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Life history and behavior of *Tamarixia triozae* parasitizing the tomato-potato psyllid, *Bactericera cockerelli*

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HIGHLIGHTS

- *Tamarixia triozae* preferred early instar hosts for feeding, and later ones for parasitism.
- Most feeding and parasitism occurred in the week after emergence and declined sharply after two weeks.
- Progeny developing in fourth and fifth instar nymphs were male-biased and female-biased, respectively.
- Offspring developing in later host instars were larger with higher egg loads.

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ABSTRACT

Tamarixia triozae is an important primary parasitoid of the tomato-potato psyllid, *Bactericera cockerelli,* a serious cosmopolitan pest of solanaceous crops. However, without better information about its life history and behavior, it will be difficult to use this parasitoid in effective biological control programs. We carried out a series of experiments to characterize its parasitism, adult feeding, and oviposition behaviors and its sex allocation in response to different life stages of its host, and their fitness consequences. We show that *T. triozae* females fed on all host instars with a preference for mid-aged ones, and preferred to parasitize later instars, thus inflicting mortality on all instars simultaneously. Host feeding and parasitism peaked during the first week of female life and declined markedly after two weeks. Parasitoids allocated more fertilized eggs to older and larger nymphs, and superparasitism declined with increasing host density. The oviposition rate of fertilized eggs peaked when females were four to five days old, with > 90 % of daughters produced during the first half of adult life. The body size and egg loads of progeny increased with increasing host instar at parasitism, demonstrating a positive relationship between the host size and offspring fitness.

1. Introduction

The tomato-potato psyllid (TPP), *Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae), is a serious pest of solanaceous crops native to the United States and Mexico, causing significant losses (Cranshaw, 1994; Crosslin et al., 2010; Butler and Trumble, 2012; Rojas et al., 2015). It has invaded New Zealand, Australia, Canada, and Ecuador, where the assessment of its economic impact is under way (Teulon et al., 2009; Ogden, 2011; FAO, 2017; WADPIRD, 2018; Castillo Carrillo et al., 2019; Olaniyan et al., 2020). The psyllid damages plants by feeding and transmission of zebra chip and other diseases (Munyaneza et al., 2008; Butler and Trumble, 2012; Rojas et al., 2015; Chen et al., 2020). To date, insecticides are still the main tactic for the control of this pest in the field (Munyaneza, 2012; Martinez et al., 2015; Wright et al., 2017). *Tamarixia triozae* (Burks) (Hymenoptera: Eulophidae), which has recently been introduced from Mexico to New Zealand for TTP control (Barnes, 2017), is an important primary ectoparasitoid of the pest (Rojas et al., 2015; Yang et al., 2015). It has a higher population growth potential than its host (Rojas et al., 2015) and about 80 % parasitism rate (Bravo and López, 2007). Furthermore, it is a synovigenic wasp, killing its hosts by both parasitization and host feeding (Martinez et al., 2015; Rojas et al., 2015; Chen et al., 2020, 2022). It can overwinter successfully and establish self-sustaining populations in New Zealand (Anderson, 2020). This parasitoid can thus be highly effective in TTP control, particularly

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in greenhouse crops.

Parasitoids foraging on host plants normally encounter hosts of different stages and sizes. The optimal foraging theory predicts that parasitoid females should adopt the host selection strategies that maximize their lifetime fitness gain (Goubault et al., 2003; Danchin et al., 2008). Many studies show that parasitoids gain better reward in offspring fitness by parasitizing larger hosts because these hosts provide more resources for their offspring (e.g., Liu et al., 2011; Hanan et al., 2015; Luo et al., 2022). However, *T. triozae* neither feed on parasitized hosts nor parasitize fed ones (Cerón-González et al., 2014; CC pers. observ.), suggesting that they must have developed a host partitioning strategy for feeding and parasitization to maximize their offspring's and their own fitness. For example, like other host-feeding parasitoid species (e.g., Kidd and Jervis, 1991; Choi et al., 2001; Ebrahimifar and Jamshidnia, 2022), *T. triozae* females may select smaller hosts for feeding and larger ones for oviposition. Although several authors have examined host stage selections in this parasitoid (Morales et al., 2013; Yang et al., 2015; Ramírez-Ahuja et al., 2017), it is still not clear how *T. triozae* females partition their hosts of different stages for feeding and parasitization when *B. cockerelli* nymphs of all instars are present simultaneously, which is the most likely scenario in the field. This knowledge may contribute to better understanding of host selection for feeding and ovipositon and evaluation of biological control effectiveness of the parasitoid.

