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Effects of host switching and successive multigenerational rearing of the parasitoid *Eretmocerus corni* (Hymenoptera: Aphelinidae) on host preference and adaptation

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Abstract

Background: The adaptive strategies of parasitoids against different hosts may evolve under successive multigenerational rearing in alternative hosts; therefore, it is crucial to validate the maintenance and optimization of parasitoid adaptations to target pests during mass rearing. *Eretmocerus corni* Haldeman (Hymenoptera: Aphelinidae) is a biological control agent for managing whitefly pests. Here, we investigated the effects on preference and adaptation of adult *E. corni* transferred from its original host, *Trialeurodes vaporariorum* Westwood (Hemiptera: Aleyrodidae), to a new host, *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae), through successive multigenerational rearing on *B. tabaci* nymphs. **Results:** The results of the choice assays showed that for the first five generations, the parasitoids showed a clear preference for the original rearing host *T. vaporariorum* nymphs. However, after 15 generations of rearing on *B. tabaci* nymphs, there was a preference for *B. tabaci* nymphs compared to *T. vaporariorum* nymphs. No-choice assays showed that there was no significant increase in the number of *B. tabaci* nymphs parasitized and total mortality in all generations, but the number of *T. vaporariorum* nymphs parasitized and total mortality were both significantly higher in the control than the 10th and 15th generations. When *E. corni* parasitized *T. vaporariorum* nymphs, the developmental time of the 1st generation offspring was significantly shorter than that of other generations. Host feeding, offspring female ratio and emergence rate did not differ among generations or between host species. **Conclusion:** Our analyses showed that successive rearing of *E. corni* on an alternative host was able to enhance the preference for that host. However, despite this increase in preference, the developmental suitability did not change significantly among generations. This study provides fundamental information for understanding the parasitism performance of *E. corni* across different whitefly hosts over multiple generations.

Keywords: *Bemisia tabaci*, *Trialeurodes vaporariorum*, biological control, parasitoid, successive rearing

Introduction

The sweetpotato whitefly, *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae), and the greenhouse whitefly, *Trialeurodes vaporariorum* Westwood (Hemiptera: Aleyrodidae) are widespread insect pests with similar morphological characteristics. *B. tabaci* was first discovered in Greece in 1889 but has since invaded several countries in South America, Oceania, Europe, Asia, Africa, etc. (Gennadius, 1889;

Ghahari *et al.*, 2013; CABI, 2017a). *T. vaporariorum* is globally distributed in many countries, including the United States, Canada, the Hawaiian Islands, Europe, Africa, Asia, Oceania, etc. (Ghahari *et al.*, 2013; CABI, 2017b; Perring *et al.*, 2018). These whiteflies frequently co-occur and cause substantial damage to economically important crops, such as vegetables, flowers and cotton (Tsueda *et al.*, 2014). Among them, *B. tabaci* comprises at least 44 cryptic species, several of which rank as some of the most destructive

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agricultural pests (MED, formerly biotype Q, and MEAM1, formerly biotype B) around the world (De Barro *et al.*, 2011; Cuthbertson and Vänninen, 2015; Kanakala and Ghanim, 2019). Numerous studies have shown that *B. tabaci* (MED) has rapidly replaced *B. tabaci* (MEAM1) as the dominant *B. tabaci* biotype in China, Spain and other parts of the Mediterranean (Liu *et al.*, 2016; Li *et al.*, 2017). In addition to causing direct damage to host plants through feeding, adult *B. tabaci* and *T. vaporariorum* can transmit over 200 plant viruses (Wan and Yang, 2016; Mu *et al.*, 2022). Notably, *B. tabaci* is crucial in transmitting various plant viruses (Polston *et al.*, 2014). As a result, *B. tabaci* has been labeled a “super pest” by some academics (Gilbertson *et al.*, 2015), demonstrating its superiority over *T. vaporariorum* in terms of its ability to spread plant diseases, thus posing an even more significant challenge to agricultural production.

Chemical control is currently the dominant approach to whitefly pest management (Horowitz *et al.*, 2020). However, continuous and extensive reliance on chemical insecticides leads multiple side effects, notably the selection of insecticide resistance in pests, negative effects on natural enemies, risks to human health, and environmental pollution (Desneux *et al.*, 2007; Damalas and Eleftherohorinos, 2011). Given these challenges, the shift toward biological control strategies emerges as an urgent and prudent approach. Biological control employs natural enemies, such as parasitoids, predators (arthropod species), and pathogenic microorganisms, to regulate pest populations through biotic interactions (Heimpel and Mills, 2017). This approach ensures agricultural sustainability while reducing potential threats to human health and the environment (Liu *et al.*, 2016; Zang *et al.*, 2021). The history of biological control of whiteflies is extensive and includes a variety of successful cases. The predatory mite *Amblyseius swirskii* Athias-Henriot (Acari: Phytoseiidae) became one of the most successful biocontrol agents against *B. tabaci* following its commercial introduction in 2005 (Calvo *et al.*, 2015; Bonsignore and Van Baaren, 2024). Among the parasitoids used are *Encarsia formosa* Gahan, *Eretmocerus mundus* Mercet, *E. eremicus* Rose and Zolnerowich, each demonstrating targeted and highly effective control of *B. tabaci* and *T. vaporariorum* (Bao-Fundora *et al.*, 2016; Perring *et al.*, 2018; He *et al.*, 2019). Notably, *E. formosa*, the primary biological control agent against *T. vaporariorum*, has been successfully commercialized (Liu *et al.*, 2015). It parasitizes and feeds on any of the four *T. vaporariorum* nymphal instars (Perring *et al.*, 2018). Nevertheless, the efficacy of *E. formosa* in controlling *B. tabaci* is not always satisfactory (Hoddle *et al.*, 1998); therefore, it is necessary to study additional biocontrol agents as potential management tools.

