



Impact of host suitability on oviposition preference toward fertilized and unfertilized host eggs in two *Trichogramma* parasitoid species

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With 4 figures and 1 table

Abstract: The preference of *Trichogramma* parasitoids is known to be modulated by the fertilization status of host eggs encountered. However whether the actual suitability of host eggs is at play for modulating the preference of *Trichogramma* when choosing fertilized vs. unfertilized host eggs has not been well documented yet. In the present study, fertilized and unfertilized eggs of *Ostrinia furnacalis* (Guenée) (Lepidoptera: Crambidae), of which the eggs are suitable for *Trichogramma ostriniae* (Pang & Chen) (Hymenoptera: Trichogrammatidae) but are suboptimal for *T. dendrolimi* Matsumura, were used to investigate host preference, host acceptance, and offspring performance of the two *Trichogramma* species. The results showed that, in a no-choice test, *T. dendrolimi* parasitized significantly more unfertilized *O. furnacalis* eggs than fertilized ones. In contrast, the number of fertilized eggs parasitized by *T. ostriniae* was significantly higher than for unfertilized eggs. The sex ratio (female proportion), developmental time and fitness of offspring wasps were similar between fertilized and unfertilized host eggs for both *Trichogramma* species. In a choice test, *T. dendrolimi* preferred unfertilized host eggs over fertilized ones, whereas *T. ostriniae* did not show a preference. The higher rate of eggs laying by *T. dendrolimi* on unfertilized eggs than on fertilized ones may explain the different parasitism performances reported for the two *Trichogramma* species.

Keywords: Trichogrammatidae; fertilization; choice test; suitability; parasitism; preference

1 Introduction

The behaviors of a parasitoids during the parasitism process, from locating host habitat to parasitizing the host, have been extensively studied (Vet & Dicke 1992; Godfray 1994). After locating a potential host, parasitoids examine the quality and suitability of the host (Desneux et al. 2009a; Desneux & Ramirez-Romero 2009; Nguyen et al. 2018; Monticelli et al. 2019) and the time taken to perform this examination may depend on the actual status of the host (Jervis & Kidds 1996). On mobile hosts (e.g. larvae), examination takes a short period of time and is often finished in

1–3 seconds or less (Völkl & Mackauer 2000; Desneux et al. 2009b but see Biondi et al. 2013), whereas on a static host, e.g. eggs, the examination process could last longer than one minute (Godfray 1994). When the quality of the host meets the requirement of the parasitoid female, then she lay egg(s) into or on the selected host (Godfray 1994). Host suitability, which is defined as the capacity of the host to be accepted and parasitized by the parasitoid adult and to provide an environment in which the parasitoid progeny can develop (Vinson & Iwantsch 1980), could be determined by evaluating both behavioral and physiological traits, notably host acceptance by the female parasitoid, and the parasitoid offspring

development (Desneux et al. 2009a; 2009c; Monticelli et al. 2019).

Trichogramma parasitoids can parasitize eggs of insects and kill embryo of the target pests; they have great potential for use in biological control programs (Smith 1996; Camerini et al. 2018; Du et al. 2018; Hou et al. 2018, Thiéry & Desneux, 2018; Zhang et al. 2018). The suitability of a variety of phytophagous insects to certain *Trichogramma* species has been studied in order to find candidate *Trichogramma* species for potential use in biological control (Pizzol et al. 2010, Tabone et al. 2010; Andrade et al. 2011; Chailleux et al. 2012; 2013). Studies demonstrated that, for a given *Trichogramma* species, the host suitability varied not only among the insect species provided (Hoffmann et al. 2001; Roriz et al. 2006; Chailleux et al. 2012) but also among the developmental stages of the host eggs (Pizzol et al. 2012; Yang et al. 2016; Hou et al. 2018), as well as the plants on which the hosts fed (Moreau et al. 2009; Thiéry & Desneux 2018). Such variation in suitability was found for both host acceptance and the suitability for successful development of parasitoid offspring. The age-dependent suitability of a host to a given *Trichogramma* species is related to the development of the embryo inside the host chorion (Olson 1998; Honda & Luck 2000). In addition, to integrate the release of *Trichogramma* with other control strategies, e.g. setting sex pheromone traps (Romeis et al. 1997; Witzgall et al. 2010) or rearing the parasitoids on alternative hosts, the suitability of host eggs with undeveloped embryos or that are unfertilized has been evaluated in various *Trichogramma* species (Young & Hamm 1967; Romeis et al. 1997; Cagnotti et al. 2016; Yang et al. 2016; Du et al. 2018). The results showed that most *Trichogramma* species preferred fertilized hosts, although there were no major differences in offspring fitness between fertilized and unfertilized host eggs. However, all the hosts used in these studies were native and/or suitable ones; the pattern may be different when considering hosts classified as suboptimal ones.

