The parasitoid *Aenasius arizonensis* prefers its natural host but can parasitize a nonnatural host in the laboratory: an opportunity for control of a new invasive mealybug

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Abstract

The absence of natural enemies in newly invaded areas is a key factor in the successful invasion of alien species. Whether a specific parasitoid can be domesticated to attack a nonnatural host that has no reported parasitic enemies in invasive areas remains unclear. Here, we analyzed two invasive mealybugs (PSS-*Phenacoccus solenopsis* and PSI-*Phenacoccus solani*) and a specific parasitoid of *P. solenopsis* (*Aenasius arizonensis*) to verify this hypothesis under laboratory conditions. *A. arizonensis* preferred to parasitize PSS, but after 6 h, it also parasitized PSI female adults. The number of visits and parasitism rate was significantly higher for PSS than for PSI. However, the contact time was influenced by the natal host. The chemical volatiles emitted by the two hosts were different and may be an important factor for host choice. Offspring fitness, measured as emergence time, longevity, and hind tibia length, in those emerging from PSS was better in those emerging from PSI, but the emergence rate was higher in the latter. We supposed that *A. arizonensis* accepts and parasitizes low-quality hosts not because of an "incomplete" evaluation but because it may be more profitable to parasitize than not given circumstances; this may provide an opportunity for the control of a new invasive mealybug in the future.

Key message

1) *Aenasius arizonensis* is a specific parasitoid of PSS, but after 6 h, it also parasitized PSI female adults. 2) PSI appeared to be a poor-quality host; however, *A. arizonensis* still parasitized PSI even after exposure to PSS, resulting in reduced offspring fitness. 3) The chemical volatiles emitted by PSS and PSI were different and may be an important factor for host choice.

Keywords *Aenasius arizonensis* · *Phenacoccus solenopsis* · *Phenacoccus solani* · Host preference · Offspring fitness

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Introduction

Worldwide, biological invasions are one of the most important threats to biodiversity and ecosystems, posing a serious risk to agricultural and forestry production. Successful invasion depends on not only the life history of the invasive species but also the characteristics of the invaded ecosystem and the susceptibility of the community (Convey et al. 2006). Many theories and hypotheses have been proposed to explain biological invasion success, such as the enemy release hypothesis, which indicates that when an alien species invades a new area, there is a lack of natural enemies, leading to the establishment of an invasive population and spatial expansion (Keane and Crawley 2002).

The cotton mealybug *Phenacoccus solenopsis* (Hemiptera: Pseudococcidae) (hereafter PSS) is native to New

Mexico, North America, and is a high-risk pest worldwide (Fand and Suroshe 2015). The insect pest feeds on plant juices and secretes honeydew, which induces sooty mold growth, seriously threatening the production of field crops, ornamental plants, fruit trees, and vegetables. More than 200 plant species in 55 families in 24 countries around the world are attacked by PSS; it has replaced the cotton bollworm as the main pest of cotton in India and Pakistan (Fand and Suroshe 2015) and poses a great threat to cotton production in China. The solanum mealybug, *Phenacoccus solani* (Hemiptera: Pseudococcidae) (hereafter PSI), is native to California, North America (Chatzidimitriou et al. 2016) and has been newly recorded in China, where it is considered to be a major threat to agricultural production and the ecological environment (Huang et al. 2020). Both PSS and PSI belong to the same genus and are invasive in China, but they have different reproductive modes; PSI is a thelytokous parthenogenetic species, with no males in the population (Huang et al. 2020), while PSS undergoes only sexual reproduction (Huang et al. 2013).

Aenasius arizonensis (Girault) (= *Aenasius bambawalei* Hayat) (Hymenoptera: Encyrtidae) is a dominant natural enemy of PSS that parasitizes second- and third-instar nymphs and female adults, with a parasitism rate as high as 62% in the field in South Asia (Fand et al. 2011; Tanwar et al. 2011). It was reported by Mahmood (2008) for the first time in Pakistan, and later was described and named *A. bambawalei* by Hayat (2009). In fact, *A. bambawalei* is a junior synonym of *A. arizonensis* (Fallahzadeh et al. 2014; Shera et al. 2017). This species was originally described from the USA as *Chalcaspis arizonensis* (Girault) and later transferred to *Aenasius* (Noyes and Woolley 1994). To date, many findings have indicated that *A. arizonensis* utilizes and completes its development period successfully only on PSS based on field and laboratory studies in South Asia (Poorani et al. 2009; Fand et al. 2011; Sahito et al. 2011; Shera et al. 2017). Laboratory rearing methods and large-scale production of this parasite have been gradually improving. Although parasitic natural enemies of PSI have been reported (Mendel et al. 2010; Zu et al. 2018), it is difficult to collect parasitoids in the wild in China, and no systematic studies have been conducted; therefore, the control efficacy and utility of parasitoids remain unknown. However, we inadvertently found that *A. arizonensis* can successfully parasitize PSI after hours of adaptation in the laboratory. This interesting observation prompted us to investigate whether this parasitoid, which normally parasitizes PSS, can be used as a natural enemy of invasive PSI.