Eretmocerus corni Haldeman (Hymenoptera: Aphelinidae) was identified in 2004 as a new species reported in China (Huang and Huang, 2004). The parasitoid was initially collected from an unidentified species of Aleyrodidae in 1936 (Blanchard, 1936). This species is considered an important natural enemies to be used as a biological control agent against *T. vaporariorum* in Argentina (López and Botto, 1997, 2005). However, it remains uncertain whether this species can be mass reared using *B. tabaci* as a host and effectively used to control whitefly populations. The preference, adaptation, and ability of *E. corni* to switch between these two hosts remain unknown. Parasitoids encounter challenges during host-switching events, potentially impacting community structure (Van Veen *et al.*, 2006; Rothacher *et al.*, 2016), species invasion dynamics (Jaworski *et al.*, 2013), and the strength of biocontrol services provided by natural enemies of pests (Jones *et al.*, 2015; Monticelli *et al.*, 2019). Preference of parasitoids for specific hosts and potential behavioral defenses against parasitoids from hosts can affect strongly population dynamics (Hassell, 2000; Vorburger and Perlman, 2018; Kruitwagen *et al.*, 2022). In addition, parasitoids must overcome host defense mechanisms during larval development (Desneux *et al.*, 2009; Contreras-Garduño *et al.*, 2023), and specialization degree may limit expansion of their host range (Van Veen *et al.*, 2008; Desneux *et al.*, 2012; Monticelli *et al.*, 2019).

In addition to host preferences, parasitoids may undergo adaptive changes during mass rearing, including evolutionary shifts or local adaptation to the rearing host (Henry *et al.*, 2008, 2010; Bertin *et al.*, 2017). Despite *E. corni*'s potential as a biological control agent, data on its adaptive strategies on different whitefly hosts remain scarcely documented. Successive rearing experiments have revealed dynamic changes in parasitoid adaptations, indicating that selection can be influenced by host experience across generations (Mandeville and Mullens, 1990; Pratisoli *et al.*, 2004; García-Robledo and Horvitz, 2012). These findings indicate some plasticity of parasitoid biological traits under prolonged rearing conditions (Uller, 2008; Pomari-Fernandes *et al.*, 2015). For example, *Trichogramma leucaniae* (Pang and Chen) could be reared on the large eggs of *Antheraea pernyi* Guérin-Ménéville (Lepidoptera: Saturniidae) with divergent adaptation for 8 successive generations (Xu *et al.*, 2020). The number of *Corcyra cephalonica* Stainton (Lepidoptera: Pyralidae) eggs parasitized by *Telenomus remus* Nixon (Hymenoptera: Scelionidae) steadily increased over successive generations before stabilizing in the F₇ generation (Pomari-Fernandes *et al.*, 2015). The induction of new host preferences through learning at early developmental stages is likely a contributing factor to species formation (König *et al.*, 2015). The differentiation of parasitoid populations with gradual adaptation to specific hosts provides further evidence for the critical role of parasitoid learning and of multigenerational genetic adaptation in host selection and specialization degree (Henry *et al.*, 2008).

We investigated the effect of successive multigenerational rearing on the preference and suitability of *E. corni* on the original host *T. vaporariorum* and the alternative host *B. tabaci*. Specifically, we compared biological parameters such as number of hosts parasitized, host feeding events, offspring developmental time, sex ratio, and emergence rate in successive rearing of *E. corni* for up to 15 generations. The results of this study will provide information for optimizing the parasitoid rearing for use against whiteflies.

Methods

HOST PLANTS

Tomato (*Solanum lycopersicum* L., Ruiqi 1) seeds were purchased from Xi'an Qunxing Seed Industry Co., Ltd. They were sown in seedling trays (29.5 cm length, 25.5 cm width) and transplanted into pots (9.2 cm diameter, 14.5 cm height) when 3 or 4 true leaves emerged. Only healthy, pest-free tomato plants with a large leaf area grown to 8 or 9 true leaves were selected for the experiment. All host plants were cultivated in a greenhouse at Guizhou University, China, with a temperature range of 25–29°C, relative humidity (RH) maintained between 50 and 70%, and a natural photoperiod of 14:10 h to 15:9 h (L:D).

HOST INSECTS

Bemisia tabaci (MED) was initially collected from tomato plants in Changchun City, China, in 2021. The wings of *B. tabaci* are covered in white powder wax that is secreted soon after the adult ecloses from the last nymphal instar (Gill, 1990). The wings are held “roof-like” over the abdomen. *T. vaporariorum* were collected from tobacco plants cultivated in a greenhouse at the Guizhou Academy of Agricultural Sciences in 2021. Adult *T. vaporariorum* have wax-covered wings held flat over the abdomen (Gerk *et al.*, 1995), a distinguishing trait from *B. tabaci*. The *B. tabaci* and *T. vaporariorum* populations were reared on tomato plants under laboratory conditions (26 ± 1°C, 65 ± 5% RH, and a 14:10 h (L:D) photoperiod) for more than 10 generations.

A total of 40–50 adults of *B. tabaci* or *T. vaporariorum* were introduced onto the underside of a tomato plant leaf within a clip cage (4.0 cm diameter × 3.5 cm height) (Dai *et al.*, 2012) and allowed to oviposit for 12 h. After this period, the adults of *B. tabaci* or *T. vaporariorum* were removed, and the tomato plants were transferred to new cages covered with a mesh screen (120 mesh). After 13–14 days,

once the nymphs had reached the third instar stage, 20 nymphs (for choice assays) or 40 nymphs (for no-choice assays) were selected per leaf. Any additional whitefly nymphs were carefully removed using an insect pin under a stereomicroscope. The petiole end of the detached tomato leaf, with the whiteflies, was wrapped in cotton and maintained hydroponically in a 25-mL clear plastic cup filled with water. This setup was placed inside a clear plastic cylindrical cup (10 cm diameter, 15 cm height).

