th). Values are means \pm SE. Means with different uppercase letters are significantly different within each biotype. Means with different lowercase letters are significantly different within each instar. Tukey test, $p < 0.05$.

than on later instars; the immature developmental period was longer (21.30 days) on the 1st instar nymphs of biotype B than on the 1st instar nymphs of biotype Q (18.22 days). The shortest immature developmental period of *E. formosa* occurred on the 4th instar of *B. tabaci* biotype Q. Among the four host instars, the immature developmental period ranged from 17.05 to 21.30 d for biotype B and from 15.05 to 18.22 d for biotype Q, with a downward trend from the 1st to the 4th instar (Fig. 3).

Emergence rate of *Encarsia formosa* as affected by *Bemisia tabaci* biotype and instar

The emergence rate of *E. formosa* was significantly affected by the host instar ($F_{3,135} = 10.33$, $P < 0.0001$) but not by the host biotype ($F_{1,135} = 0.25$, $P = 0.616$) or by the interaction between biotype and instar ($F_{3,135} = 0.19$, $P = 0.906$). Most *E. formosa* individuals were able to develop to the adult stage regardless of which instar of biotypes Q or B was parasitized. Emergence of *E. formosa* was lower on 1st instars of *B. tabaci* of both biotypes than on later instars. Parasitoid emergence did not differ among the 2nd, 3rd, and 4th instars of *B. tabaci* of either biotype (Fig. 4).

Longevity of *Encarsia formosa* as affected by *Bemisia tabaci* biotype and instar

The longevity of *E. formosa* was significantly affected by host instar ($F_{3,150} = 26.67$, $P < 0.0001$) but not by host biotype ($F_{1,150} = 0.17$, $P = 0.684$) or the interaction between

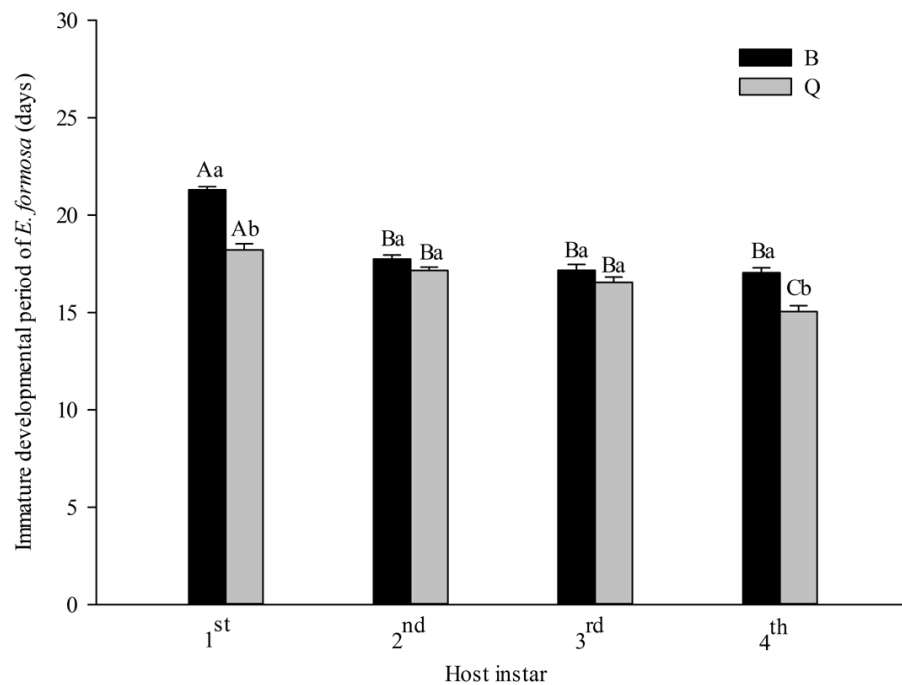


Figure 3 Immature developmental period of *Encarsia formosa* as affected by host biotype (*Bemisia tabaci* biotype Q or B) and instar (1st, 2nd, 3rd, or 4th). Values are means \pm SE. Means with different uppercase letters are significantly different within each biotype. Means with different lowercase letters are significantly different within each instar. Tukey test, $p < 0.05$.

instar and biotype ($F_{3,150} = 0.73$, $P = 0.539$). On both biotypes, longevity tended to increase with host instar. Parasitoid longevity did not significantly differ between biotype B and Q (Fig. 5).