Due to the nature of haplodiploidy, female parasitic wasps can control offspring sex ratio by adjusting the proportion of fertilized eggs at oviposition (King, 1988). Previous studies show that they usually allocate more fertilized eggs to larger hosts (e.g., Charnov et al., 1981; Favaro et al., 2018; Pérez-Rodríguez et al., 2019) because their offspring developing from larger hosts have larger body size (e.g., Hanan et al., 2015; Luo et al., 2022) and higher reproductive fitness (e.g., Hanan et al., 2015; Khatri et al., 2016). However, it is not clear how *T. triozae* females allocate the sex of their offspring based on the host stage they attack and whether host stage at parasitization has any effect on their offspring fitness. This knowledge can help design mass rearing programs for effective parasitoid production. Furthermore, although only one offspring survives on each parasitized host, *T. triozae* females often deposit more than one egg under a host (Rojas et al., 2015). To date, it is unknown whether their egg and sex allocation to each host varies with the host stage and density, making it difficult to understand the mechanisms behind their superparasitism.

Parasitoids of different ages may adjust their daily feeding, oviposition and sex allocation patterns in response to host stage, knowledge of which is currently lacking for *T. triozae* but important for the development of effective pest control programs and decision on the timing of releases. In some parasitoids, younger females may have maximal feeding (Zhang et al., 2014) and oviposition (Wade et al., 2008; Bodino et al., 2019), achieving greatest pest suppression soon after release to the field but these activities decline when they are older, reducing biocontrol effectiveness. Mated females may maximize the use of sperm and produce more daughters in their early life (Latham and Mills, 2010; Mawela et al., 2021) to ensure the survival and persistence of their next generation in the field while this reproductive feature may lead to sperm depletion over age, reducing daughter production in their later life (e.g., Pérez-Lachaud and Hardy, 1999; Santolamazza Carbone et al., 2007; Hu et al., 2012).

The aim of this study was to determine parasitoid age- and host stage-dependent host feeding, parasitization and sex allocation and their fitness consequences in *T. triozae*. We exposed mated females of *T. triozae* to *B. cockerelli* nymphs of all instars daily, recorded their lifetime feeding, parasitization, superparasitism and sex allocation on each instar, and established their offspring fitness. Knowledge generated here provides essential information for the development of effective rearing and releasing programs for the control of TTP.

2. Material and methods

2.1. Breeding colony and environmental conditions

We established the colonies of *B. cockerelli* and *T. triozae* using adults from BioForce Limited, Auckland, New Zealand. We utilized the bell pepper (*Capsicum annuum* L.) as host plants for colony maintenance and experiments. To ensure the psyllid colony was parasite-free, we kept psyllid and parasitoid colonies separate in two climate rooms. We reared psyllids on five 2-month-old plants, each in a pot (9.5 cm in height × 10.5 cm in top diameter × 8.5 cm in bottom diameter) with potting mix, in an aluminium-framed cage (43 × 42 × 40 cm) with a metal mesh (aperture size = 0.25 mm × 0.25 mm) on the back and both sides and Perspex on the top and front and aluminium alloy on the bottom. We maintained the parasitoid colony on the 3rd–5th instar psyllid nymphs feeding on five potted, 2-month-old plants in another aluminium-framed cage of the same size. Colonies were maintained and experiments carried out at 25 ± 1 °C, 40–60 % RH and a photoperiod of 14L:10D hours.

2.2. Preparation of insects for experiments

To obtain psyllids of different instars (1st–5th instars) for experiments, we randomly collected about 200 male and female adults from the colony, released them onto two potted, clean, 2-month-old pepper plants in an aluminium-framed cage mentioned above. We allowed adults to lay eggs for 24 h, and then removed all adults from the infested plants using an aspirator and transferred those plants into a nylon mesh-framed cage (65 × 50 × 50 cm, aperture size: 0.075 mm × 0.075 mm). We placed two clean plants of similar conditions into the aluminium-framed cage and repeated the above process daily until we obtained sufficient nymphs of desirable instars for experiments. During this period, we examined the aluminium-framed cage daily and added new adults from the colony to assure there were about 200 adults in the cage. When the nymphs reached the 5th instar on the first two infested plants in the nylon mesh-framed cage, we harvested all nymphs from infested plants in all cages to obtain nymphs of different instars for experiments. We determined nymph instars under a stereomicroscope (Leica MZ12, Germany) according to Vega-Chávez (2010).