PARASITOID

A laboratory colony of *E. corni* was initiated using parasitized *T. vaporariorum* nymphs collected from *Althaea rosea* (L.) at the Fumin County of Kunming City, Yunnan Province, in December 2021. The individual parasitoids were identified morphologically as *E. corni* by Prof. Zhuhong Wang (Fujian Agriculture and Forestry University, China) using the key in Huang and Huang (2004).

The experiment was designed to investigate the effects of rearing *E. corni* across five different generations (G_0 (Control), G_1 , G_5 , G_{10} , and G_{15}) on two host species (*B. tabaci* and *T. vaporariorum*). Specifically, G_1 , G_5 , G_{10} , and G_{15} represent *E. corni* reared continuously on *B. tabaci* nymphs on tomato for 1, 5, 10, and 15 generations, respectively. The control group (G_0) of parasitoids was continuously reared on *T. vaporariorum* nymphs on tomato for approximately 10 generations. Then, four pairs of *T. vaporariorum*-reared *E. corni* were introduced into a clear plastic cylindrical cup (10 cm diameter, 15 cm height) containing tomato leaves and 60 third-instar *B. tabaci* nymphs for 2 days. The third instar of whitefly nymphs was the most favorable host stage for *Eretmocerus* spp. (McAuslane and Nguyen, 1996; Qiu et al., 2004; Ebrahimifard and Jamshidnia, 2022), thus, third instar nymphs were selected as hosts tested. The clear plastic cylindrical cup for rearing parasitoids was according to the method by Dai et al. (2012, 2013). After parasitoids were removed, the first generation of *E. corni* reared on *B. tabaci* was observed until it emerged. This procedure was repeated for 15 generations.

The rearing of parasitoids described above, and the choice and no-choice assays mentioned later, were conducted in a conditioned room with $26 \pm 1^\circ\text{C}$, $65 \pm 5\%$ RH, and a 14:10 h (L:D) photoperiod at the Key Laboratory of Green Pesticide and Agricultural Bioengineering, Guizhou University, China.

THE BIOLOGICAL TRAITS OF *E. CORNI* IN DIFFERENT GENERATIONS IN CHOICE ASSAYS

Under choice condition, a tomato leaf with 20 third-instar *B. tabaci* and a tomato leaf with 23 instar *T. vaporariorum* nymphs were provided in the same plastic cylindrical cup. A pair of newly emerged (<24 h) female and male *E. corni* were introduced into the plastic cup, allowed to mate and oviposit for 24 h, and then removed. The number of hosts parasitized and fed was assessed under a stereomicroscope 12 days after parasitoid removal. When the host died as a result of host feeding, the bodies became flat and desiccated. On the other hand, if the hosts were parasitized, the parasitized nymphs and mycetome displacement could be observed during examination (Zang and Liu, 2008). A total of 25 replications were performed for each treatment.

THE BIOLOGICAL TRAITS OF *E. CORNI* IN DIFFERENT GENERATIONS IN NO-CHOICE ASSAYS

Under no-choice conditions, one pair of newly emerged (<24h) *E. corni* were placed in a plastic cylindrical cups with either a tomato leaf with 40 third instar *B. tabaci* or a tomato leaf with 40 third instar *T. vaporariorum*. As in the previous experiment, the whitefly nymphs were subjected to parasitism by *E. corni* for 24 h. The number of parasitized and fed hosts was investigated using the methods described above. The parasitized hosts were monitored every 24 h, and the time to emergence of adult parasitoids, the number of *E. corni* offspring that emerged, and the sex of *E. corni* were recorded until all *E. corni* had emerged or no

more *E. corni* emerged. A total of 25 replications were performed for each treatment.

STATISTICAL ANALYSES

Generalized linear mixed models (GLMMs) assuming a Poisson distribution with a log-link function were employed to analyze the number of hosts parasitized, host feeding events, and total mortality by *E. corni* in choice assays. Generalized linear models (GLM) were applied to analyze all data in the no-choice assays. The number of hosts parasitized, host feeding events, and total mortality by *E. corni* were analysed assuming a Poisson distribution with a log-link function. Developmental time was assumed to be a Gaussian distribution with an identity function. The proportion of females and emergence rate were assumed to have a binomial distribution (lmer, *lme4* package, Bates et al., 2015) and a logistic function.

All statistical analyses were performed in R 4.4.2 (R Core Team, 2024). Initial models included generation (G_0 (Control), G_1 , G_5 , G_{10} , and G_{15}), host species (*B. tabaci* and *T. vaporariorum*), and their interaction (generation \times host species) as fixed effect. When a significant interaction was detected, we performed post hoc comparisons by building separate models. For choice assays, we constructed separate models for each generation and compared differences between host species within these models (family = Poisson, link = log, with host species as a fixed effect). For no-choice assays, we built individual models for each host species and compared differences across generations within these models (family = Poisson, link = log, with generation as a fixed effect). All post hoc pairwise comparisons were performed using *emmeans* package (Lenth, 2025) and *P*-values were corrected using the false discovery rate (FDR) method ($\alpha = 0.05$). Figures were generated using GraphPad Prism version 8.0 (GraphPad Software, Inc., San Diego, CA, USA).