DISCUSSION

For parasitoids, differences in the host suitability in terms of initial parasitism, host-feeding, or parasitoid development may result from differences in host quality, which may vary with host age (Colinet *et al.*, 2005). Several models indicated that parasitoid fitness was related to host quality as affected by host size or age (Nicol & Mackauer, 1999; Chau & Mackauer, 2001). The results of the present study indicate that commercially produced *E. formosa* that was mass reared on *T. vaporariorum* could parasitize, feed on, and complete its life cycle on all nymphal stages of *B. tabaci* biotypes B and Q. *Encarsia formosa* preferentially parasitized the 3rd instar of biotype B and the 2nd, 3rd, and 4th instars of biotype Q. Similar results were reported in other studies. *Encarsia formosa* reared on *T. vaporariorum* preferentially parasitized the 3rd instar of *B. argentifolii* (= biotype B) (Qiu *et al.*, 2004). Zhang *et al.* (2003) reported that two strains of *E. formosa* reared on *B. tabaci* biotype B preferred to parasitize the 3rd instar rather than the other three instars, and Liu *et al.* (2014) found that the parasitism of *E. formosa* maintained on *B. tabaci* biotype B did not significantly differ between the 2nd and the 3rd instar of *B. tabaci* biotype Q.

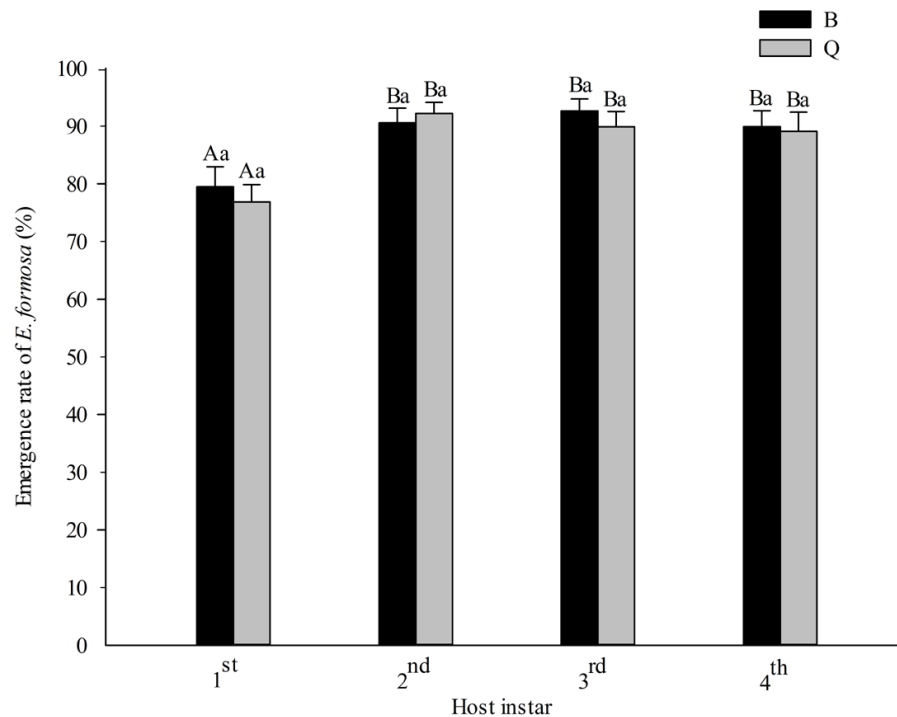


Figure 4 Emergence rate of *Encarsia formosa* as affected by host biotype (*Bemisia tabaci* biotype Q or B) and instar (1st, 2nd, 3rd, or 4th). Values are means \pm SE. Means with different uppercase letters are significantly different within each biotype. Means with different lowercase letters are significantly different within each instar. Tukey test, $p < 0.05$.