To acquire parasitoids for experiments, we randomly collected five females of *T. triozae* from the colony, released them into a plastic cylinder with a bell pepper leaf infested by 100 4th-instar psyllid nymphs and allowed them to stay in the cylinder for 24 h. The cylinder consisted of two identical transparent containers (6.5 cm in diameter × 8.5 cm in height). The bottom container was filled with tap water and covered by a lid bearing a hole (1.0 cm in diameter) at the centre through which we inserted the petiole of the infested leaf. The top container had two holes (3 cm in diameter) covered by a metal mesh at the opposite sides of the wall for ventilation. We set up a total of 10 such cylinders. We collected parasitoid pupae seven days after oviposition and individually placed them in glass vials (5 cm in height × 1.5 cm in diameter) plugged with cotton wools until adult emergence. We individually introduced the newly emerged wasps to the glass vials with a cotton ball saturated with 10 % honey solution as food and maintained them there for 24 h. Because both sexes become sexually mature on the day they emerge (Chen et al., 2020), we individually paired 1-day-old virgin females and males in the glass vials with honey food until mating ended. Mating usually occurs within 90 mins after pairing and lasts about 15 min (CC pers. observ.).

2.3. Effect of host stage on lifetime host feeding and parasitization

To determine lifetime parasitism and host feeding in relation to host stage, we transferred 30 psyllid nymphs of five different instars (6 individuals × 5 instars) onto a pepper leaf with its petiole embedded in water-saturated cotton wool wrapped with parafilm in a Petri dish (8.5 cm in diameter × 2.4 cm in height). We covered the dish with the lid bearing two holes (1 cm in diameter), one covered with metal mesh for ventilation and one with a cotton wool plug for introducing wasps. We introduced a 1-d-old mated female parasitoid into the dish and allowed it to stay for 24 h. We then transferred the wasp to another dish with a leaf and 30 fresh psyllid nymphs as above and allowed it to stay for 24 h. We repeated this process until the wasp died, which lasted about 20 days. During the experiment, psyllid nymphs were the only food for the wasp and each wasp was exposed to more than 600 nymphs in its lifetime. A cotton ball saturated with water was provided to the wasp and refreshed every day. We tested 18 female wasps, each of which was considered a replicate.

For each replicate, we examined all dishes after removing the wasp and recorded the number and instar of hosts fed and parasitized, and number of eggs laid under the stereomicroscope. Host feeding was determined by the presence of body fluid (Martinez et al., 2015) or an inverted V-shape mark on the hollowed body (Morales et al., 2013). During oviposition female wasps paralyse psyllid nymphs and then deposit eggs on the ventral side of the hosts and secret adhesive substance to attach the eggs to the host cuticle (Martinez et al., 2015). Therefore, we turned over all host nymphs and put them on the surface of 1 % agar to determine oviposition and counted the number of eggs laid under each parasitized nymph.

2.4. *Effect of host stage at parasitization on parasitoid offspring fitness*

We separated the parasitized nymphs according to their instars in each dish. We then transferred those of the same instar onto a randomly selected leaf on a potted, 2-month-old pepper plant in a nylon mesh-framed cage. Immediately after the transfer of psyllid nymphs, we enclosed the leaf with a transparent resealable plastic bag (17.5 cm in length × 10 cm in width) bearing small holes made by insect pins for ventilation and filled the space between the leaf petiole and the zip seal of the bag with cotton wool. Parasitoid pupae were collected seven days after parasitism and individually placed in the glass vials plugged with cotton wool until emergence. For a given host instar, the emergence rate was calculated as the number of emerged offspring divided by the number of hosts parasitized. The developmental time from egg to adult emergence and sex of emerged wasps were recorded.