The change in host suitability as host age changes mostly relates to the host embryo development (Honda & Luck 2000). It was supposed that *Trichogramma* could inject venom to suppress embryo development of putative host and so the immature parasitoid can complete its development inside the host egg (Honda & Luck 2000; Zhu et al. 2014). On the other hand, host embryo may rely on innate immune system to counteract parasitism (Reed et al. 2007; Abdelatif & Hilker 2008). For the particular case of low host suitability related to poor parasitoid ability to suppress host embryo development, unfertilized eggs may be more suitable than fertilized ones for the *Trichogramma* immatures. Therefore the fertilization status of host eggs encountered may modulate the preference of *Trichogramma* females between the two kinds of host eggs.

The Asian corn borer, *Ostrinia furnacalis* (Guenée) (Lepidoptera: Crambidae) is one of the most notorious agri-

cultural pests of maize in Asia, and both *Trichogramma ostriniae* Pang et Chen (Hymenoptera: Trichogrammatidae) and *T. dendrolimi* Matsumura have been used in biological control of the pest in China (Wang et al. 2014; Yang et al. 2016). Field and laboratory studies indicated that *O. furnacalis* eggs is suitable hosts for *T. ostriniae* but that it is suboptimal for *T. dendrolimi*, especially when the age of host eggs increased (Li et al. 2002; Zhu et al. 2014; Huang et al. 2017). However, the effects of fertilization status of *O. furnacalis* eggs on oviposition preference have not been reported in the two *Trichogramma* species yet. We hypothesized that the oviposition preference may differ among *Trichogramma* species, for which the host egg has different suitability, when the parasitoid females are able distinguishing the fertilization status of host eggs encountered. The two *Trichogramma* species and *O. furnacalis* eggs were chosen to compare the preference of the parasitoids toward fertilized and unfertilized host eggs. The subsequent impact on the quality of parasitoids emerging from these hosts was also evaluated.

2 Material and methods

2.1 Biological materials

Trichogramma dendrolimi was reared in the laboratory using a strain provided by the Institute of Biological Control of Jilin Agricultural University. The *Trichogramma ostriniae* colony was initiated using individuals that emerged from parasitized *O. furnacalis* eggs that were collected in a maize field in Jiangsu Province, China. Both *Trichogramma* species were continually reared on *Corcyra cephalonica* (Stainton) (Lep.: Pyralidae) eggs (Wu et al. 2018; Iqbal et al. 2019).

Ostrinia furnacalis was collected from a corn field in the suburb of Nanjing, Jiangsu Province, China. The larvae were reared on a modified artificial diet (Zhou et al. 1980) in plastic boxes. After pupation, the pupae were collected and placed in a screened cage (25 cm × 25 cm × 40 cm), for which the top was screened with a wire mesh (0.5 cm × 0.5 cm grids). After adults emerged, 10% sugar solution was provided as a food source. A piece of tracing paper was used to collect eggs. Fertilized and unfertilized eggs were obtained by simultaneously placing 100 female and 100 male pupae or 200 female pupae into a cage, respectively, and a 10% sucrose solution in degreased cotton was provided as food to emerged moths. UV-treated fertilized (UV/fertilized) eggs, which could be used as control to fertilized and unfertilized eggs, were obtained by exposing fertilized eggs to an UV lamp (253.7 nm, 15 W, Danqi Industrial Co. Ltd., Shanghai, China) at 45 cm away for 6 h. The tracing paper with egg masses was cut into pieces based on one egg mass (fertilized eggs: 20–40 eggs per egg mass; unfertilized eggs: 5–25 eggs per egg mass) on each piece. All insect cultures were reared under laboratory conditions (25 ± 1°C, 70 ± 10% RH, 14:10 L:D photoperiod).