Results

HOSTS PARASITIZED BY *E. CORNI* IN DIFFERENT GENERATIONS IN CHOICE AND NO-CHOICE ASSAYS

Number of hosts parasitized: In choice assays, the number of hosts parasitized by *E. corni* were not affected by generation, but they were affected by host species ($\chi^2 = 43.67$, $df = 1$, $P < 0.001$) and its interaction ($\chi^2 = 49.11$, $df = 4$, $P < 0.001$) with the generation (Table 1). The number of *T. vaporariorum* nymphs parasitized during 24 h by *E. corni* was significantly higher than *E. corni* on *B. tabaci* nymphs in G_0 , G_1 , and G_5 (G_0 : $\chi^2 = 46.46$, $df = 1$, $P < 0.001$; G_1 : $\chi^2 = 26.21$, $df = 1$, $P < 0.001$; G_5 : $\chi^2 = 49.89$, $df = 1$, $P < 0.001$), indicating that *E. corni* exhibits a significant parasitism preference for *T. vaporariorum* nymphs in these early generations (Fig. 1a). However, with increasing generations, the number of *B. tabaci* nymphs parasitized by *E. corni* was significantly higher compared to *E. corni* on *T. vaporariorum* nymphs in G_{15} ($\chi^2 = 9.96$, $df = 1$, $P = 0.003$) (Fig. 1a).

In no-choice assays, although the number of host parasitized by *E. corni* was not affected by the generation and host species, it was affected by the interaction of generation and host species ($\chi^2 = 12.34$, $df = 4$, $P = 0.015$). The number of parasitized *B. tabaci* nymphs by *E. corni* was not significantly different among generations (Fig. 1b). However, the number of parasitized *T. vaporariorum* nymphs by *E. corni* was significantly lower in G_{10} and G_{15} than G_0 ($\chi^2 = 12.37$, $df = 4$, $P = 0.015$) (Fig. 1b).

Number of hosts feeding events: The number of host feeding events was not affected by generation, host species, and their interaction whether choice (generation: $\chi^2 = 1.35$, $df = 4$, $P = 0.854$; host species: $\chi^2 = 0.18$, $df = 1$, $P = 0.894$; generation \times host species: $\chi^2 = 3.14$, $df = 4$, $P = 0.535$) or no-choice assays (generation: $\chi^2 = 2.41$, $df = 4$, $P = 0.660$; host species: $\chi^2 = 0.69$, $df = 1$, $P = 0.405$; generation \times host species: $\chi^2 = 0.73$, $df = 4$, $P = 0.947$) (Fig. 2a,b).

Total mortality: In choice assays, the total mortality caused by *E. corni* was not affected by generation, but was affected by host

Table 1. A generalized linear mixed models (GLMMs) of the effects of generations, host species, and their interactions on the performance of *Eretmocerus corni* reared on *Bemisia tabaci* nymphs across generations in choice assays.

Parameters	Source	χ^2	df	P
Number of whitefly nymphs parasitized	Generation	1.45	4	0.835
	Host species	43.67	1	<0.001
	Generation × Host species	49.11	4	<0.001
	Error	240		
Number of host-feeding events	Generation	1.35	4	0.854
	Host species	0.18	1	0.894
	Generation × Host species	3.14	4	0.535
	Error	240		
Total mortality of whitefly nymphs	Generation	1.06	4	0.901
	Host species	40.46	1	<0.001
	Generation × Host species	51.02	4	<0.001
	Error	240		