To measure the effect of host instar at parasitization on the body size of parasitoid offspring at emergence, we randomly sampled 19 and 30 newly emerged females from the 4th and 5th instar nymphs (no females emerged from the 3rd instar – see Results), and 12, 30 and 28 newly emerged males from the 3rd, 4th and 5th instar nymphs (no 1st and 2nd nymphs were parasitized – see Results), respectively. We measured the hind tibial length of these adults as an index of body size (Khatri et al., 2016) under the stereomicroscope. To determine the egg load of newly emerged females, after tibial measurement we dissected these females in 70 % alcohol on a slide under the stereomicroscope. Because immature eggs absorb the stain while mature eggs prevent the stain (Edwards, 1954), we added one droplet of stain (1 % acetocarmine) into the alcohol. The ovaries were covered with a slide cover, spread by gently pressing 3–5 min after staining and eggs counted under the stereomicroscope. The number of mature eggs in the ovaries was recorded as egg load at emergence.

2.5. *Statistical analysis*

We performed all analyses using SAS 9.4 (SAS Institute Inc., NC, USA). Because our data were not normally distributed (Shapiro-Wilk test, UNIVARIATE Procedure), we used a generalized linear model (GLIMMIX procedure) to analyze them with the instar as a fixed factor and the replicate as a random factor in the model. A Gamma distribution and a log function were applied to the number of eggs laid under each parasitized nymph, developmental time and hind tibial length; a Poisson distribution and a log function to the lifetime number of hosts fed and parasitized, number of eggs laid, and egg load, and a Binomial distribution and a *logit* function to the emergence rate and proportion of daughters produced. A Tukey-Kramer test was used for multiple comparisons between the instars.

According to Archontoulis and Miguez (2015), we developed two Gaussian functional models, $y = a\, e^{(-0.5\{[(x-c)-(x_0-c)]/b\}^2)}$, to fit the daily host feeding on nymphs of different instars, and $y = a\, e^{(-0.5\{\ln[(x-c)/(x_0-c)]/b\}^2)}$, to fit the daily number of parasitism on and daughter emergence from nymphs of different instars, where x is the age of female wasps (days), a is the peak at age x_0, b is the coefficient controlling the width of the peak, and c (=1 day) is the time before the females got access to hosts. The difference in each estimated parameter in the Gaussian functional models was compared between treatments: if the 95 % confidence limits (CLs) overlap, then there is no significant difference. We did not fit the data on host feeding for the 1st and 5th instar nymphs, and on parasitism and daughter emergence for 3rd instar nymphs because only a few 1st and 5th instar nymphs were fed, few 3rd instar nymphs were parasitized, and no daughter emerged from the 3rd instar nymphs.

3. Results

3.1. *Effect of host stage on lifetime host feeding and parasitization*

The female parasitoids fed on hosts of all instars but significantly preferred the 2nd, 3rd and 4th to the 1st and 5th instar nymphs for feeding with the highest number of the 3rd instar nymphs fed ($F_{4,68}$ = 241.19, P < 0.0001) (Fig. 1a). They significantly preferred the 4th and 5th to the 3rd instar nymphs for oviposition with the highest number of parasitism and eggs laid on the 5th instar nymphs ($F_{2,34}$ = 213.56, P < 0.0001 for parasitism; $F_{2,34}$ = 314.12, P < 0.0001 for eggs laid) but did not parasitize the 1st and 2nd instar nymphs (Fig. 1b). Furthermore, the parasitoids deposited significantly more eggs under the 4th and 5th instar nymphs (1.34 and 1.47 eggs per nymph, respectively) than under the 3rd instar nymphs (1.11 eggs per nymph) ($F_{2,27}$ = 6.46, P = 0.0051).

Daily host feeding and parasitization patterns varied with host stage and parasitoid age (Fig. 2, Table S1). Daily number of hosts fed by parasitoids on the 3rd and 2nd instar nymphs peaked about six and seven days after emergence, respectively, significantly earlier than that

