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Effect of host feeding on life traits of *Tamarixia radiata* (Hymenoptera: Eulophidae), parasitoid
of the Asian citrus psyllid

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ABSTRACT

The parasitoid *Tamarixia radiata* (Waterston) (Hymenoptera: Eulophidae) is being used worldwide for the biological control the Asian citrus psyllid (ACP), *Diaphorina citri* Kuwayama (Hemiptera: Liviidae). The parasitoid is strongly synovigenic, as it is born with very few mature eggs. Synovigenic insects need to feed on host haemolymph in order to mature additional eggs, and are able to resorb mature eggs in order to allocate resources toward maintenance. We investigated the effect of host feeding on parasitism behavior, longevity and egg load dynamics, and estimated egg maturation and resorption rates. We showed that, whilst host feeding does not increase survival or longevity, it results in increased parasitization rates when parasitoids are seven days old, and that a single host meal leads to an average gain of three eggs. We discuss the importance of these data to predict the foraging and parasitization behavior of *T. radiata* into the field, and to potentially improve current efforts to control ACP, for example by exploiting the host feeding gains to improve the nutritional status of mass reared *T. radiata* females upon release.

INTRODUCTION

As the foraging behavior is one of the main contributors to oviposition decisions made by natural enemies, behavioral ecology can inform the practice of biological control (Mills and Heimpel 2018), and help making it a more predictive science. Synovigenic parasitoids emerge as adults

with few mature eggs ready to be laid, but are able to mature additional eggs by using the nutritional resources accumulated as larva and by acquiring proteins and lipids through feeding on host haemolymph and tissues (Heimpel and Collier 1996; Jervis and Kidd 1986). Larval reserves become quickly exhausted (Rivero and West 2002), hence host feeding is essential to reproductive success. However, in using a host for food, the wasp is foregoing an immediate gain in her lifetime reproductive success for nutrients that can be used to mature more eggs or energy that may enable her to search for more hosts. Therefore there is a dynamic trade-off between current and future reproduction, and this dilemma is influenced by the parasitoid's physiology, nutritional reserves, life expectancy, experience, and by environmental conditions, such as host availability, host quality and mortality risk (e.g., predation). The effect of these physiological and environmental factors has been addressed by a number of dynamic state-variable models (e.g. (Chan and Godfray 1993; Heimpel and Collier 1996; Mangel and Heimpel 1998; Rosenheim 1999; Rosenheim et al. 2000) and empirical studies (e.g., (Collier 1995; Heimpel et al. 1998; Heimpel and Rosenheim 1995; Heimpel et al. 1997). The general paradigm is that higher egg loads, decreasing life expectancy and decreasing host availability lead to behaviors favoring current over future reproduction, and that host feeding should occur when egg reserves are low (Heimpel and Rosenheim 1995).

Due to environmental stochasticity, females may die before exhausting their eggs when hosts are rare, or exhaust their eggs before dying when hosts are abundant (Rosenheim 2011). Egg limitation is particularly acute in synovigenic species, which are able to resorb eggs to get energy for survival (Jervis et al. 2001), at the expense of oviposition, as a female that is resorbing eggs might be unable to oviposit even if the host is available, with a destabilizing effect on host-parasitoid equilibrium (Briggs et al. 1995). Therefore, avoiding or limiting oosorption could

improve the efficacy of a synovigenic parasitoid. Egg resorption may be partially or totally avoided by increasing the egg load through host feeding. However, high rates of host feeding by an egg limited parasitoid at low host density may hinder establishment and performance. An increase in egg load at emergence and a decrease in the egg maturation rate can reduce the need for host feeding and mitigate the negative effect of oosorption on biological control (Shea et al. 1996; Vanaclocha et al. 2014). Therefore, providing a mass reared synovigenic parasitoid the opportunity to host feed upon emergence may ensure that their ability to increase the egg load would be enhanced or maintained during pre-release storage.