Here, we chose PSS and PSI as hosts and studied the subsequent host preferences of *A. arizonensis* that emerged from the different hosts. We aimed to answer the following questions: (1) How long does it take for laboratory and

field populations of *A. arizonensis* to adapt to a new host? (2) What are the preferences of *A. arizonensis* that emerged from the two mealybug species when selecting subsequent hosts? (3) What are the differences in offspring fitness between *A. arizonensis* that emerged from different hosts? (4) Chemical volatiles of insect pests play a key role in host searching and host recognition by parasitoids (Colazza et al. 2014), and specialist parasitoids respond to not only their host but also some nonhost species that emit similar chemical volatiles (Hedlund et al. 1996); therefore, if host volatiles are responsible for host choice, are the body volatiles of the two species of mealybugs similar?

Materials and methods

Insects and material preparation

The tested insects included PSS, PSI, and *A. arizonensis*. PSS and PSI were collected from *Hibiscus mutabilis* and succulent plants in the field and reared under artificial climate conditions (27 ± 1 °C, $70 \pm 5\%$ RH, and a photoperiod of 14 L:10 D) on potato tubers; their populations were maintained for more than 30 generations. The *A. arizonensis* population was reared for many generations (> 30 generations) in our laboratory on PSS. A laboratory population of *A. arizonensis* was isolated and reared on PSI as a host for more than 10 generations. The field population of *A. arizonensis* was collected from *Hibiscus rosa-sinensis* in the middle of October 2018 in Beihai City (21.487°N, 109.129°E), Guangxi Province, China, and the host was PSS; no PSI had been reported in this area in the past 5 years according to the investigation data provided by Guangxi Academy of Agricultural Sciences (see Supplement 1 for more details). Different populations of *A. arizonensis* mentioned above (i.e., laboratory populations with PSS and PSI as the hosts, respectively; field population with PSS as the host) were reared independently in insect cages (length $\times$ width $\times$ height = 50 cm $\times$ 50 cm $\times$ 60 cm) with sprouted potato tubers that had been cleaned.

Host adaptation times in laboratory and field populations of *Aenasius arizonensis*

Our preliminary tests found that *A. arizonensis* parasitized female adults and second- and third-instar nymphs of PSI but emerged from only parasitized female adults. Therefore, we chose 5-day-old female adult PSS (unmated) and PSI for the experiments. PSS females are larger than PSI females (1.60 mm in width and 3.12 mm in length vs. 0.63 mm in width and 1.11 mm in length) according to the descriptions by Huang et al. (2012) and Zhi et al. (2018).

PSS (20 individuals) and PSI (15 individuals) females were carefully selected with a brush and placed on the buds of the potato tubers, and one potato tuber was placed in a plastic box with a volume of approximately 1.5 L. After the mealybugs fed continuously on the buds, 2 mated (2-day-old) *A. arizonensis* females with no oviposition history were introduced into the plastic box with a simple suction device. After mealybug female adults had been exposed to the parasitoids for 0.5 h, 1 h, 3 h, 6 h, 12 h, and 24 h, respectively, the parasitoids were removed from the boxes. The mealybugs were observed every day, and the numbers of parasitized mealybugs (i.e., mummies) were recorded for 20 days; additional methodological details were similar to those described by Zhang et al. (2016). The tests were conducted under controlled climate conditions with a photoperiod of L 14:D 10 and $75 \pm 5\%$ RH. The parasitoid parasitized PSS or PSI under certain parasitism time as a treatment, and each treatment included 5 replicates. Three different populations of *A. arizonensis* were tested, i.e., field and laboratory populations with PSS as the host and a laboratory population with PSI as the host. Since PSI has not been found to be parasitized by *A. arizonensis* in the wild, we could not test a field population of *A. arizonensis* with PSI as the host in our experiment.