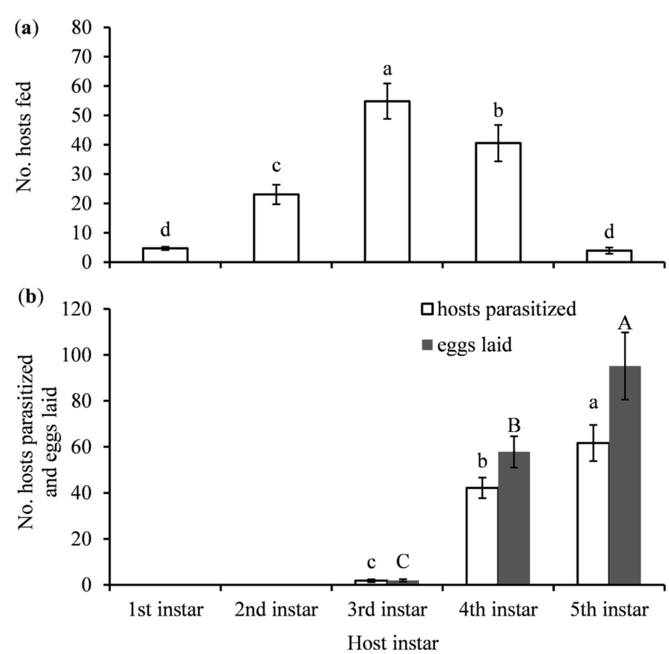

Fig. 1. Mean (±SE) lifetime number of hosts fed (**a**), parasitized and eggs laid (**b**) by *T. triozae* on *B. cockerelli* nymphs of different instars. Columns with different letters are significantly different (P < 0.05).

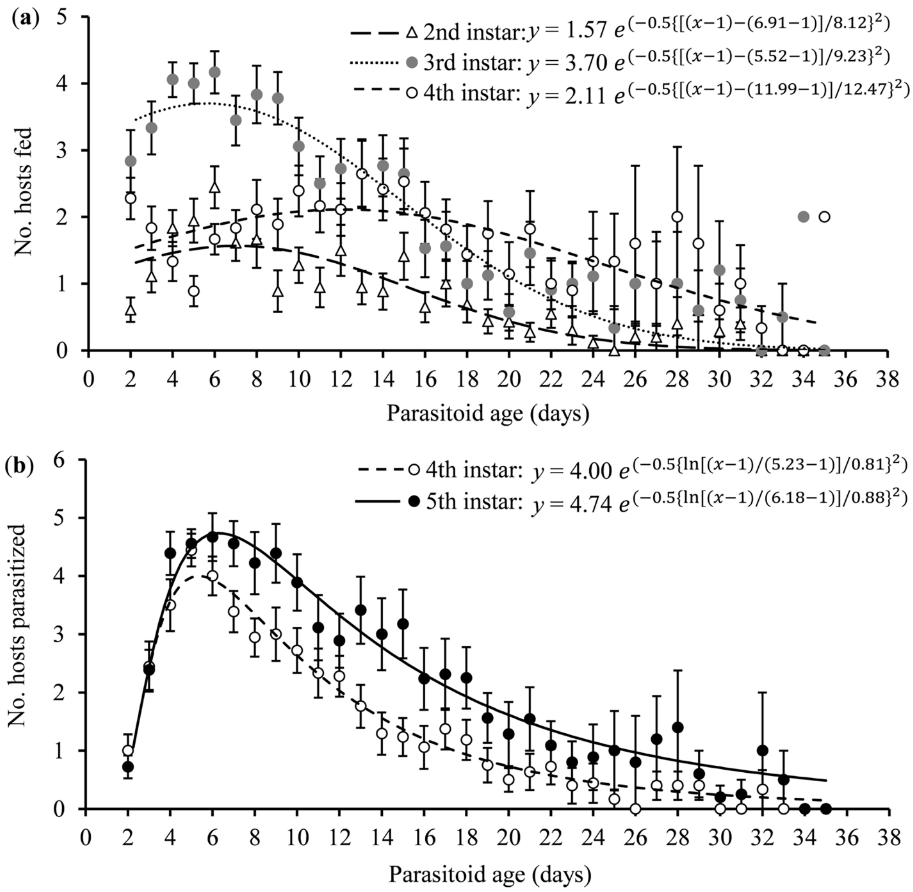

Fig. 2. Mean (±SE) daily number of hosts fed (**a**) and parasitized (**b**) by *T. triozae* females on *B. cockerelli* nymphs of different instars.

on the 4th instar nymphs which peaked about 12 days after emergence (non-overlapping 95 % CLs). The host feeding peak on the 3rd instar nymphs was significantly higher than that on other nymph stages (non-overlapping 95 % CLs). Daily parasitism on the 4th instar nymphs peaked about five days after emergence, significantly earlier than that on the 5th instar nymphs which peaked about six days after emergence (non-overlapping 95 % CLs). The parasitism peak on the 5th instar nymphs was significantly higher than that on the 4th instar nymphs (non-overlapping 95 % CLs). However, there was no significant difference in the width of daily host feeding and parasitism curves between instars (overlapping 95 % CLs).