Tamarixia radiata (Waterston) (Hymenoptera: Eulophidae) represent an ideal model to test the effect of host feeding on a mass reared augmentative biological control agent. *T. radiata* is a solitary arrhenotokous ectoparasitoid of the Asian citrus psyllid (ACP), *Diaphorina citri* Kuwayama (Hemiptera: Liviidae), an important citrus pest that vectors *Candidatus Liberibacter asiaticus* (CLAs), a bacterium that causes the lethal ~~and incurable~~ citrus greening disease, also known as huanglongbing (HLB) (Bové 2006). Native to the Indian subcontinent, *T. radiata* has been and is being used as biological control agent in all areas where ACP has spread (Tena et al. 2017). However, average year-round parasitism by *T. radiata* are generally very low in Florida and California, although parasitism rates vary greatly depending on location and time of year (Kistner et al. 2016; Qureshi et al. 2009). A better understanding of the foraging behavior of this parasitoid could translate into better performance in the field. *T. radiata* is a strongly synovigenic parasitoid born with few mature eggs (Chen and Stansly 2014a) that performs non-concurrent destructive host feeding, that is, feeds and parasitizes different nymphal stages (2nd and 3rd versus 3rd, 4th and 5th instar, respectively), and is able to resorb eggs in the absence of host food (Chen and Stansly 2014b). *T. radiata* has been mass reared at the University of California,

Riverside (UCR) since 2011 (Hoddle and Hoddle 2013), and released as part of augmentative biological control programs in California and Arizona. Mass rearing involves temporary storage of the wasps, and in California *T. radiata* harvested from mass-rearing cages are held in small containers with honey prior to field releases for up to seven days (David Morgan, pers. comm.) As food provided to females during the holding period may affect the number of eggs formed in ovaries, and in turn parasitization efficiency upon release, pre-release conditioning should aim at maximizing the fitness of parasitoids. Chen and Stansly (2014b) evaluated eight holding diets for *T. radiata*, concluding that none of the artificial diet could match the benefits of host haemolymph on egg load. Tena et al. (2017) showed that in the laboratory non-host deprived *T. radiata* females were over twice as likely to oviposit than host-deprived females and did not need to host feed when offered a patch of host nymphs, whereas host-deprived females tended to host feed and abandon host patches without parasitizing, and speculated that this behavior could be due to lack of mature eggs or the need to rest after host feeding.

The present study aimed at better understanding the impact of host feeding on the biology of *T. radiata*. We first evaluated how a set number of host meals affect parasitization behavior, then assessed the impact of host feeding on longevity, studied the egg load dynamics as affected also by size and age, and estimated egg maturation and resorption rates. These parameters are fundamental to predict the foraging behavior and potentially optimize the performance of *T. radiata* in the field.

MATERIAL AND METHODS

Experimental arenas

Tamarixia radiata wasps were sourced from a mass rearing culture established in 2011 at the Insectary & Quarantine facility of UCR (Hoddle, 2012). Wasps were aspirated from the rearing

cages in the early morning until the cages were emptied, and newly emerged females were collected within two hours, and if necessary at 2 hour-intervals afterwards. Females were then randomly assigned to three diets: 1) single host feeding: a single female was placed in a plastic vial (2.5 x 5.2 cm) and provided with a drop of honey and a second instar *D. citri* nymph on a *M. koenigii* seedling (< 2 cm) whose root (between 0.5 to 1.5 cm) was wrapped in a moist cotton ball covered by a thin layer of aquarium sand; 2) multiple host feeding: a female was put in the same test unit but it was provided with three second instar *D. citri* nymphs and left in the plastic vial for three days; 3) honey (control diet): a single female was kept in a glass vial (0.8 cm x 3.0 cm) with a drop of honey. After the host feeding exposure time, nymphs were coded as alive, dead with signs of host-feeding (nymph completely emptied) or without obvious signs, and only females taken from vials with nymphs showing clear signs of host feeding were transferred to a small glass vial with a drop of honey until use.