***Aenasius arizonensis* host preferences**

Short-term foraging

Five female adult PSS and PSI were selected and placed on opposing sides of a plastic culture dish (9 cm in diameter, 1.4 cm in depth). One mated (2-day-old) *A. arizonensis* female with no oviposition history was introduced into the plastic culture dish with a simple suction device. Laboratory populations of *A. arizonensis* reared on PSS (15 replicates) and on PSI (10 replicates) were tested. The contact time on, the number of attacks on, and the number of visits by *A. arizonensis* to individuals from both mealybug populations were observed and recorded for half an hour. The contact time was defined as the time from first *A. arizonensis* contact with the mealybug to its departure; if *A. arizonensis* attacked a mealybug during the contact, it was not recorded as the contact time. If *A. arizonensis* grasped the mealybug while bending its body and attempting to lay eggs, an attack was recorded. Repeated contact of the antenna of *A. arizonensis* with the mealybug body was recorded as a visit; occasional contact and immediate departure (< 3 s) were not considered visits.

Long-term foraging

Three plastic culture dishes (two 9 cm in diameter and one 6 cm in diameter and 1.4 cm in depth) and two plastic straws

(0.5 cm in diameter and 5 cm in length) formed the selection test arena; the plastic culture dishes were connected by plastic straws (see Fig. 3 for details). A budded potato tuber with a thickness not more than the depth of a culture dish was placed in each large culture dish. Female adults of PSS (10 individuals) and PSI (10 individuals) were, respectively, placed on potato tubers in different large dishes. After the mealybugs fed continuously on the buds, 2 mated (2-day-old) *A. arizonensis* females with no oviposition history were introduced into the smaller dish with a simple suction device; observations were recorded at 1 h, 6 h, 12 h, 18 h, and 24 h. The locations of the *A. arizonensis* (PSS side, middle or blank, PSI side) at each time point were recorded. The results of observations at different times were finally calculated as averages, and each observation time was a replicate, i.e., 5 replicates in total. Afterward, (24 h later), the *A. arizonensis* were removed from the system, the mealybugs were observed every day, and the numbers of mummies were recorded for 20 days. The parasitoids reared on PSS and PSI were used as treatments, and each treatment included 20 replicates. These experiments were conducted in an enclosed and odor-free room.

Differences in offspring fitness between *Aenasius arizonensis* emerging from different hosts

The mummies obtained in all of the above experiments were collected and placed separately in 1.5 mL centrifuge tubes, and *A. arizonensis* emergence was observed daily. Finally, the emergence time (from mummy formation to adult emergence) and the number of *A. arizonensis* females and males were counted and recorded. *A. arizonensis* is a solitary parasitoid, and after the parasitoids emerged, they were transferred into individual plastic culture dishes and fed a 10% honey–water solution, and their survival was observed daily; the emergence rate (i.e., the percentage of successful emergence individuals in a group) and longevity of the parasitoids were obtained. The hind tibia length of parasitoids is often used as an important index to evaluate size and fecundity (Heimpel and Rosenheim 1995), and its measurement error is very small (Stenberg and Hamback 2010). Therefore, we measured the hind tibia length of *A. arizonensis* under a Nikon SMZ1500 zoom stereomicroscope (Nikon, Japan). Each emergence time, longevity, and hind tibia length test included 25 replicates, and each parasitoid was considered a biological replicate. Each emergence rate test and offspring sex ratio analysis included 5 replicates, and each replicate (group) tested a sufficient number of individuals (mummies). In total, 174 mummies and 99 mummies were tested for emergence rate, and 158 individuals (adult females) and 96 individuals (adult females) were calculated for sex ratio, respectively, on PSS and PSI as hosts.

Mealybug body volatile analysis

Whether *A. arizonensis* parasitized PSI because the volatiles of the two mealybugs were similar, thus confusing *A. arizonensis*, was analyzed. To verify this hypothesis, we detected the body volatiles of the two species of mealybugs. The volatile compounds of female adults of the two species of mealybugs were collected by headspace-solid phase microextraction (HS-SPME). Five-day-old female adult PSS (unmated) and PSI were carefully picked with a brush and put into a 20-ml glass container. Each glass container contained 150 female adults and was allowed to sit for 10 min at room temperature before rapid microextraction. Headspace volatiles were collected on a 100- μ m polydimethylsiloxane SPME fiber assembly (Supelco, Bellefonte, PA) at 20 ± 1 °C for 90 min. SPME fibers were preconditioned by heating at 250 °C for 1 h. Three replicates were performed, with 150 female adults per replicate.