3.2. Effect of host stage at parasitization on parasitoid offspring fitness

The emergence rate of parasitoid offspring significantly increased with the increase of host instars at parasitization ($F_{2,27} = 21.75$, $P < 0.0001$) (Fig. 3a). Both sons and daughters emerged from hosts parasitized at the 4th and 5th instars while only sons emerged from those parasitized at the 3rd instar. Emerged offspring were male-biased if the parasitoids parasitized the 4th instar nymphs but female-biased if parasitization occurred at the 5th instar ($F_{2,23} = 71.55$, $P < 0.0001$) (Fig. 3b). We show that both host stage and parasitoid age at parasitization affected parasitoid daughter emergence patterns (Fig. 4, Table S2). The highest number of daughters emerged from the 4th instar nymphs parasitized by 4-d-old parasitoids while that occurred from the 5th instar nymphs parasitized by 5-d-old parasitoids (non-overlapping 95 % CLs). Daughter emergence peak from the 5th instar nymphs was significantly higher than that from the 4th instar nymphs (non-overlapping 95 % CLs). However, there was no significant difference in peak width between the two instars (overlapping 95 % CLs). Furthermore, 90 % of daughters were produced from the 4th and 5th instar nymphs by

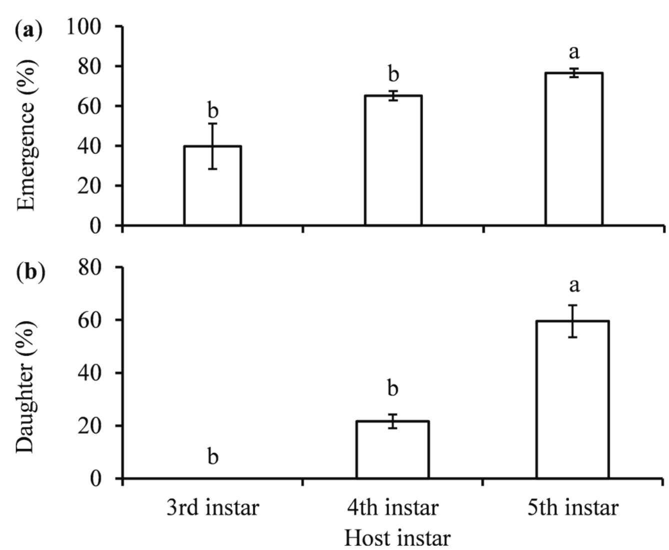

Fig. 3. Mean (±SE) emergence rate (**a**) and daughter percentage (**b**) of *T. triozae* offspring that developed from *B. cockerelli* nymphs parasitized at different instars. Columns with different letters are significantly different ($P < 0.05$).

the parasitoids of 3–11 days old.

Sons required significantly longer time to complete development on the 3rd instar than on the 4th and 5th instar nymphs (Developmental time: mean ± SE = 10.07 ± 0.05, 9.58 ± 0.04 and 9.74 ± 0.07 days for the 3rd, 4th and 5th instars, respectively; $F_{2,23} = 8.13$, $P = 0.0021$) but

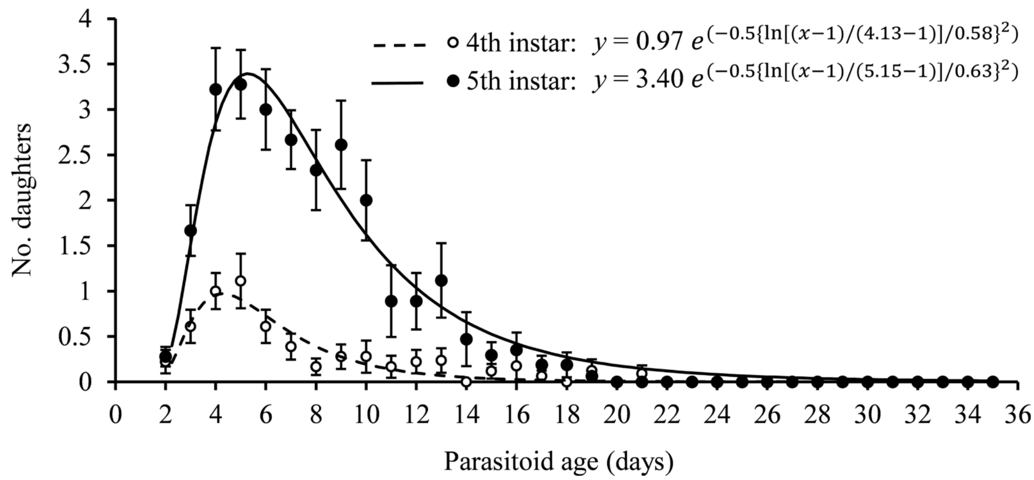

Fig. 4. Mean (±SE) number of daughters emerging from *B. cockerelli* nymphs of different instars parasitized by *T. triozae* over lifetime.