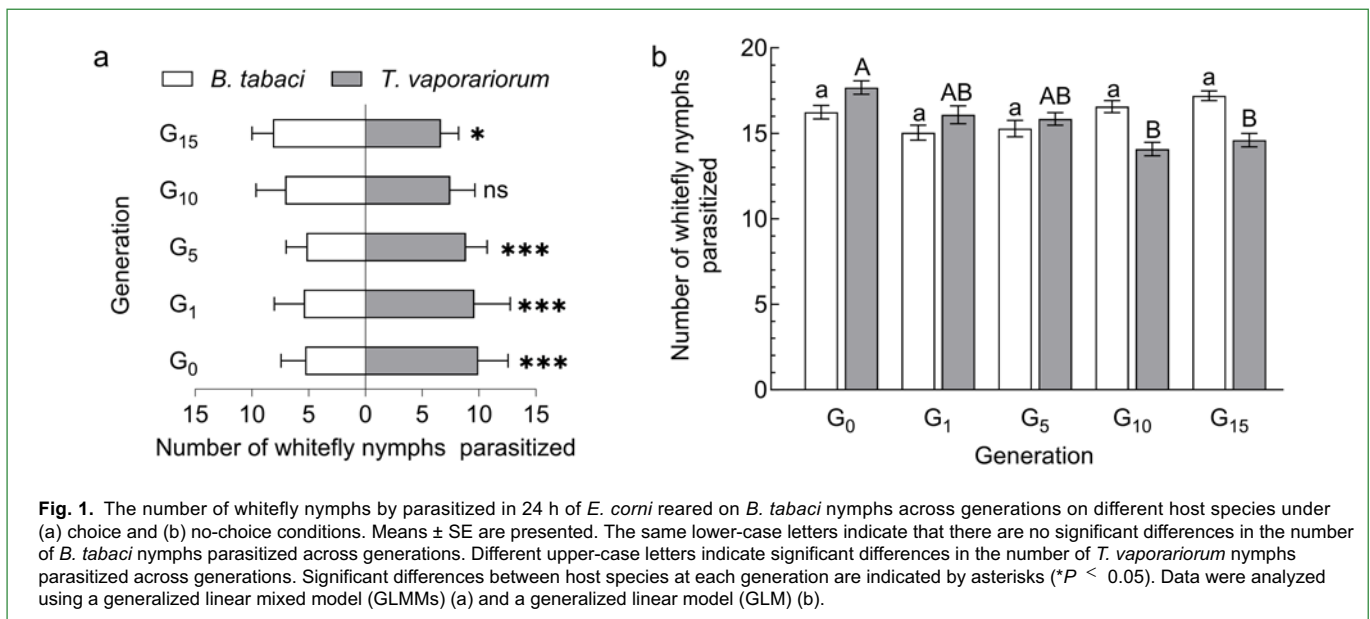


Fig. 1. The number of whitefly nymphs by parasitized in 24 h of *E. corni* reared on *B. tabaci* nymphs across generations on different host species under (a) choice and (b) no-choice conditions. Means ± SE are presented. The same lower-case letters indicate that there are no significant differences in the number of *B. tabaci* nymphs parasitized across generations. Different upper-case letters indicate significant differences in the number of *T. vaporariorum* nymphs parasitized across generations. Significant differences between host species at each generation are indicated by asterisks (* $P < 0.05$). Data were analyzed using a generalized linear mixed model (GLMMs) (a) and a generalized linear model (GLM) (b).

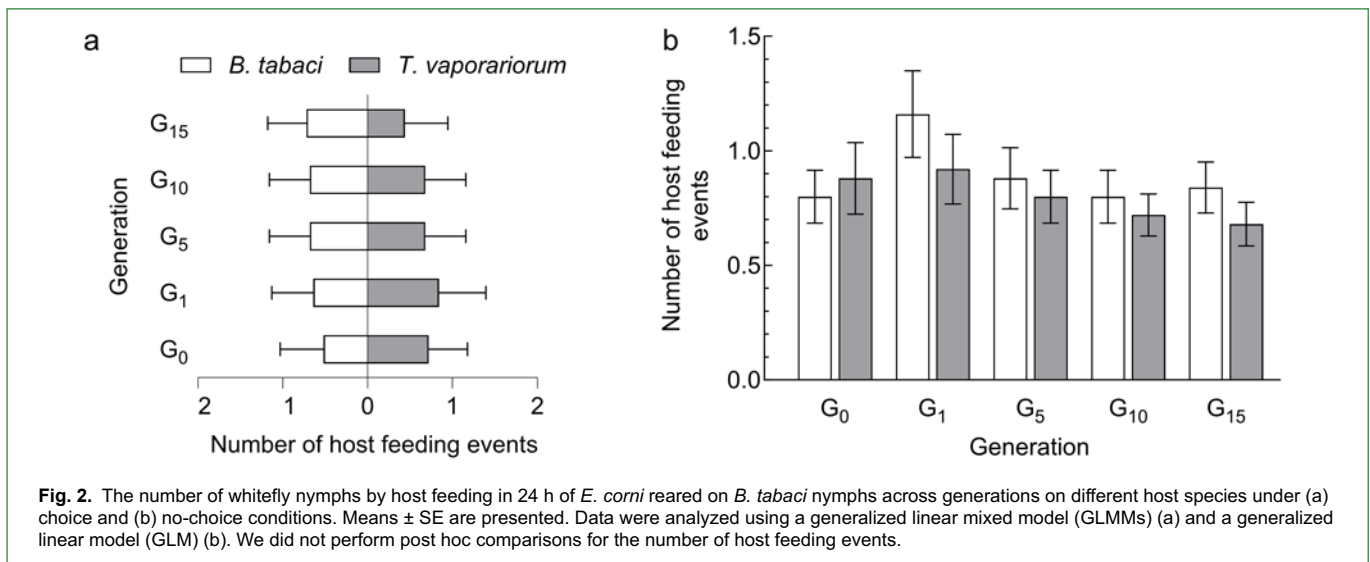


Fig. 2. The number of whitefly nymphs by host feeding in 24 h of *E. corni* reared on *B. tabaci* nymphs across generations on different host species under (a) choice and (b) no-choice conditions. Means ± SE are presented. Data were analyzed using a generalized linear mixed model (GLMMs) (a) and a generalized linear model (GLM) (b). We did not perform post hoc comparisons for the number of host feeding events.

species ($\chi^2 = 40.46, df = 1, P < 0.001$), and by the interaction between the host species and generation ($\chi^2 = 51.02, df = 4, P < 0.001$). The total mortality of *T. vaporariorum* nymphs caused by *E. corni* was significantly higher than that of *E. corni* on *B. tabaci* nymphs in G_0, G_1 , and G_5 ($G_0: \chi^2 = 38.49, df = 1, P < 0.001$; $G_1: \chi^2 = 23.57, df = 1, P < 0.001$; $G_5: \chi^2 = 35.67, df = 1, P < 0.001$). However, the total mortality number of *B. tabaci* nymphs caused by *E. corni* was significantly higher than those of *E. corni* on *T. vaporariorum* nymphs in G_{15} ($\chi^2 = 9.42, df = 1, P = 0.004$) (Fig. 3a).

In no-choice assays, although the total mortality caused by *E. corni* was not affected by the generation and host species, but it was affected by the interaction of generation and host species ($\chi^2 = 11.91, df = 4, P = 0.018$). The total mortality of *B. tabaci* nymphs caused by *E. corni* was not significantly different among generations (Fig. 3b). However, the total mortality of *T. vaporariorum* nymphs caused by *E. corni* was significantly lower in G_{10} and G_{15} than G_0 ($\chi^2 = 13.26, df = 4, P = 0.010$) (Fig. 3b).

DEVELOPMENTAL SUITABILITY OF *E. CORNI* REARED ON ALTERNATIVE HOST ACROSS GENERATIONS ON DIFFERENT WHITEFLY NYMPHS

The developmental time was affected by generation and host species (generation: $\chi^2 = 35.86, df = 4, P < 0.001$; host species: $\chi^2 = 6.63, df = 1, P = 0.010$), but it was not affected by the interaction of generation and host species. When *E. corni* parasitized *T. vaporariorum* nymphs, the shortest development time was at G_1 (Fig. 4a). The only difference in development time among host species was in the control group, G_0 (Fig. 4a). The female proportion (Fig. 4b) or emergence rate (Fig. 4c) of *E. corni* were not affected by generation, host species, and their interaction (Table 2).