The volatile compounds collected by HS-SPME were analyzed by gas chromatography-mass spectrometry (GC–MS) using an Agilent 7890 GC coupled with an Agilent 5977B MS (Agilent Technologies Inc., Wilmington, NC) equipped with an HP-5 (Agilent, 30 m $\times$ 0.25 mm i.d., 0.25- μ m film thickness) column. The SPME sample was injected into the inlet port (250 °C) in splitless mode and desorbed for 5 min before the fiber assembly was withdrawn. The carrier gas was helium (1.0 ml/min). Following injection, the column temperature was maintained at 40 °C for 5 min, increased to 260 °C at 10 °C/min, and held at 260 °C for 13 min. The MS detector was operated in electron impact ionization mode (70 eV), and mass spectra in the range of 30–350 μ were recorded. Volatile compounds were identified by comparison with the NIST mass spectra library (NIST/EPA/NIH, 2014).

Statistical analysis

For each test, Shapiro–Wilks tests were applied to determine whether the data had a normal distribution and homogeneity of variance. When the data were normally distributed and exhibited similar variances, they were further analyzed, and when necessary, data were normalized by either square root or logarithmic transformations. The parasitism rates of *A. arizonensis* (laboratory or field population) between mealybug species (between-subject) and between different time points (within-subject) were analyzed and compared using repeated-measures ANOVA and Tukey's HSD tests. The contact times, numbers of attacks, and numbers of visits by *A. arizonensis* were statistically compared between mealybugs and between different natal hosts by analysis of variance (ANOVA) and a general linear model (GLM), respectively; mean differences between two species of mealybugs were analyzed by GLM *t*-test, respectively. According to the occurrence times of *A. arizonensis* in the different locations

(i.e., the PSS side, middle or blank, and PSI side) at the different observation times, the frequency (choice tendency) was calculated, and differences in frequency between different locations were compared using a Chi-square test. Two-way ANOVA was used to compare the parasitism rate of *A. arizonensis* between mealybug species and natal host species, and multiple comparisons were performed with Tukey's HSD tests. GLM *t*-tests were also used to compare the emergence time, longevity, hind tibia length, emergence rate, and offspring sex ratio in *A. arizonensis* that parasitized PSS and PSI. Two-way ANOVA was also used to compare differences between the volatile compounds emitted by the different mealybug species, and multiple comparisons were performed with Tukey's HSD tests. All statistical analyses were conducted in SPSS version 14.0 (SPSS Inc., Chicago, IL, USA). The data are expressed as means $\pm$ standard errors.

Results

Host adaptation times in laboratory and field populations of *Aenasius arizonensis*

In the laboratory, *A. arizonensis* parasitized both PSS and PSI; the parasitism rates at the different time points are shown in Fig. 1a. When *A. arizonensis* emerged from PSI parasitized PSS, there was a certain parasitism rate at each parasitism time; the parasitism rate was 9% at 0.5 h, increased significantly after 12 h, and reached 55% at 24 h. When *A. arizonensis* that emerged from PSI parasitized PSI, parasitism did not occur until 1 h after contact, and the parasitism rate was 25.3% at 24 h. The parasitism rates at different parasitism times of *A. arizonensis* that emerged from PSS and parasitized PSS and PSI are shown in Fig. 1b. In *A. arizonensis* that parasitized PSS, the parasitism rate increased significantly after 6 h, reaching a peak at 62%, while those that parasitized PSI engaged in 3 h of contact before parasitizing the host, and the value was 17.3% at 24 h. The PSS parasitism rate of field-collected *A. arizonensis* also reached 62%, but when *A. arizonensis* parasitized PSI, parasitism did not occur until 6 h, and the value was 22.7% at 24 h (Fig. 1c). Additionally, there were statistically significant interactions between host species and parasitic time for different parasitoid populations (field parasitoids emerged from PSS, $F_{5,59} = 5.6$, $p < 0.001$; laboratory parasitoids emerged from PSS, $F_{5,59} = 8.9$, $p < 0.001$; laboratory parasitoids emerged from PSI, $F_{5,59} = 3.1$, $p = 0.018$).

Aenasius arizonensis host preferences

When *A. arizonensis* that emerged from PSS parasitized PSS, the contact time (20.0 vs. 8.2 times, $t = 3.9$, $df = 14$, $p < 0.001$), number of attacks (1.3 vs. 0.4 times, $t = 2.3$,

Fig. 1 Parasitism rates (%) of *Aenasius arizonensis* in two species of invasive mealybugs (PSS: *Phenacoccus solenopsis*; PSI: *Phenacoccus solani*) at different time points (0.5 h, 1 h, 3 h, 6 h, 12 h, and 24 h). Three populations of *A. arizonensis* were tested, i.e., laboratory populations with PSI (a) and PSS (b) as the hosts and field populations with PSS as the host (c). Bars labeled with different lower-case letters are significantly different at $p=0.05$ from each other in

the same series (mealybug group); bars labeled with “**” or “***” are significantly different at $p=0.05$ or $p=0.01$ between two species of mealybugs, and bars labeled with “ns” are not significantly different at $p=0.05$ between two species of mealybugs at each time point; all multiple comparisons were performed using Tukey’s (HSD) test. Values are the means (+SE) of 5 replicates

Fig. 2 Contact time (a, d), the number of attacks (b, e), and the number of visits (c, f) by *Aenasius arizonensis* (that emerged from different hosts) on two species of invasive mealybugs (PSS: *Phenacoccus solenopsis*; PSI: *Phenacoccus solani*). Mean differences between two species of mealybugs were analyzed by GLM t -test, respectively.