the host stage at parasitization had no impact on daughter developmental time (Developmental time: mean ± SE = 10.00 ± 0.05 and 10.06 ± 0.05 days for the 4th and 5th instars, respectively; $F_{1,17} = 0.83$, $P = 0.3749$). Daughters needed significantly longer time to complete development than sons regardless of the host stage parasitized ($F_{1,17} = 53.15$, $P < 0.0001$ for the 4th instar; $F_{1,17} = 11.04$, $P = 0.0040$ for the 5th instar). There was no significant interaction between the host stage parasitized and sex of emerged offspring in their effects on developmental period ($x_1^2 = 1.02$, $P = 0.3115$).

Offspring body size of both sexes significantly increased with the increase of the host stage at parasitization (Tibial length of sons: mean ± SE = 129.07 ± 3.47, 160.87 ± 1.67 and 190.82 ± 3.00 μm for the 3rd, 4th and 5th instars, respectively; $F_{2,38} = 86.24$, $P < 0.0001$. Tibial length of daughters: mean ± SE = 170.06 ± 1.98 and 203.45 ± 1.82 μm for the 4th and 5th instars, respectively; $F_{1,18} = 99.53$, $P < 0.0001$), and regardless of host stage at parasitization, daughters were significantly larger than sons ($F_{1,18} = 13.52$, $P = 0.0017$ for the 4th instar; $F_{1,27} = 13.38$, $P = 0.0011$ for the 5th instar). There was also no significant interaction between the host stage parasitized and sex of emerged offspring in their effects on offspring body size ($x_1^2 = 0.11$, $P = 0.7420$). In addition, newly emerged daughters from hosts parasitized at the 5th instar had significantly higher egg load than those from hosts parasitized at the 4th instar (Egg load: mean ± SE = 0.05 ± 0.05 and 1.67 ± 0.27 for the 4th and 5th instars, respectively; $F_{1,18} = 13.19$, $P = 0.0019$).

4. Discussion

We demonstrate that *T. triozae* females partitioned hosts of different instars for feeding and parasitization. When all instars of *B. cockerelli* nymphs were present, which should be the most common scenario in the field, the parasitoids preferred mid-aged nymphs for feeding and older for parasitization. Because the parasitoids need to pierce the hosts with ovipositors before feeding or parasitization (Martinez et al., 2015; Rojas et al., 2015) and do not parasitize fed hosts (Cerón-González et al., 2014), they rationalize their effort for optimal fitness gain for both mothers and their offspring. Older hosts are more nutritious for parasitoid offspring development (Li and Mills, 2004; Liu et al., 2011) but more difficult to punctuate (Kidd and Jervis, 1991; Zhang et al., 2015) due to their thicker integument (Veronesi et al., 2022) and defensive behaviour (Liu et al., 2011). Therefore, they choose to feed on younger hosts and parasitize older ones, consistent with the optimal foraging theory (Kishani Farahani et al., 2015). As both adult feeding and parasitization destroy the hosts (Martinez et al., 2015; Rojas et al., 2015), the host partitioning behavior may allow the parasitoids to control the pest effectively by killing hosts of different life stages simultaneously.

Although only one offspring survives on each parasitized host (Rojas et al., 2015), *T. triozae* females deposited more than one egg under a host with more eggs allocated to older nymphs. This host stage-dependent egg investment may help increase parasitoid offspring survival because the offspring from older nymphs at parasitization were more likely to develop to adults. Comparing the findings between the current and Rojas et al.'s (2015) studies, we found that the egg allocation was also host density dependent. In the current study, the parasitoids deposited an average of 1.4 eggs per host of the 4th or 5th instar while they laid about 1.15 eggs under each host when the density of the same stage nymphs was twice as that in our study (Rojas et al., 2015). These findings suggest: (1) when the number of nymphs suitable for parasitization is lower, the parasitoid may increase superparasitism to avoid collapse of the host population for the survival of future generations, but (2) when the number of nymphs suitable for parasitization is higher, the parasitoid may reduce superparasitism to maximize the use of available resources. This behavior may make the parasitoids more effective and persistent in the field.