Effect of host feeding on parasitism rates

Each host-fed wasp was introduced in a Petri dish (60 mm Ø) containing a *M. koenigii* leaf placed into an Eppendorf vial (0.5 mL) filled with water and capped with a small cotton ball and infested with 20 fourth instar *D. citri* nymphs. The wasps from each treatment were introduced at three days old (i.e., right after checking for host feeding in the multiple host feeding treatment, and two days after host feeding for the single host feeding treatment) or seven days old. After 24 hours the wasps were transferred into a glass vial and killed at -20°C for dissection (see below) aimed at checking the number of mature eggs left in the abdomen. Parasitism was checked after five days from the introduction of parasitoids, and compared by ANOVA test.

Effect of single and multiple host feeding on survival.

In this experiment, we examined longevity and survivorship of *T. radiata* given only honey or honey, one or up to three second instar nymphs. At the end of the host feeding exposure period, all females were singly kept with honey at $27\pm 1^\circ\text{C}$, $50\pm 10\%$ RH and a photoperiod of 16:8 (L:D hours). Vials were checked daily, honey was added when necessary, and the date of female death was recorded. At least 20 females per diet treatment were evaluated. Cox regression was used to compare survival of *T. radiata* among treatments calculated using the Kaplan and Maier curves.

Effect of a single host feeding meal on egg load dynamics

Females of *T. radiata* fed honey only or honey + a single second instar *D. citri* nymph and kept at 18°C , which is the pre-release storage temperature, after the first 24 hours (host feeding exposure time) were killed at -20°C every day and dissected. Twenty females were frozen right after collection from the mass rearing cages to assess the egg load at emergence. The hind tibia length was measured as proxy for wasp size by using a Zeiss Axioskop 40 microscope at 10x magnification before dissection. Then a drop of water was added onto the female, which was then covered by a coverslip, and mature eggs were squeezed out of the abdomen by exerting a light pressure on the thorax with a pair of pins and counted. At least 21 females were dissected per time point per diet. Given a positive correlation between wasp size and egg load (see results), data were analyzed by ANCOVA using the *lm* function in the statistical software package “R” (<http://www.R-project.org>), with diet and age as factors, size as covariate, and egg load as response variable. Prior to the analysis, the assumptions of normality, homoscedasticity, and equality (i.e., interaction terms not significant) and linearity of slopes (i.e., trend lines roughly equal) were checked. Model simplification to find the minimal most adequate model was carried out starting from the most complex model including interactions among all terms.

RESULTS

A total of 1,184 *T. radiata* wasps were given the opportunity to host feed once or multiple times to assess parasitism rates, survival and egg load dynamics. Of 1,005 wasps that were set up for single host feeding, 32.9% (n= 331) host fed and 11.3% (n= 114) showed ambiguous signs that could have resulted from probing or non-destructive host feeding, hence discarded. Of 179 wasps set up for multiple host feeding, 67.6% (n=121) host fed on two (36.31%) or three (31.3%) second instar nymphs.

Effect of host feeding on parasitism rates

Parasitism rates achieved by 3-day old *T. radiata* females were similar among diets (honey = 0.2 ± 0.024 SE; honey and single host feeding = 0.208 ± 0.034 SE; honey and multiple host feeding = 0.256 ± 0.041 SE) ($F_{2, 72} = 0.469$, $P = 0.627$). However, parasitism rates by 7-day old wasps that host fed once or multiple times were higher than those of wasps fed only honey ($F_{2, 97} = 15.614$, $P < 0.001$) (Figure 2A). The maximum parasitism rates achieved on this experimental arena were 0.5, 0.7 and 0.75 for the wasps exposed to honey, honey + one nymph or honey + two or three nymphs, respectively. The egg load did not differ among 3-day old wasps ($F_{2, 72} = 0.637$, $P = 0.532$), whereas when the wasps were 7-day old the egg load was higher in both host feeding treatments than for the honey diet ($F_{2, 97} = 10.417$, $P < 0.001$), without difference between the two host feeding treatments (single host feeding = 3.876 ± 0.218 SE eggs; multiple host feeding = 3.752 ± 0.217 SE eggs) (Figure 2B). The fraction of eggs used for parasitization was similar among diets at both time points (3-day old: $F_{2, 72} = 2.524$, $P = 0.087$; 7-day old: $F_{2, 97} = 0.9$, $P = 0.41$) (Figure 2C).