2.2 Parasitism incidence rate (PIR) of

Trichogramma species on *O. furnacalis* eggs

A < 24-h-old egg mass containing approximately 25 eggs of *O. furnacalis* was glued onto a 2 cm × 2 cm piece of graph paper to make an egg card. The egg card was then placed into a glass tube (9.5 cm × 3.5 cm), and a 1 cm × 1 cm wet filter paper was put into the tube to maintain humidity. A < 24-h-old mated female wasp was introduced into the glass tube for 6 h. After the female wasp was removed the eggs were checked at 12-h intervals, and hatched host larvae were removed immediately. The parasitism was determined by observing the eggs that turned gray-dark within approximately 4 days after the exposure to parasitoids. The preference was assessed through estimating the parasitism incidence rate (PIR). The PIR was calculated by dividing the number of wasps that effectively accepted parasitizing *O. furnacalis* eggs (during the 6-h exposure) by the total number of wasps tested. The number of *O. furnacalis* eggs turning gray-dark was also counted. For *T. ostriniae*, 20, 10, and 10 females were used in the first, second, and third replicate, respectively, of each of the three egg treatments (fertilized, unfertilized and UV/fertilized eggs). Same number of *T. dendrolimi* wasps were used following the same experimental process. The experiments were performed under laboratory conditions at 25 ± 1°C, 70 ± 10% RH and 14:10 (L:D) photoperiod.

2.3 Suitability of *O. furnacalis* eggs for development of *Trichogramma* offspring

One host egg card (about 25 eggs) was exposed to a < 24-h-old female wasp for 6 h in a glass tube (9.5 cm × 3.5 cm) under 25 ± 1°C, 70 ± 10% RH and a 14:10 (L:D) photoperiod. After the wasp was removed, the host eggs were checked at 12-h intervals to remove hatched borer larvae immediately. From the 5th day on, the eggs were checked at 24-h intervals, and the emerged wasps were sexed and female wasps were placed under -20°C for subsequent egg load estimates. After excluding the samples in which no parasitism occurred or no female offspring were produced, the data of 30, 30, and 32 replicates for *T. dendrolimi* and 33, 30, and 23 replicates for *T. ostriniae* in the fertilized, UV/fertilized and unfertilized treatments, respectively, were analyzed. The emergence rate was calculated by dividing the number of host eggs with emerged hole by the number of host eggs that turned into grey. The development time was defined as the period from (i) exposing host eggs to parasitoids and (ii) the emergence of parasitoids. 30 emerging parasitoid females were randomly selected from each treatment to evaluate the egg load and to measure the hind tibia length (HTL) under a microscope (Nikon SMZ 800; Nikon Instrument Inc., Tokyo, Japan).

2.4 Choice test

Two egg cards, one with 25 fertilized eggs and one with 25 unfertilized eggs, were placed in a glass tube (9.5 cm

× 3.5 cm) in laboratory at 25 ± 1°C, 70 ± 10% RH and a 14:10 (L:D) photoperiod. A mated, < 24-h-old female wasp was released at the point between the two cards. The wasp was removed 6 h later, and the two egg cards were incubated, separately, in glass tubes. The cards were checked at 24-h intervals, and the number of eggs that turned grey was recorded. 30 replicates were performed for each of the two *Trichogramma* species.

2.5 Host acceptance at oviposition

One < 24 h-old mated female wasp was introduced into a plastic Petri dish (3.5 cm × 10 cm) in which an egg card bearing six host eggs was in place. The female wasp's behavior was observed under a stereoscopic microscope under 25 ± 1°C, 70 ± 10% RH. A host egg attacked one time was determined by observing that the female wasp pierced the egg with her ovipositor. A minimum of 20 wasps were observed in each of 3 replicates for each *Trichogramma* species on fertilized or unfertilized eggs of *O. furnacalis*. The process of host acceptance involves external examination, which should be considered in analyzing the parasitism behavior of female wasp. However, because *O. furnacalis* eggs cover one another, a female wasp may touch more than one egg during external examination, and it is difficult to determine how much time the female takes in examining the exterior of the egg that she ultimately decides piercing. Thus, the host eggs that were pierced by a female were dissected under a microscope to determine host acceptance. The proportion of host eggs with zero, one, or two wasp eggs was calculated by dividing the number of host eggs, that containing the corresponding number of wasp eggs, by the number of host eggs attacked once.