A previous report indicated the *E. formosa* reared on *T. vaporariorum* preferred to parasitize the 3rd and 4th instars rather than the 1st and 2nd instars of *B. tabaci* biotype B (Hu, Gelman & Blackburn, 2003). The results of the current study suggest that the rate of parasitism of *E. formosa* was significantly higher on the 3rd instar than on the 4th instar of *B. tabaci* biotype B. In our research, the 4th instar hosts had developed into the 4th instar for 1–2 days before they were used in the experiments. Because *B. tabaci* biotype B and Q do not develop uniformly on tomato plants (Zhang et al., 2014), some of the 4th instar individuals used in our experiments may have developed into pharate adults and thus escaped parasitism, which would cause us to underestimate the rate of oviposition on the 4th instar of *B. tabaci* biotypes B and Q. The rate of parasitism of *E. formosa* was the lowest when the 1st instar of either species was the host, and this result agrees with previous reports (Hu, Gelman & Blackburn, 2003; Zhang et al., 2003). The parasitism rate of the commercially produced *E. formosa* was slightly higher on *B. tabaci* biotype B than on biotype Q, indicating that parasitism by *E. formosa* differs to some extent between the two *B. tabaci* biotypes. We suspect that this may be explained by differences in the nutritional quality or body size between the two whitefly biotypes (X Liu, 2015, unpublished data).

Although it is well known that *E. formosa* not only efficiently parasitizes its hosts but also destructively feeds on them, only a few studies have assessed the feeding rate of *E. formosa* on different *B. tabaci* instars (Liu et al., 2014). The present study found that *E. formosa*

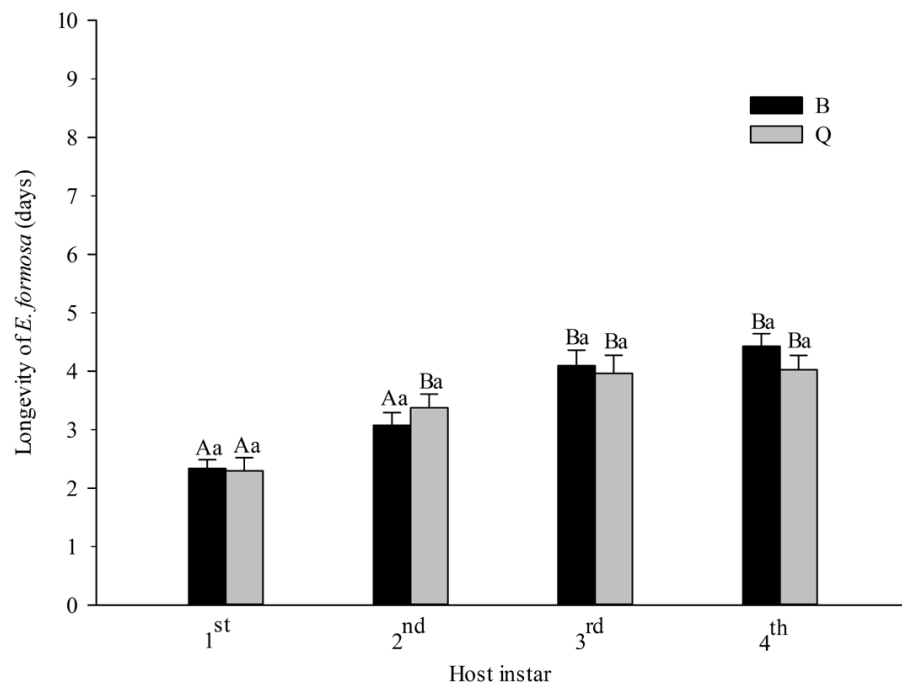


Figure 5 Longevity of *Encarsia formosa* as affected by host biotype (*Bemisia tabaci* biotype Q or B) and instar (1st, 2nd, 3rd, or 4th). Values are means \pm SE. Means with different uppercase letters are significantly different within each biotype. Means with different lowercase letters are significantly different within each instar. Tukey test, $p < 0.05$.

mass reared on *T. vaporariorum* had a higher host-feeding rate on 1st instar nymphs than on later instars of *B. tabaci*, which agrees with Wang *et al.* (2015). The host-feeding rate of *E. formosa* reared on *T. vaporariorum* was higher on biotype Q than on biotype B. This might be related to the time required for a parasitoid to feed on a host and to the difference in body size of biotype B and Q; parasitoids require less time to feed on younger hosts than older hosts probably because the former are smaller (Yang & Wan, 2011; Zhang *et al.*, 2014). Because the parasitoid must consume a greater number of younger hosts than older hosts to obtain enough nutrition to ensure its development, the feeding rate is higher on younger than on older nymphs (Zang & Liu, 2008; Yang & Wan, 2011; Wang *et al.*, 2015). All four instars of *B. tabaci* biotype B are larger than the corresponding instars of biotype Q (unpublished data). This is likely the main reason why *E. formosa* fed on more nymphs of biotype Q than biotype B.