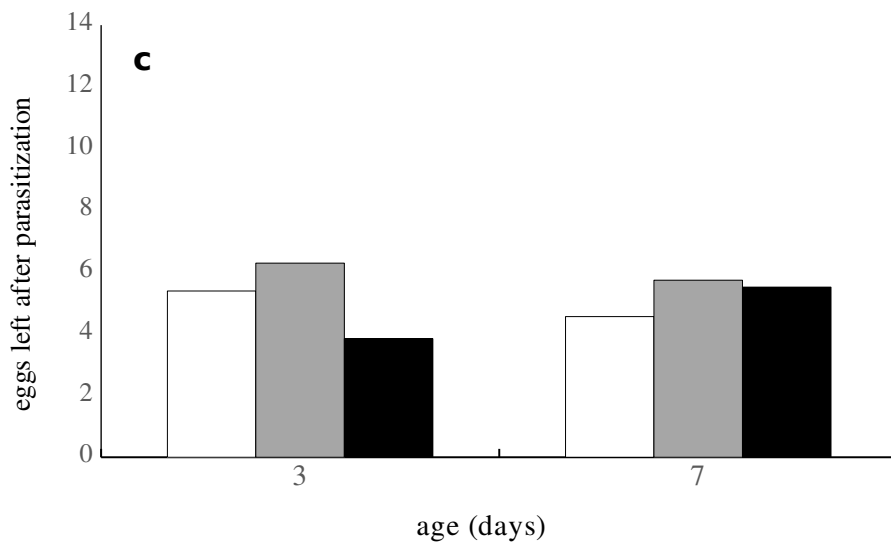
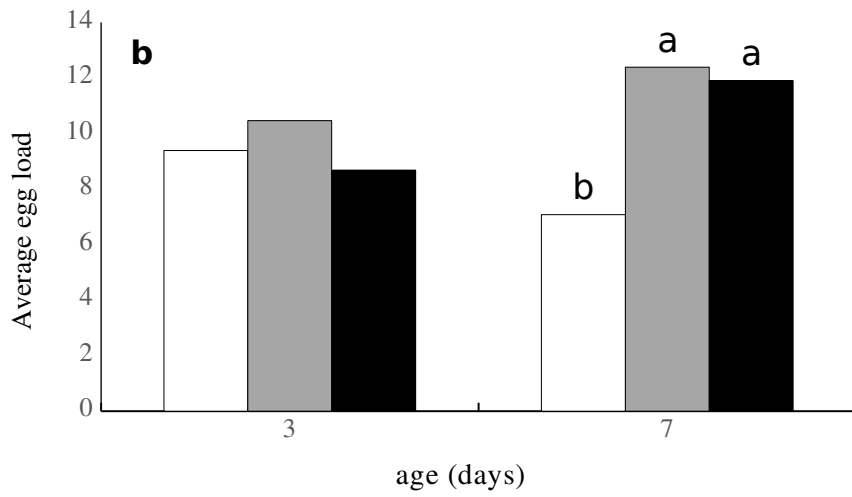
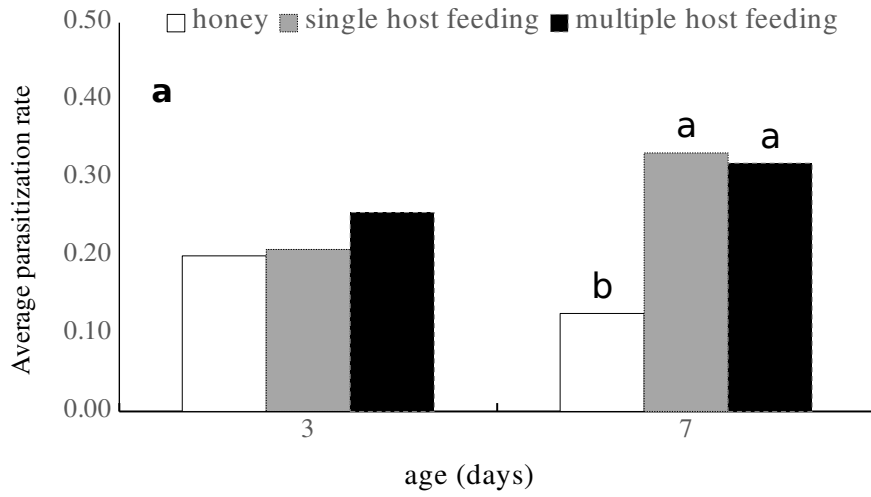