Bars labeled with “**” or “***” are significantly different at $p=0.05$ or $p=0.01$ from each other, and bars labeled with “ns” are not significantly different at $p=0.05$ from each other. Values are the means (+SE) of 5 replicates. Values are the means (+SE) of 15 and 10 replicates for parasitoid emerged from PSS and PSI, respectively

$df=14$, $p=0.004$), and number of visits (4.1 vs. 2.5 times, $t=2.2$, $df=14$, $p=0.041$) were significantly higher than those in *A. arizonensis* that emerged from PSS and parasitized PSI (Fig. 2a, b, and c). When *A. arizonensis* that emerged from PSI parasitized PSS, the contact time (9.2 vs. 7.9 times, $t=0.39$, $df=9$, $p=0.698$) and number of attacks (0.8 vs. 1.0 times, $t=0.33$, $df=9$, $p=0.904$) were not significantly different than those in *A. arizonensis* that emerged from PSI and parasitized PSI (Fig. 2d, e), but the number of visits (4.7 vs. 1.9 times, $t=2.8$, $df=9$, $p=0.014$) was significantly higher in the former than in the latter (Fig. 2f). Additionally, the contact time was influenced by the natal host and mealybug species interaction ($F=8.7$, $df=2$, $p<0.001$); however, there was no significant impact on the number of attacks ($F=1.0$, $df=2$, $p=0.372$) or number of visits ($F=3.1$, $df=2$, $p=0.055$).

There was no significant difference in the frequency of *A. arizonensis* spent at each location (i.e., close to PSS or PSI) regardless of whether the parasitoids emerged from PSS or

PSI (Fig. 3a, $\chi^2=17.0$, $df=14$, $P=0.858$; Fig. 3c, $\chi^2=20.0$, $df=14$, $P>0.788$). However, there was a significant difference in the parasitism rate; the parasitism rate of PSS was higher than that of PSI, regardless of which host the parasitoids emerged (Fig. 3b, d, $F_{1,79}=31.2$, $p<0.001$). There was no statistically significant interaction between mealybug species and host species for the parasitism rate ($F_{1,79}=0.21$, $p=0.652$).

Differences in offspring fitness between *Aenasius arizonensis* emerging from different hosts

The offspring fitness of *A. arizonensis* that emerged from the different hosts is shown in Fig. 4. The emergence time of *A. arizonensis* females that emerged from PSS was shorter than that of females that emerged from PSI (Fig. 4a, $t=2.38$, $df=24$, $p=0.024$), but there was no significant difference between *A. arizonensis* males that emerged from the different hosts (Fig. 4b, $t=0.65$,

Fig. 3 The frequency (%) (a, c) and parasitism rate (%) (b, d) of *Aenasius arizonensis* on the hosts *Phenacoccus solenopsis* (PSS) and *Phenacoccus solani* (PSI). Bars labeled with different lowercase letters are significantly different at $p=0.05$ from each other, and bars

labeled with “***” are significantly different at $p=0.01$ from each other based on Tukey’s (HSD) test. Values are the means (+SE) of 5 replicates for the frequency test and 20 replicates for the parasitism rate test

Fig. 4 Emergence times, longevity, hind tibia lengths, emergence rates, and offspring sex ratios in *Aenasius arizonensis* emerging from the hosts *Phenacoccus solenopsis* (PSS) and *Phenacoccus solani* (PSI). **a**, **c**, and **e** showed the measurements of *A. arizonensis* females, while **b**, **d**, and **f** showed the measurements of *A. arizonensis* males. The sex ratio is the proportion of female to male numbers.