As a koinobiont parasitoid wasp (Nechols & Tauber, 1977; Blackburn, Gelman & Hu, 2002; Hu, Gelman & Blackburn, 2002), *E. formosa* requires a longer time to develop to the adult stage when parasitizing younger rather than older instars (Wang *et al.*, 2015). The immature developmental period (time from oviposition through adult emergence) of commercially produced *E. formosa* decreased as the age of the host instar attacked increased, regardless the biotype (i.e., the immature developmental of *E. formosa* was longer on 1st instars than on later instars). Similar results were reported when *B. tabaci* biotype B and *T. vaporariorum* were parasitized by *E. formosa* reared on *T. vaporariorum*

(Hu, Gelman & Blackburn, 2002; Hu, Gelman & Blackburn, 2003; Wang et al., 2015) and when *B. tabaci* biotype B was parasitized by two *E. formosa* strains reared on *B. tabaci* biotype B (Zhang et al., 2003). Differences in *E. formosa* developmental period on different instars of *B. tabaci* biotype B and Q could be due to differences in host size and host developmental rate (Hu, Gelman & Blackburn, 2003), although the environment was constant in the current study.

Most *E. formosa* individuals were able to develop to the adult stage regardless of which instar of biotypes Q or B they parasitized, but the 1st instars of *B. tabaci* of both biotypes were less suitable than the later instars for emergence of *E. formosa*. This result agrees with Hu, Gelman & Blackburn (2003) and Zhang et al. (2003), who found that *E. formosa* emerged more synchronously and at a higher rate when older instars rather than younger instars served as hosts. In other studies, however, the emergence rate of several parasitoids did not differ among host instars (Urbaneja & Stansly, 2004; Liu, 2007; Yang & Wan, 2011). This apparent discrepancy may be due to the differences among parasitoids, host species, experimental methods, host plants, or environmental conditions.

The longevity of *E. formosa* offspring was significantly greater when the 3rd and 4th instars rather than the 1st or 2nd instars of *B. tabaci* biotype B and Q served as hosts, and longevity was shortest with the 1st instar of both whitefly species. These results agree with some previous reports (Hu, Gelman & Blackburn, 2003; Zhang et al., 2003). We speculate that the female parasitoids would probably choose host instars (e.g., the 3rd and 4th instars) that contained more nutrition for prolonging the longevity of progenies (Colinet et al., 2005; Luo & Liu, 2011; Wang et al., 2015).

The present study demonstrates that parasitic or host-feeding characteristics of *E. formosa* that was commercially produced using *T. vaporariorum* differed between the biotypes B and Q of *B. tabaci*. Other reports involving several host-parasitoid interactions indicate that the host species used to rear parasitoids affects its subsequent preference for hosts (Luo & Liu, 2011; Wang et al., 2013; Dai et al., 2014; Wang et al., 2015). In a system involving *Phaseolus vulgaris* L. (Ambra'), the whitefly *B. tabaci*, and the parasitoid *Encarsia sophia* Girault and Dodd (Hymenoptera: Aphelinidae), almost all biological parameters of *E. sophia* were superior when the parasitoid was maintained on *T. vaporariorum* rather than on *B. tabaci* (Luo & Liu, 2011). *Eremocerus hayati* Zolnerowich and Rose maintained on *B. tabaci* biotype B preferred to feed on the 1st, 2nd, and 3rd instars of *B. tabaci* biotype Q rather than the 4th instar nymph, and preferred to parasitize the 2nd instar of *B. tabaci* biotype Q rather than the other instars (Zhang et al., 2014). *Eremocerus hayati* reared on *B. tabaci* biotype Q had a significantly higher host-feeding rate on the 1st instar of *B. tabaci* biotype Q than on the other three instars, and preferred to parasitize 2nd and 3rd instars of biotype Q rather than the 1st and 4th instars (Dai et al., 2012). In contrast, the clutch size, sex ratio, and fitness of the first generation of *Hyssopus pallidus* Askew (Hymenoptera: Eulophidae), a gregarious ectoparasitoid of the tortricid moths *Cydia molesta* Busck and *Cydia pomonella* L. (Lepidoptera, Tortricidae), were not influenced by original rearing host species even though those species differed considerably in size (Johanna, Rott & Silvia, 2007).