Figure 1. Effect of host feeding on parasitism rates by *T. radiata* (A), egg load (B) and eggs left after parasitization (C) at two different ages (3 and 7 days old); honey (3do: n=26; 7do: n=27), single host feeding (3do: n=24; 7do: n=34) and multiple host feeding (3do: n=26; 7do: n=39). Different letters indicate significant differences.

Effect of single and multiple host feeding on survival.

Survival of *T. radiata* did not differ among treatments (Wald test = 1.45, $P = 0.485$) (Fig. 1). The maximum longevity was 44, 53 and 46 days for honey, single and multiple host feeding diet, respectively. Females that host fed once lived in average for 19.6 (± 2.98 SE) days, females that host fed at least twice for 18.6 (± 1.83 SE) days, and females fed only honey for 18.1 (± 1.33 SE) days. There was no effect of the wasp size on longevity ($F_{1, 91}=0.069$, $P = 0.792$).

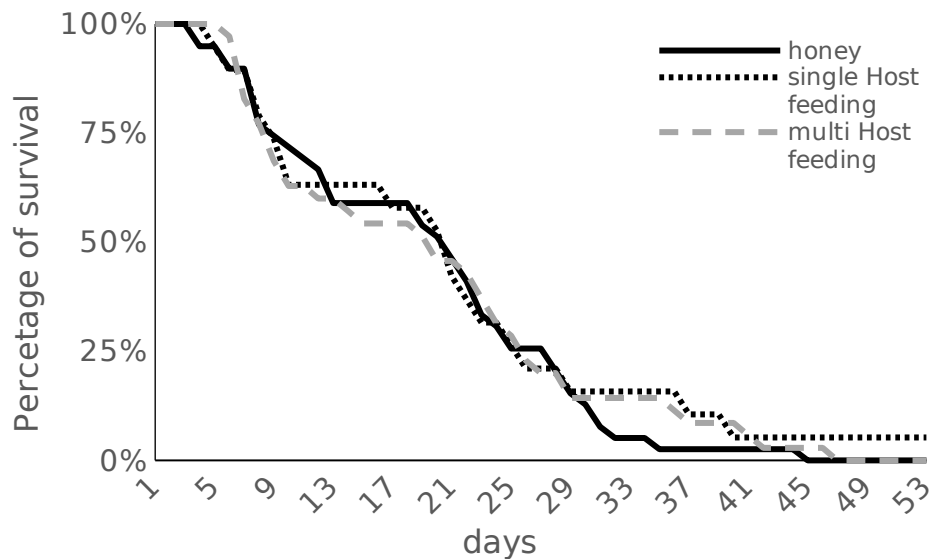


Figure 2. Survival curves for *T. radiata* females feed on three different diets; honey only (n=39), honey + one host feeding (n=19) and honey + multiple host feeding (n=35).

Effect of a single host feeding meal on egg load.