2.6 Statistical analysis

The effects of host eggs, wasp species and their interaction on PIR, number of eggs parasitized, emergence rate, hind tibia length and egg load of female wasp offspring, developmental time, and proportion of female progeny in the no-choice tests were analyzed using two-way ANOVA (host eggs × wasp species). In addition, (i) the *Trichogramma* species were analyzed separately to evaluate the effect of host egg types on the traits tested, and (ii) the traits recorded for the two *Trichogramma* species were compared also per host egg type. The PIR, emergence rate, and proportion of female progeny data did not follow a normal distribution and were all arcsine-transformed before being analyzed. The means were separated using Tukey's honestly significant difference (HSD) as post-hoc test (at $P = 0.05$ level). The comparison of number of eggs parasitized between host egg treatments in the choice test and the comparison of the proportion of eggs in the host acceptance test were performed using a paired t -test and a t -test, respectively, after the proportion were arcsine transformed. All statistical analyses were performed using SPSS 20.0 (SPSS Inc., Chicago, IL, USA).

3 Results

3.1 The parasitism incidence rate of two *Trichogramma* species

There was a significant impact of both host eggs and *Trichogramma* species factors, as well as their interaction, on the parasitism incidence rate (PIR) ($F_{2,18} = 37.20$, $P < 0.01$; $F_{1,18} = 319.94$, $P < 0.01$; $F_{2,18} = 180.02$, $P < 0.01$, respectively, Fig. 1A). The PIR of *T. dendrolimi* on unfertilized eggs was significantly higher than on fertilized or UV/

fertilized eggs ($F_{2,8} = 16.03$; $P < 0.01$). In contrast, the PIR of *T. ostrinae* on unfertilized eggs was significantly lower than on fertilized or UV/fertilized eggs ($F_{2,8} = 813.20$; $P < 0.01$). The PIR of wasps on fertilized eggs ($F_{1,5} = 24.86$; $P < 0.01$), UV/fertilized eggs ($F_{1,5} = 28.27$; $P < 0.01$), or unfertilized eggs ($F_{1,5} = 3.59$; $P = 0.02$) differed between the two *Trichogramma* species.

There was a significant effect of both host eggs and *Trichogramma* species factors, as well as their interaction, on the number of eggs parasitized ($F_{2,178} = 3.13$; $P < 0.05$;