In conclusion, this study showed that parasitism of *B. tabaci* by *E. formosa* commercially produced on *T. vaporariorum* differed in some respects depending on whitefly biotype (B or Q) and host instar. Our results indicate that the commercially-produced *E. formosa* is able to control all instars of *B. tabaci* biotypes B and Q, making this parasitoid a promising tool for the management of the two biotypes in China. Where *B. tabaci* biotype B and Q coexist in the field (*Chu et al., 2010; Pan et al., 2011*) and whether commercially-produced *E. formosa* preferentially parasitizes one biotype or the other remains to be determined.

ADDITIONAL INFORMATION AND DECLARATIONS

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Xin Liu conceived and designed the experiments, performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables.
- Youjun Zhang contributed reagents/materials/analysis tools, reviewed drafts of the paper.
- Wen Xie analyzed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables.
- Qingjun Wu contributed reagents/materials/analysis tools.
- Shaoli Wang conceived and designed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.

Data Availability

The following information was supplied regarding data availability:

Raw data has been uploaded as [Supplemental Information](#).

Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.1863#supplemental-information>.

REFERENCES

- Agekyan NG. 1982.** Biological features of *Encarsia formosa* Gahan (Hymenoptera, Aphelinidae). *Entomological News* **60**:90–94.
- Blackburn MB, Gelman DB, Hu JS. 2002.** Co-development of *Encarsia formosa* (Hymenoptera: Aphelinidae) and the greenhouse whitefly, *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae): a histological examination. *Archives of Insect Biochemistry and Physiology* **51**:13–26 DOI [10.1002/arch.10045](https://doi.org/10.1002/arch.10045).
- Boykin LM, Bell CD, Evans G, Small I, Barro PJD. 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**:228–238 DOI [10.1186/1471-2148-13-228](https://doi.org/10.1186/1471-2148-13-228).
- Chau A, Mackauer M. 2001.** Host-instar selection in the aphid parasitoid *Monoctonus paulensis* (Hymenoptera: Braconidae, Aphidiinae): assessing costs and benefits. *Canadian Entomologist* **133**:549–564 DOI [10.4039/Ent133549-4](https://doi.org/10.4039/Ent133549-4).
- Cheng HK, Tian YQ, Wei BC, Zhao JH, Ye CQ, Wei SX, Wang JZ, Wang RJ. 1989.** A technique for commercial-scale production of *Encarsia Formosa*. *Chinese Journal of Biological Control* **5**:178–181.
- Chu D, Wan FH, Zhang YJ, Brown JK. 2010.** Change in the biotype composition of *Bemisia tabaci* in Shandong Province of China from 2005 to 2008. *Environmental Entomology* **39**:1028–1036 DOI [10.1603/EN09161](https://doi.org/10.1603/EN09161).
- Chu D, Zhang YJ, Brown JK, Cong B, Xu BY, Wu QJ, Zhu GR. 2006.** The introduction of the exotic Q biotype of *Bemisia tabaci* from the Mediterranean region into China on ornamental crops. *Florida Entomologist* **89**:168–174 DOI [10.1653/0015-4040\(2006\)89\[168:TIOTEQ\]2.0.CO;2](https://doi.org/10.1653/0015-4040(2006)89[168:TIOTEQ]2.0.CO;2).
- Colinet H, Salin C, Boivin G, Hance TH. 2005.** Host age and fitness-related traits in a koinobiont aphid parasitoid. *Ecological Entomology* **30**:473–479 DOI [10.1111/j.0307-6946.2005.00716.x](https://doi.org/10.1111/j.0307-6946.2005.00716.x).
- Dai P, Ruan CC, Zang LS, Wan FH. 2012.** Host feeding and parasitism of *Eretmocerus hayati* on different nymphal stages of *Bemisia tabaci* Q. *Journal of Biosafety* **21**:9–13.
- Dai P, Ruan CC, Zang LS, Wan FH, Liu LZ. 2014.** Effects of rearing host species on the host-feeding capacity and parasitism of the whitefly parasitoid *Encarsia formosa*. *Journal of Insect Science* **14**:Article 118 DOI [10.1093/jis/14.1.118](https://doi.org/10.1093/jis/14.1.118).
- De Barro PJ, Liu SS, Boykin LM, Dinsdale AB. 2011.** *Bemisia tabaci*: a statement of species status. *Annual Review of Entomology* **56**:1–19 DOI [10.1146/annurev-ento-112408-085504](https://doi.org/10.1146/annurev-ento-112408-085504).
- Gerling D, Alomar O, Arno J. 2001.** Biological control of *Bemisia tabaci* using predators and parasitoids. *Crop Protection* **20**:779–799 DOI [10.1016/S0261-2194\(01\)00111-9](https://doi.org/10.1016/S0261-2194(01)00111-9).