Females of *T. radiata* emerged with an average of about five eggs (4.74 ± 0.63 SE). The average egg load peaked at day 3 for both diets. Providing honey only, females matured about seven eggs on the first two days of life, and one host feeding meal on a second instar *D. citri* nymph resulted in the maturation of about three additional eggs over the same time period. At age four, females started to resorb eggs, at a rate of 0.72 eggs/day ($R^2 = 0.21$; $F_{1, 208} = 55.628$; $P < 0.001$; $Y = 10.94 - 0.72X$) and 0.83 eggs/day ($R^2 = 0.21$; $F_{1, 194} = 51.855$; $P < 0.001$; $Y = 14.85 - 0.83X$), down to about 3 and 6 eggs at day 11 (T11) for the honey and honey + host feeding diet, respectively (Figure 3). Model simplification led to the following model as the minimal most adequate one to explain the observed pattern of egg load dynamics: $\text{eggs} \sim \text{size} + \text{age} + \text{diet}$ ($F_{3, 534} = 97.68$, $P < 0.001$). All factors were highly significant: size ($F_{1, 534} = 181.54$, $P < 0.001$), age ($F_{1, 534} = 39.66$, $P < 0.001$), and diet ($F_{1, 534} = 71.82$, $P < 0.001$). The regression model showed that a single host feeding meal resulted into an overall average gain of 2.7 eggs, and that an increase of 100 μm of the hind tibia length resulted into an average increase of 5.7 eggs. The average egg load difference by day between diets was significant on each day, except for day seven and eight (Table S1). The positive correlation between egg load and size change on the different wasps ages. At emergence there was not effect of wasp size on egg load ($F_{1, 17} = 0.52$, $P = 0.48$) (Figure 4A). On contrary, the effect of the wasp size was significant at day three and day seven on both diets (T3 honey: $F_{1, 21} = 12.9$, $P = 0.002$, T3 host feeding: $F_{1, 20} = 26.2$, $P < 0.001$, T7 honey: $F_{1, 20} = 13.09$, $P = 0.002$ and T7 host feeding: $F_{1, 20} = 29.64$, $P < 0.001$) (Figure 4B and 4C).

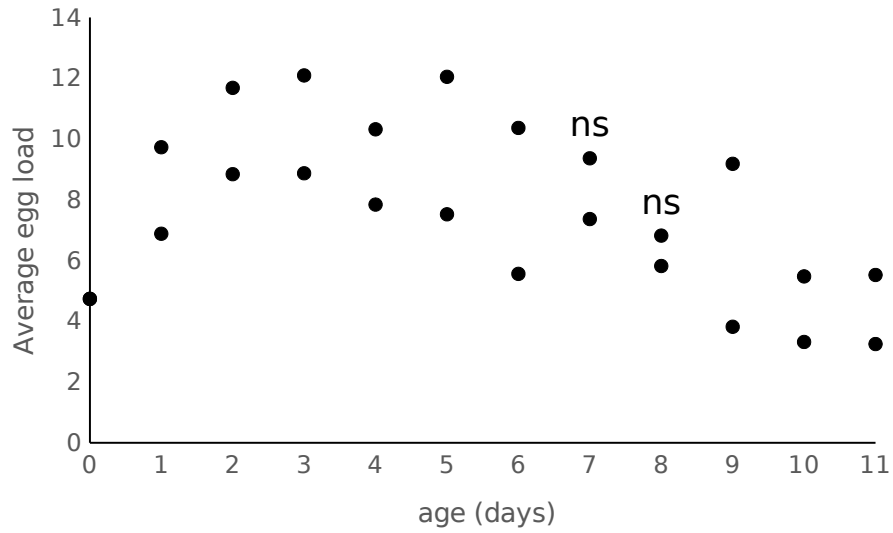
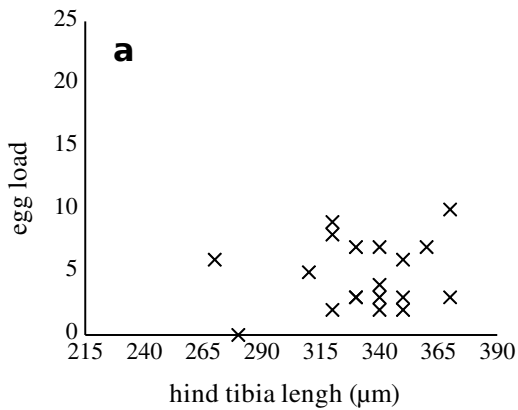


Figure 3. Egg load dynamics as average egg load by day of *T. radiata* on two different diets: honey (open circles) and honey + single host feeding (solid circles). Sample sizes: T0 n=19, honey: T1, T2, T4, T5, T6 n=25, T3 n=23, T7 to T10 n=22, at T11 n=24; honey + single host feeding: at T1 to T9 n=22, T10, T11 n=21. ns = not significant.