Our results indicate that *T. triozae* females adjusted their daily feeding and parasitization patterns in response to host stage and their own age. They mainly fed on the 3rd nymphs in their early life when they had maximum parasitism on the 4th and 5th instar hosts but they increased their feeding on the 4th instar nymphs after they reached mid-age and their parasitism sharply declined. The increase of feeding on more nutritious 4th instar nymphs at older age is probably due to the combination of declined fecundity and increased demand of nutrition for adult survival. Overall, *T. triozae* completed 90 % of their lifetime feeding and parasitism when they were 17 days old. Because our experimental condition (25 °C) is optimal for the development of both *B. cockerelli* (Lewis et al., 2015) and *T. triozae* (Vega-Chávez et al., 2016), our findings may provide important knowledge for development of field release programs for biological control of TPP under similar conditions.

The present study reveals that although *T. triozae* preferred to parasitize the 4th and 5th instar nymphs, adults emerged from the 4th instar nymphs at parasitization were highly male-biased and those from the 5th instar nymphs were highly female-biased. These results strongly imply that the parasitoids allocate significantly more fertilized eggs to the oldest and largest nymphs, which was also reported in other parasitoids (e.g., Charnov et al., 1981; Favaro et al., 2018; Pérez-Rodríguez et al., 2019). Using the 5th instar nymphs as hosts for *T. triozae* during mass rearing may thus increase daughter production and reduce rearing cost. The sex allocation patterns also shifted with the age of parasitoids, i.e., females laid the highest number of fertilized eggs per day when they were four to five days old, with > 90 % of daughters produced during their first half of life. We suggest that the females may maximize the use of sperm in their early life to ensure the survival and persistence of their next generation in the field. As a result, they may quickly run out of sperm as they age (Pérez-Lachaud and Hardy, 1999; Santolamazza Carbone et al., 2007; Hu et al., 2012) and after they reach mid-age, they produce male-biased offspring.

We show that regardless of the host stage at parasitization, females had longer developmental time and larger body than males, suggesting that females need more resources and time to build up larger body size for reproduction (King, 1988, 2000; He et al., 2005). Like other parasitoids (e.g., Liu et al., 2011; Hanan et al., 2015; Luo et al., 2022), the host stage affected offspring body size of both sexes in *T. triozae*, which increased with the increase of the host age at parasitization. Furthermore, newly emerged daughters from hosts parasitized at the 5th instar carried more mature egg than those from hosts parasitized at the 4th instar. Although we have not measured male reproductive potential, other studies show that larger parasitoid males mate more times (Ji et al., 2004; Lacoume et al., 2006) and produce more sperm (He and Wang, 2006; Kant et al., 2012). In accordance with other parasitoids (e.g., Hu et al., 2002; Hanan et al., 2015; Li et al., 2018), larger and older hosts increase the fitness of *T. triozae* offspring.

In conclusion, *T. triozae* females adjust their behaviors in response to host stage and their own age. They feed on hosts of all instars with a preference for mid-aged ones and almost always parasitize late instar hosts, thus inflicting mortality on all instars simultaneously. The parasitoids increase and reduce superparasitism at lower and at higher host density, respectively. This may help maintain their own population in the field. Maximum feeding and parasitization occur during the first week of their life and these activities sharply decline when they are two weeks old. The parasitoids allocate more fertilized eggs to the oldest and largest nymphs. They lay the highest number of fertilized eggs per day when they are four to five days old, with > 90 % of daughters produced during their first half of life. Parasitoids' offspring body size and egg load increase with the increase of host instar at parasitization, demonstrating a positive relationship between host size and offspring fitness.

CRediT authorship contribution statement

Chen Chen: Conceptualization, Methodology, Investigation, Formal analysis, Writing – original draft, Writing – review & editing. **Xiong Z. He:** Conceptualization, Methodology, Formal analysis, Writing – review & editing. **Peng Zhou:** Investigation, Formal analysis, Writing – review & editing. **Qiao Wang:** Conceptualization, Methodology, Formal analysis, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Availability of data and material

The datasets from the current study are available from the corresponding author on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocontrol.2023.105152.

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