- Grille G, Lorenzo ME, Burla JP, Franco J, Basso C. 2012.** Parasitoid niches of *Encarsia formosa* and *Encarsia lycopersici* (Hymenoptera: Aphelinidae) exploiting *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). *Florida Entomologist* **95**:1024–1030 DOI [10.1653/024.095.0431](https://doi.org/10.1653/024.095.0431).
- Hoddle MS, Van Driesche RG, Sanderson JP. 1998.** Biology and use of the whitefly parasitoid *Encarsia formosa*. *Annual Review of Entomology* **43**:645–669 DOI [10.1146/annurev.ento.43.1.645](https://doi.org/10.1146/annurev.ento.43.1.645).
- Hu JS, Gelman DB, Blackburn MB. 2002.** Growth and development of *Encarsia formosa* (Hymenoptera: Aphelinidae) in greenhouse whitefly, *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae): effect of host age. *Archives of Insect Biochemistry and Physiology* **49**:125–136 DOI [10.1002/arch.10015](https://doi.org/10.1002/arch.10015).
- Hu JS, Gelman DB, Blackburn MB. 2003.** Age-specific interaction between the parasitoid, *Encarsia formosa* and its host, the silverleaf whitefly, *Bemisia tabaci* (Strain B). *Journal of Insect Science* **3**:Article 28.
- Jiao XG, Xie W, Wang SL, Wu QJ, Pan HP, Liu BM, Zhang YJ. 2013.** Differences in host selection and performance between B and Q putative species of *Bemisia tabaci* on three host plants. *Entomologia Experimentalis et Applicata* **147**:1–8 DOI [10.1111/eea.12040](https://doi.org/10.1111/eea.12040).
- Johanna H, Rott AS, Silvia D. 2007.** How two different host species influence the performance of a gregarious parasitoid: host size is not equal to host quality. *Journal of Animal Ecology* **76**:376–383 DOI [10.1111/j.1365-2656.2006.01206.x](https://doi.org/10.1111/j.1365-2656.2006.01206.x).
- Lee W, Park J, Lee GS, Lee S, Akimoto S. 2013.** Taxonomic status of the *Bemisia tabaci* complex (Hemiptera: Aleyrodidae) and reassessment of the number of its constituent species. *PLoS ONE* **8**:e63817 DOI [10.1371/journal.pone.0063817](https://doi.org/10.1371/journal.pone.0063817).
- Liu TX. 2007.** Life history of *Eretmocerus melanoscutus* (Hymenoptera: Aphelinidae) parasitizing nymphs of *Bemisia tabaci* Biotype B (Homoptera: Aleyrodidae). *Biological Control* **42**:77–85 DOI [10.1016/j.biocontrol.2007.03.008](https://doi.org/10.1016/j.biocontrol.2007.03.008).
- Liu BM, Preisser EL, Chu D, Pan HP, Xie W, Wang SL, Wu QJ, Zhou XG, Zhang YJ. 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 DOI [10.1128/JVI.03571-12](https://doi.org/10.1128/JVI.03571-12).
- Liu TX, Stansly PA, Gerling D. 2015.** Whitefly parasitoids: distribution, life history, bionomics, and utilization. *Annual Review of Entomology* **60**:273–292 DOI [10.1146/annurev-ento-010814-021101](https://doi.org/10.1146/annurev-ento-010814-021101).
- Liu XY, Xiang WS, Wang SL, Zhang YJ, Wu QJ, Xie W. 2014.** Parasitic characteristics of *Encarsia formosa* on the sweetpotato whitefly, *Bemisia tabaci* Q biotype. *Acta Phytocologica Sinica* **41**:7–11.
- Luo C, Jones CM, Devine G, Zhang F, Denholm I, Gorman K. 2010.** Insecticide resistance in *Bemisia tabaci* biotype Q (Hemiptera: Aleyrodidae) from China. *Crop Protection* **29**:429–434 DOI [10.1016/j.cropro.2009.10.001](https://doi.org/10.1016/j.cropro.2009.10.001).
- Luo C, Liu TX. 2011.** Fitness of *Encarsia sophia* (Hymenoptera: Aphelinidae) parasitizing *Trialeurodes vaporariorum* and *Bemisia tabaci* (Hemiptera: Aleyrodidae). *Insect Science* **18**:84–91 DOI [10.1111/j.1744-7917.2010.01394.x](https://doi.org/10.1111/j.1744-7917.2010.01394.x).