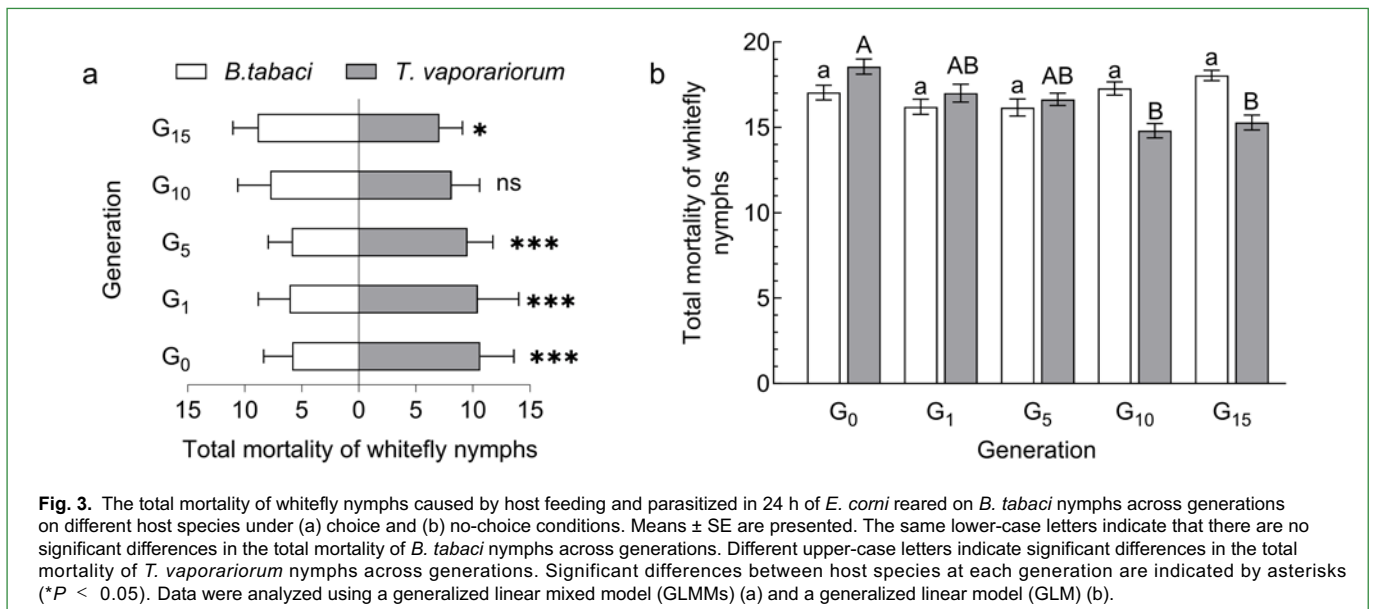
Discussion

We found that for the first five generations, the parasitoids showed a preference for the original hosts in choice assays. However, as the number of generations increased while being reared on *B. tabaci* nymphs, the 15th generation of *E. corni* showed a preference for *B. tabaci* nymphs compared to *T. vaporariorum* nymphs, suggesting that the preference of the parasitoid for *T. vaporariorum* nymphs gradually weakened. Similarly, in no-choice assays, the number of *T. vaporariorum* nymphs parasitized and total mortality were both significantly higher in G_0 than G_{10} and G_{15} . Overall, our study confirmed that rearing parasitoids on alternative hosts for multiple consecutive generations has the potential to improve their efficacy against those hosts.

In our study, the 15th generation of *E. corni* showed a preference for *B. tabaci* nymphs compared to *T. vaporariorum* nymphs under choice condition. Previous studies have shown that the choice of rearing host species can influence the reproductive performance and host-selection behavior of Hymenoptera parasitoids (Jones et al., 2015). Similar results were found in *E. formosa* where significantly more *B. tabaci* nymphs were killed when reared on it than when reared on *T. vaporariorum* (Dai et al., 2014). Bertin et al. (2017) observed that females emerging from *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs showed a marked preference for parasitism on this host over *Diatraea saccharalis* Fabr (Lepidoptera: Crambidae) eggs and parasitism on *D. saccharalis* eggs was reduced when *Trichogramma galloi* Zucchi was reared on *E. kuehniella* eggs. Furthermore, switching to *E. kuehniella* as a novel host environment significantly inhibited the viability of *Venturia canescens* Gravenhorst (Hymenoptera: Ichneumonidae). However, after three consecutive generations of reproduction, its survival in the novel host recovered significantly (Jones et al., 2015). This finding indicated that the host preference of parasitoids may potentially change with multiple successive generations of rearing, further confirming the plasticity of parasitoids in alternative host selection (Kalyanaraman et al., 2021).

We observed no difference in the number of host parasitized and in total mortality of *B. tabaci* nymphs from G_1 to G_{15} in the no-choice assays. Similarly, there was no significant difference in the number of hosts parasitized by *Telenomus remus* Nixon (Hymenoptera: Scelionidae) after 30 generations of rearing on the alternative host *Spodoptera litura* Fabricius (Lepidoptera: Noctuidae), compared to its original host *Spodoptera frugiperda* J. E. Smith (Lepidoptera: Noctuidae) (Chen et al., 2023). Research has demonstrated that using alternative hosts for rearing parasitoids imposes selection pressures may lead to different evolutionary trajectories (Henry et al., 2008, 2010; Bertin et al., 2017). For instance, parasitism increased from the 1st to the 10th generation of *Trichogramma atopovirilia* (Oatman and Platner) and *Trichogramma bruni* Nagaraja in an alternative host (Dias et al., 2008). The *T. remus* colony has been reared on *Spodoptera frugiperda* J. E. Smith (Lepidoptera: Noctuidae) eggs under laboratory conditions for approximately 250 generations and may be better adapted to *S. frugiperda* eggs than those reared on *C. cephalonica* eggs, which have only been reared for 19 generations (Pomari-Fernandes et al., 2016). These results suggest that different parasitoids may develop different potential adaptations to alternative hosts after multiple generations.