Bars labeled with “*” or “**” are significantly different at $p=0.05$ or $p=0.01$ from each other, and bars labeled with “ns” are not significantly different at $p=0.05$ from each other based on the GLM t -test. Values are the means (+SE) of 25 replicates for emergence times, longevity, and hind tibia lengths test, and 5 replicates for emergence rates and offspring sex ratios test

$df=24$, $p=0.566$). There was a large difference in longevity between *A. arizonensis* females and males that emerged from both hosts (Fig. 4c, $t=9.20$, $df=24$, $p<0.001$; Fig. 4d, $t=13.70$, $df=24$, $p<0.001$). The hind tibia length in *A. arizonensis* females that emerged from PSS was longer than that in *A. arizonensis* females that emerged from PSI (Fig. 4e, $t=5.30$, $df=24$, $p<0.001$), but there was no significant difference between *A. arizonensis* males (Fig. 4f, $t=2.03$, $df=24$, $p=0.051$). The emergence rate of *A. arizonensis* that emerged from PSI was higher than that of *A. arizonensis* that emerged from PSS (Fig. 4g, 97.1% vs. 90.8%, $t=4.84$, $df=4$, $p=0.008$); the offspring sex ratio was not significantly different between the hosts (Fig. 4h, 1.47 vs. 1.39, $t=0.57$, $df=4$, $p=0.540$).

Mealybug body volatile analysis

Chemical analysis of volatiles collected from female adults of PSS and PSI revealed 15 and 21 compounds, respectively, 8 of which overlapped: δ -4-carene, β -phellandrene, (-)- β -elemene, β -caryophyllene, (-)-9-aristolene, α -caryophyllene, cyclopentadecane, and pentadecane. The most abundant compound among these eight compounds in PSS was β -phellandrene, followed by δ -4-carene. However, the most abundant compound in PSI was β -caryophyllene. The relative concentrations of the volatile compounds collected from the two species of mealybugs were significantly different among compounds and between mealybug species (Fig. 5; $F_{7,47}=24.68$, $p<0.001$).

Fig. 5 Average relative content (%) of shared volatile compounds identified from female adult *Phenacoccus solenopsis* (PSS) and *Phenacoccus solani* (PSI). Chromatographic profiles are shown at the top of the bar graph. Codes 1~8 on axis X indicate the volatile compounds δ -4-carene (1), β -phellandrene (2), (-)- β -elemene, β -caryophyllene (4), (-)-9-aristolene, α -caryophyllene, cyclopentadecane, and pentadecane, respectively. Bars labeled with different low-

case letters are significantly different at $p=0.05$ from each other in the same series; bars labeled with “*” or “**” are significantly different at $p=0.05$ or $p=0.01$ between two species of mealybugs, and bars labeled with “ns” are not significantly different at $p=0.05$ between two species of mealybugs for each volatile compound; all multiple comparisons were performed using Tukey’s (HSD) test. Values are the means (+SE) of 3 replicates

Discussion

The lack of natural enemies in newly invaded areas is a key factor in the successful invasion of an alien species (Colautti et al. 2004; Heger and Jeschke 2014). Therefore, researchers have used native parasitoids to parasitize exotic host species for biological control purposes (Zapalá et al. 2012; Golec et al. 2019); however, few studies have focused on whether accompanying parasitoids of invasive pests can be used to control other invasive pests. *A. arizonensis* was considered an obligatory parasitoid of the invasive mealybug, PSS, and it was generally believed

that the parasitoid utilized and completed its development period successfully only on this mealybug in South Asia (Poorani et al. 2009; Fand et al. 2011; Sahito et al. 2011). For example, Shera et al. (2017) indicated that successful parasitization, complete development of immature stages within the host and adult emergence were observed only in PSS, whereas other mealybug species (*Saccharicoccus sacchari*, *Paracoccus marginatus*, *Drosicha mangiferae*, *Nipaecoccus viridis*, and *Ferrisia virgata*) were not found suitable as hosts by the parasitoid in Punjab, India. However, the Universal Chalcidoidea database showed that *Pseudococcus longispinus* (Targioni and Tozzeti) was

also the primary host of *A. arizonensis* (Noyes 2021). The results from this study showed that laboratory-reared and field-collected *A. arizonensis*, which generally parasitizes PSS, can parasitize PSI with 6 h at the most and complete development in female adults only. Therefore, we may need to fully consider the host species, different developmental stages of the host, and the different geographical populations to truly judge the parasitic potential of the parasitoid. Previous studies found that the *A. arizonensis* parasitism rate in PSS in the field can exceed 62%, and even at numerous sites in the southern areas of Israel the parasitism level by *A. arizonensis* was close to 100% (Spodek et al. 2018). These results were consistent with the fact that specialist parasitoids have high host utilization efficiency (Stiling and Comelissen 2005). However, the present study did not support these results, as we found that *A. arizonensis* contacted PSI for the first time and had adapted to PSI hosts for 10 generations had parasitism rates of more than 20%, which were relatively stable. Therefore, we suggest that *A. arizonensis* is not truly a highly specific parasitoid and can expand to new hosts, but the width of the scope of expansion and adaptability to the environment needs further study.