- Luo C, Yao Y, Wang RJ, Yan FM, Hu DX, Zhang ZL. 2002. The use of mitochondrial cytochrome oxidase mtCOI gene sequences for the identification of biotypes of *Bemisia tabaci* (Gennadius) in China. *Acta Entomologica Sinica* **45**:759–763.
- Natskova V. 1987. Economical method for mass rearing of *Encarsia formosa*. *Bulletin SROP* **10**:121–124.
- Nechols JR, Tauber MJ. 1977. Age-specific interaction between the greenhouse whitefly and *Encarsia formosa*: influence of host on the parasite's oviposition and development. *Environmental Entomology* **6**:143–149 DOI [10.1093/ee/6.1.143](https://doi.org/10.1093/ee/6.1.143).
- Nicol CMY, Mackauer M. 1999. The scaling of body size and mass in a host parasitoid association: influence of host species and stage. *Entomologia Experimentalis et Applicata* **90**:83–92 DOI [10.1046/j.1570-7458.1999.00425.x](https://doi.org/10.1046/j.1570-7458.1999.00425.x).
- Pan HP, Chu D, Ge DQ, Wang SL, Wu QJ, Xie W, Zhang YJ. 2011. Further spread of and domination by *Bemisia tabaci* biotype Q on field crops in China. *Journal of Economic Entomology* **104**:978–985 DOI [10.1603/EC11009](https://doi.org/10.1603/EC11009).
- Pan HP, Chu D, Yan WQ, Su Q, Liu BM, Wang SL, Wu QJ, Xie W, Jiao XG, Li RM, Yang N, Yang X, Xu BY, Zhang YJ. 2012. Rapid spread of *Tomato yellow leaf curl virus* in China is aided differentially by two invasive whiteflies. *PLoS ONE* **7**:e34817 DOI [10.1371/journal.pone.0034817](https://doi.org/10.1371/journal.pone.0034817).
- Parrella G, Scassillo L, Giorgini M. 2012. Evidence for a new genetic variant in the *Bemisia tabaci* species complex and the prevalence of the biotype Q in southern Italy. *Journal of Pest Science* **85**:227–238 DOI [10.1007/s10340-012-0417-2](https://doi.org/10.1007/s10340-012-0417-2).
- Qiu YT, Van Lenteren JC, Drost YC, Posthuma-Doodeman JAM. 2004. Life-history parameters of *Encarsia formosa*, *Eretmocerus eremicus* and *E. mundus*, aphelinid parasitoids of *Bemisia argentifolii* (Hemiptera: Aleyrodidae). *European Journal of Entomology* **101**:83–94 DOI [10.14411/eje.2004.017](https://doi.org/10.14411/eje.2004.017).
- Rao Q, Luo C, Zhang H, Guo X, Devine GJ. 2011. Distribution and dynamics of *Bemisia tabaci* invasive biotypes in central China. *Bulletin of Entomological Research* **101**:81–88 DOI [10.1017/S0007485310000428](https://doi.org/10.1017/S0007485310000428).
- Rauch N, Nauen R. 2003. Identification of biochemical markers linked to neonicotinoid cross resistance in *Bemisia tabaci* (Hemiptera: Aleyrodidae). *Archives Insect Biochemistry and Physiology* **54**:165–176 DOI [10.1002/arch.10114](https://doi.org/10.1002/arch.10114).
- Takahashi KM, Filho EB, Lourencao AL. 2008. Biology of *Bemisia tabaci* (Genn.) B-biotype and parasitism by *Encarsia formosa* (Gahan) on collard, soybean and tomato plants. *Scientia Agricola* **65**:639–642 DOI [10.1590/S0103-90162008000600011](https://doi.org/10.1590/S0103-90162008000600011).
- Teng X, Wan FH, Chu D. 2010. *Bemisia tabaci* Biotype Q dominates other biotypes across China. *Florida Entomologist* **93**:363–368 DOI [10.1653/024.093.0307](https://doi.org/10.1653/024.093.0307).
- Urbaneja A, Stansly PA. 2004. Host suitability of different instars of the whitefly *Bemisia tabaci* 'biotype Q' for *Eretmocerus mundus*. *BioControl* **49**:153–161 DOI [10.1023/B:BICO.0000017365.37010.e0](https://doi.org/10.1023/B:BICO.0000017365.37010.e0).
- Wang XS, Chen QZ, Zhang SZ, Liu TX. 2015. Parasitism, host feeding and immature development of *Encarsia formosa* reared from *Trialeurodes vaporariorum* and *Bemisia tabaci* on *Trialeurodes ricini*. *Journal of Applied Entomology* **139**:647–726 DOI [10.1111/jen.12208](https://doi.org/10.1111/jen.12208).