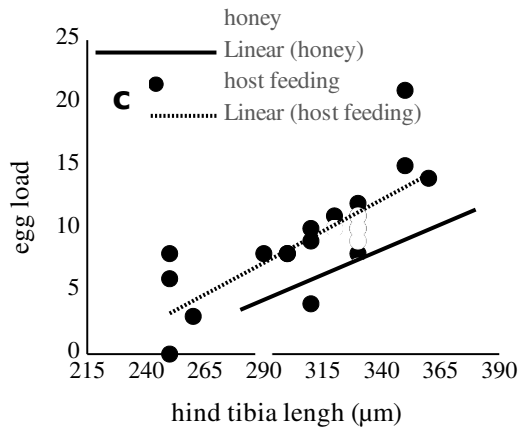
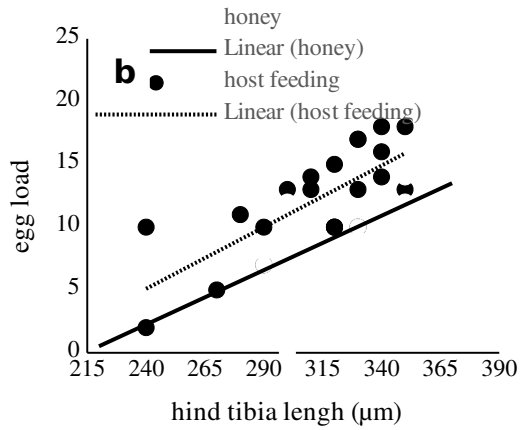


Figure 4. Influence of wasp size [hind tibia length (HTL)] on the egg load of *T. radiata* fed honey (open circles, solid line) and honey + single host feeding (solid circles, dotted line) at three wasp ages: A) emergence day (T0), B) 3 days (T3) and C) 7 days (T7). Linear regression for T3 (A) honey: $EL = 0.086(HTL) - 18.53$, $r^2 = 0.35$, $P = 0.002$, and honey + host feeding: $EL = 0.098(HTL) - 18.47$, $r^2 = 0.54$, $P < 0.001$. For T7-old parasitoids (B) fed honey: $EL = 0.079(HTL) - 18.85$, $r^2 = 0.37$, $P = 0.002$, and host feeding diet: $EL = 0.1(HTL) - 21.93$, $r^2 = 0.58$, $P < 0.001$.

DISCUSSION

The establishment and success of synovigenic parasitoids partly depends on their foraging behavior, as the egg load is probably the most important physiological trait determining host-feeding and oviposition decisions (Rosenheim et al., 2000). *T. radiata* is a synovigenic parasitoid and the most important natural enemy of the Asian citrus psyllid, yet his performance in the field in ongoing biological control projects are not always satisfactory. As host feeding is critical for synovigenic parasitoids, a better understanding of his effect on *T. radiata* could lead to an improvement of its performance. Here we have first shown the effect of egg load on parasitism rates, and then quantified the effect of host feeding on egg load dynamics of *T. radiata*. Females that host fed once or multiple times parasitized at a similar rate as honey fed females when three days old, whereas the effect of host feeding was higher when the wasps were seven days old, the age when they are usually released into the fields. At this age, females that host fed either once or multiple times were almost three times as likely to oviposit as the honey fed wasps, which in turn were parasitizing at rates that were nearly half of those on the same sugary diet at age three. Dissection of females after oviposition showed that the pattern of egg usage was similar (50-60%), irrespective of age and diet, and that it was the underlying egg load that drove the parasitization behavior.

Single and multiple host feeding did not have an effect on survival or longevity of *T. radiata*. This was not unexpected, as it has been shown that host feeding may or may not have an effect on longevity of parasitoids, likely reflecting differences in the metabolism of nutrients or energy (Heimpel & Collier 1996).