Although *A. arizonensis* can parasitize PSI, it is obvious that the parasitoid significantly preferred to parasitize PSS. The selection preference of parasitoids for different hosts is influenced by the future growth and development of their offspring and resource availability (Harvey et al. 1995; Rivero 2000). In addition, host selection preferences are influenced by differences in parasitic mechanisms (such as paralyzing the host), offspring survival rates, and reproductive ability (Rojas et al. 1999; Gao et al. 2016). Here, we found that if parasitoids emerged from PSS, they preferred to reside around and attack PSS, and the parasitism rate was significantly higher than in those that emerged from PSI. However, the parasitization of the two mealybug species was not affected by natal hosts. We observed that after long-term adaptation (more than 10 generations), the tendency of *A. arizonensis* to parasitize its natural host, PSS, decreased, while its tendency to parasitize the new host, PSI, increased; this is reflected by the contact time and the number of attacks. Learning and contact experience have obvious influences on host location and selection in parasitoids (Giunti et al. 2015), and many specialist parasitoids have shown a stronger learning ability than generalist parasitoids, especially when the host insects feed on multiple plant species (Liu et al. 2003). Therefore, we suggest that the continuous rearing of *A. arizonensis* on the new host, PSI, enhanced host acceptance. However, it seemed that the parasitoids were more efficient in parasitizing their natural host; in other words, the parasitism rate was higher in PSS than in PSI even though the contact time and attack rate of the parasitoid on its original host decreased. This indicated that *A. arizonensis* did not lose its preference for its natural host, similar to *Trichogramma*

dendrolimi after rearing for 12 continuous generations on a nonnatural host (Takada et al. 2001). Shin et al. (1994) also reported a similar phenomenon when *Sitophilus oryzae* was used to rear *Anisopteromalus calandrae* and *Lariophagus distinguendus* in the laboratory; the functional responses and attack rate of the two parasitoids were significantly decreased when they were reared on the nonnatural host *Callosobruchus chinensis*. The introduction of a new pest may cause a rapid change in the host's habits. *Cotesia glomerata* originally parasitized the larvae of *Pieris rapae*; however, after the invasion of *Pieris brassicae*, the parasitism rate of *C. glomerata* in *P. rapae* decreased significantly, while the parasitism rate in *P. brassicae* increased (Tanaka et al. 2007). In conclusion, we suggest that variations in host selection preferences may be caused by differences in the suitability of parasitoids to different host types.

The acceptance and fitness of parasitoids concerning target pests is an important quality evaluation index (Henter and Lenteren 2011). Therefore, by comparing offspring fitness indices, such as emergence time, longevity, and hind tibia length, we found that offspring fitness, especially longevity, was better in offspring emerging from PSS than in those that parasitized PSI. The longevity of the parasitoids emerging from PSS was nearly 20 days longer than that of the parasitoids emerging from PSI. Previous studies have shown that there were significant differences in the longevity of parasitoids emerging from the same host at different developmental stages (Liu et al. 2016) and that longevity varied greatly when adapting to different hosts (Eben et al. 2000). Host size and host quality are significantly correlated with the longevity of parasitoids (Bernal et al. 1999; Häckermann et al. 2007). We suggest that in our study, this result was due to differences in body size or nutrients provided by the two species of mealybugs, which led to obviously reduced longevity in *A. arizonensis* that emerged from the new host. Whether long-term domestication on new hosts can be achieved to improve the longevity of *A. arizonensis* is worth further study. Additionally, we found that the hind tibia length in *A. arizonensis* females that emerged from PSS was longer than that in those that emerged from PSI. The hind tibia length of parasitoids is usually used as an important index to evaluate its size and fecundity, and there is a significant positive correlation (Heimpel and Rosenheim 1995). Consequently, females that emerged from PSS and parasitized PSS were larger, with greater potential for reproduction. Overall, PSI is a relatively poor host for *A. arizonensis* because the offspring fitness of the parasitoids was significantly reduced after development in this host.