In field and greenhouse environments, *B. tabaci* and *T. vaporariorum* frequently coexist (Tsueda et al., 2014; Perring et al., 2018). This



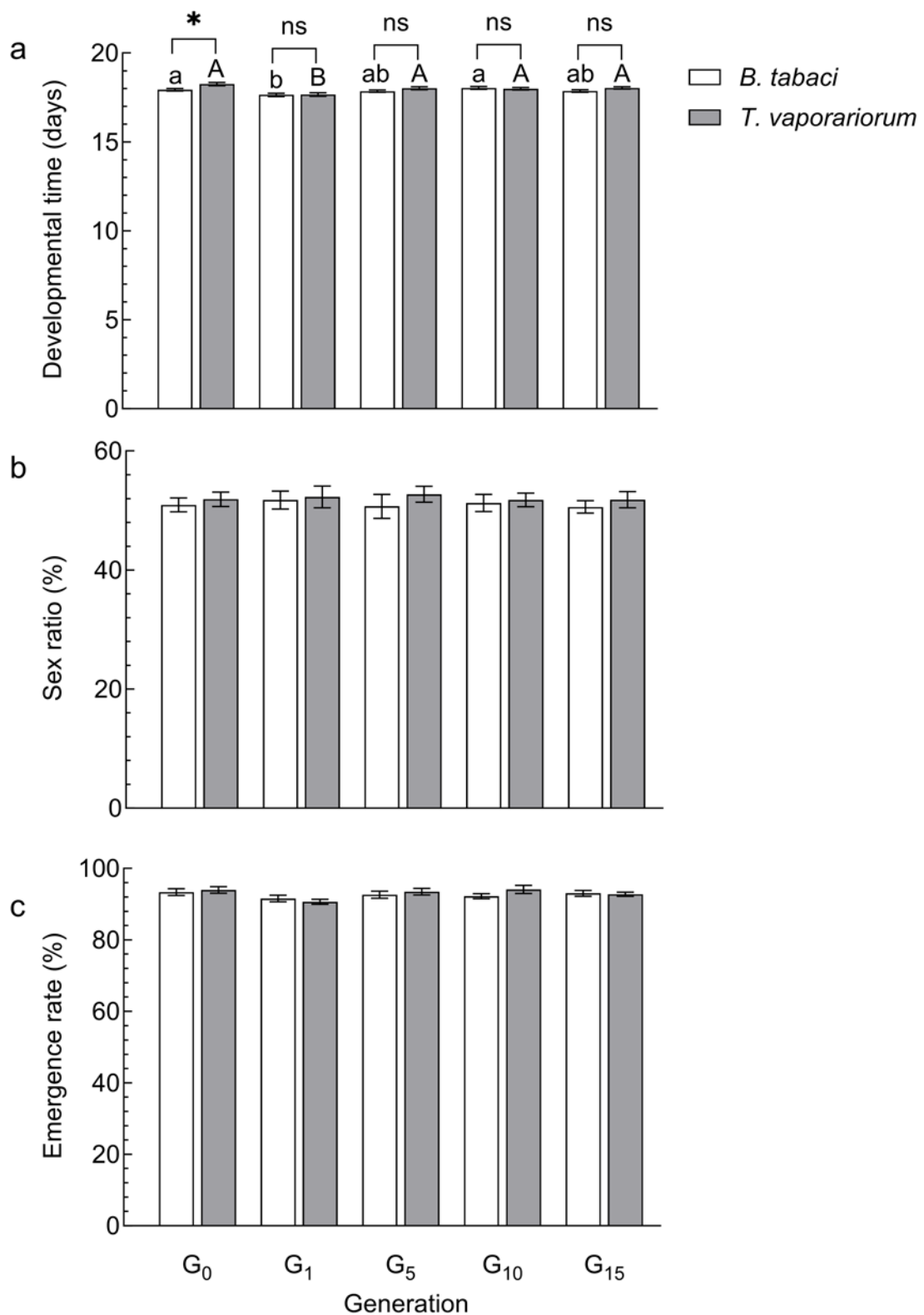


Fig. 4. Developmental time (a), sex ratio (b), and emergence rate (c) of *E. corni* reared on *B. tabaci* nymphs across generations parasitizing different host species. Means ± SE are presented. Different lower-case letters indicate significant differences across generations when *E. corni* parasitized *B. tabaci* nymphs. Different upper-case letters indicate significant differences across generations when *E. corni* parasitized *T. vaporariorum* nymphs. Significant differences between host species at each generation are indicated by asterisks (* $P < 0.05$). Data were analyzed using a generalized linear model (GLM) (a, b, c). We did not perform post hoc comparisons for the sex ratio and emergence rate.

sympatric distribution raises important biocontrol considerations, as our study demonstrates that *E. corni*'s host preference shifts toward its rearing host (*B. tabaci*) across generations, potentially compromising its efficacy against *T. vaporariorum* in mixed

infestations. This adaptation dynamic suggests that mass-reared *E. corni* populations may require complementary management strategies when targeting both whitefly species. One promising approach would be to integrate *E. corni* with *E. formosa* – a

Table 2. A generalized linear models (GLM) of the effects of generations, host species, and their interactions on the performance of *Eretmocerus corni* reared on *Bemisia tabaci* nymphs across generations in no-choice assays.