These two experiments indicated that multiple host feeding did not provide any additional benefit in terms of parasitism rate, egg load or survival. Therefore, we then studied the effect of a single host feeding on the egg load dynamics, showing that one meal on a 2nd instar ACP nymph

resulted into an average gain of three eggs. *T. radiata* females were born with about five eggs, and were able to mature about four more eggs when fed on honey over two days, presumably using larval reserves, and additional three eggs when host fed over the same time span. Therefore, host feeding nearly doubled the egg maturation rate, from about 2 eggs/day to about 3.5 eggs/day. Host feeding on 2nd instar ACP nymphs could represent the minimum host feeding gain, and feeding on 3rd instar nymphs, which are nearly double in size, could result in an even larger gain of eggs. However, Collier (1995b) did not find such gain for *Aphytis melinus* fed on 2nd and 3rd instar California red scale nymphs, speculating that nutrients from host feeding might be stored in the fat body and not immediately used. Kapranas and Luck (2008) instead recorded an effect of host size on egg load for one of the two congeneric parasitoids they tested, and speculated that egg maturation could be dynamic. We found a positive correlation between egg load and size, which is known also in other systems, e.g. *Aphytis* spp. (Heimpel & Rosenheim, 1995; Rosenheim & Rosen, 1991), and the size effect was more marked in host fed females, which matured more eggs per meal. Host feeding by *T. radiata* did not retard or slow down oosorption, which started at day 4 for both diets and continues at a similar pace of less than 1 egg/day that was slightly faster for host fed individuals. This contrasts with observations by Heimpel and Rosenheim (1995) for *A. melinus*, where adding yeast to a sugar diet did slow down oosorption.

A comparison of the egg load at day three and seven from the oviposition and egg load dynamics experiments shows two interesting differences. First, at day three there was no difference in the egg load in the former, but a difference of about three eggs in the latter experiment. Second, at day seven the egg load was higher in the former than in the latter experiment for host fed females. These two discrepancies may have the same explanation, that is,

the presence of hosts and the parasitization activity itself could stimulate a dynamic maturation of eggs, and this effect could be more marked later in life. Furthermore, the egg usage suggests that *T. radiata* females are not willing to go below the number of eggs they are born with. This could represent the threshold at which these wasps feel the urge to host feed, thus explaining also why only about a third of wasps host fed over 24 hours when provided one host upon emergence, and two thirds host fed at least twice when provided with three hosts over the first three days of life.

Our study has implications for the foraging ecology of *T. radiata* and for its use as an augmentative biological control agent. Ellers et al. (2000) showed that stochasticity in relatively rich host environments increases the risk of egg limitation, but synovigenic parasitoids that replenish their egg supply throughout their life can diminish such risk. Nonetheless, synovigenic species may still experience periods of egg limitation, depending on the interaction between egg maturation rate, host encounter rate, and host phenology (Heimpel et al., 1998; Casas et al., 2000). As *T. radiata* carry a limited number of mature eggs, it is likely to experience periods of egg limitation under field conditions. Considering that females require time to host feed, mature additional eggs and rest after a host meal (Tena et al., 2017), the release of host fed females could provide a jump start in parasitization upon releases in the field, in particular at low host densities. Therefore host feeding could be exploited at the mass rearing level. Currently at UCR three to four days old *T. radiata* are allowed to host feed for two days before being introduced into the “mass sting” cages that produce the wasps that ultimately get released (Soper, et al. 2014), but no pre-release host feeding is carried out. Our experiments suggest that such conditioning step may be more effective not upon emergence but when the egg load is stationary right before oosorption starts, that is, when wasps are two to three days old. In conclusion, the

egg load dynamics, the effect of egg load on parasitization rates, the egg maturation and resorption rates will be used to build a model to predict the foraging and oviposition behavior in the field with and without pre-release host feeding. Field experiments will then be carried out to test such model, and in turn the timing and effectiveness of pre-release host feeding in terms of biological control efficacy.

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