However, the emergence rate of *A. arizonensis* was higher in PSI than in PSS. Preliminary observations found that *A. arizonensis* parasitized female adults and second- and third-instar nymphs of PSI but emerged from only parasitized female adults; in addition, mummies that formed in the second- and

third-instar nymphs eventually decayed and deteriorated. This may be due to excessive host body fluids or unsuitable conditions for parasitoid development. The higher emergence rate in PSI female adults may be due to the thinner body wall of the host or the softness of the host's epidermis (Zhao 2004). A thinner host wall is more conducive to the insertion of a parasitoid's ovipositor, reducing energy costs (Boisseau et al. 2017). We suspect that this may be an important reason why *A. arizonensis*, after a short period of adaptation, was attracted to and chose to parasitize PSI to some extent. Previous studies found that parasitoids could detect the quality of their hosts, and males tended to emerge from inferior hosts (Campan and Benrey 2004; Stenberg and Hamback 2010); larger hosts supported more female offspring and larger broods (Bernal et al. 1999). Moreover, the offspring sex ratio is, to some extent, related to the host's developmental stage. For example, the mealybug parasitoid *Anagyrus* spec. nov near *sinope*, which parasitizes third-instar or pre-reproductive adult females, is characterized by a higher proportion of female parasitoids than that from younger nymphs and ovipositing adults because the relative gain in reproductive benefits from increased body size was greater in female progeny than in male progeny (Chong and Oetting 2006). However, Häckermann et al. (2007) found that the sex ratio was not influenced by host species that differed considerably in size. Similarly, we found that the offspring sex ratio in *A. arizonensis* was not significantly different between hosts, which had a significant difference in size. Generally, parasitoids can recognize the physiological condition, size, and age of the host and whether it has already been parasitized. Therefore, what influences *A. arizonensis* to select to deposit a high proportion of female offspring in PSI, which appears to be a poor-quality host, is worth further study.

Specialist parasitoids respond not only to their host but also to some nonhost species that emit similar chemical volatiles (Hedlund et al. 1996); they use this volatile information to make assessments about new hosts and can quickly adapt to changing circumstances (Rolff and Kraaijeveld 2001). However, through the determination and analysis of body volatiles from female adult PSS and PSI, we found that the chemical volatiles emitted by the two species of mealybugs differed. While eight of the chemicals were the same, the concentrations of the compounds were significantly different. The volatiles emitted by mealybugs are mainly derived from powdery wax on the body surface, excreted honeydew, and sex pheromones. However, we observed that the volatiles between the two species of mealybugs were different. Previous studies showed that the waxy secretions of scale insects had obvious attraction effects on host searching and oviposition by natural enemies (Takahashi et al. 1990; Millar and Hare 1993), and the volatiles of wax secretions were different in different scale insects and the same scale insects at different developmental stages (Xie et al. 2004). Here, we

found that the wax powder layer of PSS was thicker than that of PSI according to our observations under a microscope, and the visible wax secretions were distinctly different. Additionally, the frequency and quantity of excreted honeydew were different (PSI is probably not a typical phloem-feeding insect, resulting in very little honeydew, unpublished data); Xu et al. (2020) showed that honeydew produced by PSS was attractive to *A. arizonensis*. Moreover, PSS reproduces sexually, and females release sex pheromones (Tabata and Ichiki 2016), while PSI is a thelytokous parthenogenetic species that does not release sex pheromones. Therefore, we suggest that eight main chemical volatiles with different concentrations are released by PSS and PSI, which may further affect the recognition and learning experience of *A. arizonensis*. However, further biological tests, such as electrophysiological and behavioral tests, are needed to determine which volatiles emitted by mealybugs affect host location in *A. arizonensis* to further validate our conclusion.

arizonensis selected and parasitized a poor-quality host even after exposure to their natural host, resulting in reduced offspring fitness. Because the chemical volatiles released by the two hosts differed, it was unlikely that host volatiles confounded *A. arizonensis* selection. In terms of the degree of attack difficulty, we found that the body size was larger, the abdomen was longer, and the resistance ability against *A. arizonensis* was greater in PSS than in PSI; moreover, PSS could free itself from the grip of *A. arizonensis* by swinging its abdomen up and down. However, host quality is still the priority for parasitoids to choose hosts, but it cannot be ruled out that some individuals choose the host based on availability and ease of parasitism; thus, factors that affect the quality of the offspring may be ignored (Henry et al. 2005). It is also possible that parasitoids accept and parasitize low-quality hosts, not because of an "incomplete" evaluation but because it may be more profitable to parasitize than not to given circumstances (egg load, host encounters, age, etc.). Therefore, we suggest that this accompanying parasitoid of the invasive mealybug PSS (i.e., *A. arizonensis*) can be further domesticated and used to control invasive PSI in the future.

Author contributions

JH and YBL conceived and designed research. JH, FYZ, JZ, and XWL conducted experiments. JH, FYZ, and JZ analyzed data. JH and JZ wrote the manuscript. All authors read and approved the manuscript.

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Declarations

Conflict of interest The authors declare that there are no conflicts of interest.

Ethical approval This article does not contain any studies with human participants and/or animals (other than insects) performed by any of the authors.

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