- Wang J, Chen HY, Zhang LS, Qiu YC. 2013.** Control effects of *Encarsia formosa* populations reared on different hosts to *Trialeurodes vaporariorum* and *Bemisia tabaci*. *Chinese Journal of Plant Protection* **39**:144–148.
- Xie W, Liu Y, Wang SL, Wu QJ, Pan HP, Zhang YJ. 2014.** Sensitivity of the whitefly *Bemisia tabaci* to several new insecticides in China: effects of insecticide type and whitefly species, strain, and stage. *Journal of Insect Science* **14**:Article 261 DOI [10.1093/jisesa/ieu123](https://doi.org/10.1093/jisesa/ieu123).
- Yang NW, Wan FH. 2011.** Host suitability of different instars of *Bemisia tabaci* biotype B for the parasitoid *Eretmocerus hayati*. *Biological Control* **59**:313–317 DOI [10.1016/j.biocontrol.2011.07.019](https://doi.org/10.1016/j.biocontrol.2011.07.019).
- Zang LS, Liu TX. 2008.** Host-feeding of three parasitoid species on *Bemisia tabaci* biotype B and implications for whitefly biological control. *Entomologia Experimentalis et Applicata* **127**:55–63 DOI [10.1111/j.1570-7458.2008.00667.x](https://doi.org/10.1111/j.1570-7458.2008.00667.x).
- Zhang J, Huang J, Lu Y, Xia T. 2016.** Effects of temperature and host stage on the parasitization rate and offspring sex ratio of *Aenasius bambawalei* Hayat in *Phenacoccus solenopsis* Tinsley. *PeerJ* **4**:e1586 DOI [10.7717/peerj.1586](https://doi.org/10.7717/peerj.1586).
- Zhang SZ, Wan H, Zhang F, Hua BZ. 2003.** Parasitic suitability of two strains of *Encarsia formosa* on *Bemisia tabaci*. *Chinese Journal of Biological Control* **19**:149–153.
- Zhang YB, Yang NW, Sun LY, Wang FH. 2014.** Host instar suitability in two invasive whiteflies for the naturally occurring parasitoid *Eretmocerus hayati* in China. *Journal of Pest Science* **88**:225–234 DOI [10.1007/s10340-014-0592-4](https://doi.org/10.1007/s10340-014-0592-4).