Parameters	Source	χ^2	df	P
Number of whitefly nymphs parasitized	Generation	5.32	4	0.256
	Host species	0.76	1	0.385
	Generation × Host species	12.34	4	0.015
	Error	240		
Number of host-feeding events	Generation	2.41	4	0.660
	Host species	0.69	1	0.405
	Generation × Host species	0.73	4	0.947
	Error	240		
Total mortality of whitefly nymphs	Generation	5.28	4	0.259
	Host species	1.039	1	0.308
	Generation × Host species	11.91	4	0.018
	Error	240		
Developmental time (days)	Generation	35.86	4	<0.001
	Host species	6.63	1	0.010
	Generation × Host species	6.92	4	0.140
	Error	240		
Sex ratio (%)	Generation	0.66	4	0.956
	Host species	0.56	1	0.453
	Generation × Host species	0.28	4	0.991
	Error	240		
Emergence rate (%)	Generation	4.61	4	0.330
	Host species	0.23	1	0.635
	Generation × Host species	1.20	4	0.878
	Error	240		

commercially successful specialist against *T. vaporariorum* (Liu *et al.*, 2015) – creating a synergistic parasitoid system. Such combined deployment could maintain pressure on both host species while mitigating the adaptation trade-offs observed in *E. corni*.

The majority of female Hymenoptera parasitoids kill their hosts not only by parasitism but also by host feeding (Jervis and Kidd, 1986). For example, the parasitoids *Encarsia sophia* (Girault and Dodd), *E. formosa*, and *Eretmocerus melanoscutus* (Zolnerowich and Rose) parasitize their hosts and feed on and kill whiteflies. In particular, *E. sophia* has host-feeding effects on pest control that are similar to or greater than parasitism (Zang and Liu, 2008). Numerous elements influence the host-feeding behavior of parasitoid insects, such as host instars (Zang and Liu, 2008; Wang *et al.*, 2025), host density (Zang *et al.*, 2011), physiological condition of the parasitoids (Heimpel and Rosenheim, 1995), and environmental conditions (Hansen and Jensen, 2002). The results of this study indicate that there is no significant difference in the feeding of *B. tabaci* nymphs and *T. vaporariorum* nymphs by *E. corni* across generations in choice and no-choice assays (Fig. 1b). Similarly, the number of whiteflies killed by host feeding did not differ between *E. formosa* reared on *T. vaporariorum* and *E. formosa* reared on *B. tabaci* (Dai *et al.*, 2014). These results may indicate that rearing generations and host species do not influence the host feeding pattern.

In our study, in all generations, *E. corni* parasitized *T. vaporariorum* nymphs exhibited the shortest developmental time at G₁ (Fig. 4a). In comparison, *T. leucaniae* reared on large *A. pernyi* eggs had progressively shortened developmental time over the first five generations, with a prolongation beginning in the 6th generation (Xu *et al.*, 2020). Parasitoids sometimes adopt rapid development to reduce the risk of mortality (Pennacchio and Strand, 2006). For example, some parasitoids secrete immune-suppressive factors to interfere with host defenses, but when facing a new host, they may adopt a “quick-win” strategy (Strand and Pech, 1995). In this study, the stabilization of developmental time in subsequent generations suggests that the developmental pressure caused by adaptation to host insufficiency may be alleviated after multiple generations of breeding (Henter and Via, 1995).

In biological control, the female ratio is a critical factor that can affect the profitability of mass parasitoid rearing (Ghaemmaghani *et al.*, 2021). According to IOBC guidelines, the female ratio of parasitoids should be greater than 0.5 in mass production programs (Lenteren *et al.*, 2003). Academic studies have shown the sex ratio of *Trichogramma pretiosum* Riley and *Tricho. brassicae* was not affected by generational variation under laboratory conditions (Prattisoli *et al.*, 2004; Ghaemmaghani *et al.*, 2021). Our experiments resulted in a similar finding that the proportion of females in the offspring was higher than 0.5 whether *E. corni*

parasitized *B. tabaci* nymphs or *T. vaporariorum* nymphs, with no significant differences among generations. Therefore, *E. corni* exhibited the potential for mass rearing on *B. tabaci* nymphs.

CONCLUSIONS

Our research suggests that *E. corni* may increase preference for alternative hosts as the number of generations of rearing on alternative hosts increases, and conversely, decrease preference for the original host. Therefore, using *B. tabaci* nymphs as a host to generate a population seems appropriate for controlled inoculative or inundative releases of *B. tabaci* in greenhouse environments. However, this experiment was conducted under laboratory conditions, further research should consider the more natural and complex environments that may be present in field applications.

CONFLICT OF INTEREST

All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

ETHICS STATEMENT

Not applicable.

CONSENT FOR PUBLICATIONS

Not applicable.

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AUTHOR CONTRIBUTIONS

Yi-Ling Wu: Investigation, data curation, formal analysis, methodology, writing – original draft, review, and editing. Ricardo Ramirez-Romero: Writing–review & editing, Validation, Methodology. Wishwajith Kandegama: Writing–review & editing, Validation. Qing-Rong Bai: Funding acquisition, data curation, formal analysis, methodology. Antonio Biondi: Writing–review & editing, Validation. Lucie Monticelli: Writing–review & editing, Methodology, Validation. Nicolas Desneux: Writing–review & editing, Methodology, Validation. Lian-Sheng Zang: Conceptualization, funding acquisition, project administration, methodology, supervision, writing – review and editing.

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DATA AVAILABILITY

The datasets analyzed during the current study available from the corresponding author on reasonable request.

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