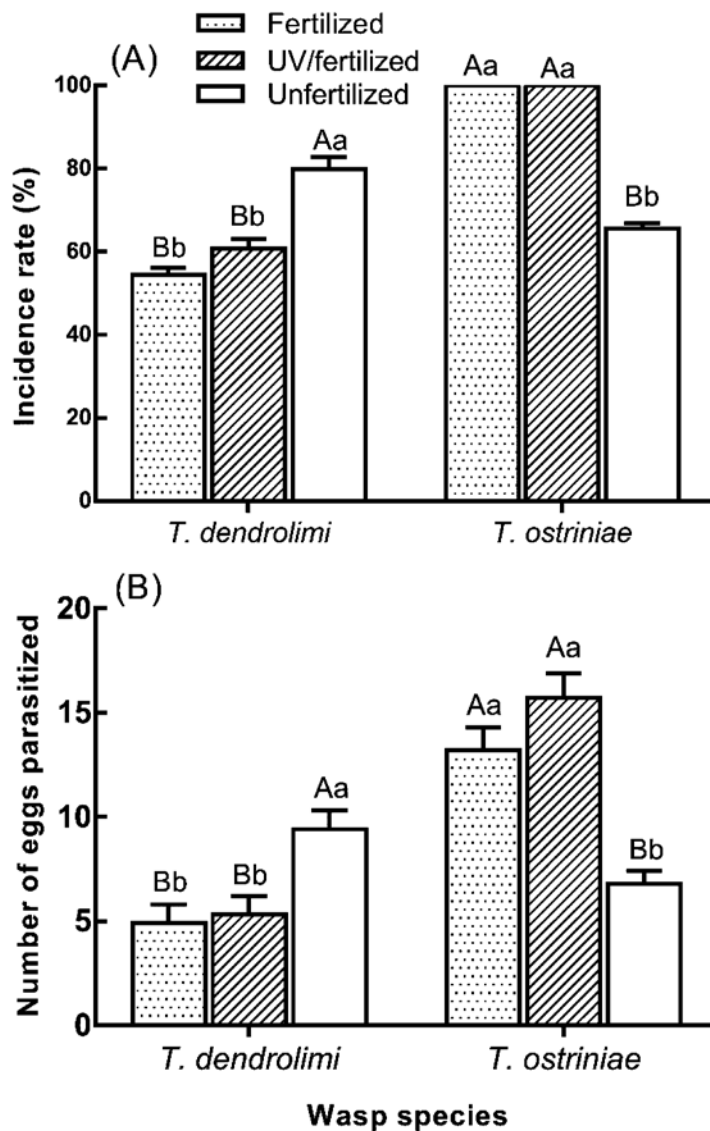


Fig. 1. Parasitism incidence rate (mean + SE) of *Trichogramma* (A) and number (mean + SE) of *Ostrinia furnacalis* eggs parasitized by *Trichogramma* (B) in no-choice tests. The uppercase letters above the histograms indicated comparisons among the three kinds of host eggs, and the lowercase letters indicated the comparisons between the two *Trichogramma* species on corresponding host eggs. Different letters indicated significant differences (at $P < 0.05$ level).

$F_{1,178} = 46.36$; $P < 0.01$; $F_{2,178} = 24.89$; $P < 0.01$, respectively, Fig. 1B). The number of unfertilized eggs parasitized by *T. dendrolimi* was significantly higher than of fertilized or UV/fertilized eggs ($F_{2,91} = 7.94$; $P < 0.01$). In contrast, the number of unfertilized eggs parasitized by *T. ostrinia* was significantly lower than that of fertilized or UV/fertilized eggs ($F_{2,85} = 17.54$; $P < 0.01$). In addition, *T. ostrinia* showed higher number of eggs parasitized for fertilized or UV/fertilized eggs than was observed for *T. dendrolimi*; the opposite was observed when comparing the number of parasitized eggs on unfertilized eggs (all $P < 0.05$).

3.2 Emergence rate, female proportion and developmental time of *Trichogramma* offspring

Overall, there was no significant impact of both host eggs and *Trichogramma* species factors on the emergence rate ($F_{2,178} = 0.40$, $P = 0.67$; $F_{1,178} = 0.17$, $P = 0.68$, respectively, Table 1). Still, both factors interacted significantly ($F_{2,178} = 4.26$; $P = 0.02$). *Trichogramma dendrolimi* showed a lower emergence rate from unfertilized eggs than from fertilized eggs ($F_{2,91} = 3.46$; $P = 0.04$), and this species also had a lower emergence rate than *T. ostrinia* from unfertilized eggs ($F_{1,54} = 2.24$, $P = 0.03$). No significant difference was found for *T. ostrinia* among the three kinds of host eggs ($F_{2,85} = 1.14$; $P = 0.33$).

No significant impact of both factors was found on the proportion of females (host eggs: $F_{1,178} = 1.20$, $P = 0.30$; *Trichogramma* species: $F_{1,178} = 3.26$, $P = 0.07$; interaction: $F_{1,178} = 0.49$, $P = 0.61$; Table 1). The developmental time was significantly affected by *Trichogramma* species factor (*Trichogramma* species: $F_{1,178} = 25.44$, $P < 0.01$) but host eggs factor ($F_{2,178} = 0.06$, $P = 0.94$) or the interaction of both factors ($F_{2,178} = 0.10$, $P = 0.91$).

3.3 Hind tibia length and egg load of offspring wasps

Host eggs and *Trichogramma* species factors (and their interaction) had no significant effects on the HTL of female offspring wasps ($F_{2,180} = 0.58$, $P = 0.56$; $F_{1,180} = 1.53$, $P = 0.22$; $F_{2,180} = 0.09$; $P = 0.91$; Fig. 2A). In contrast, the egg load of emerging females was significantly affected by both host eggs and *Trichogramma* species factors ($F_{2,180} = 3.36$, $P = 0.04$; $F_{1,180} = 12.46$, $P < 0.01$; Fig. 2B), with significantly more egg load for emerging *T. dendrolimi* females than for *T. ostrinia* females (independently of egg type, with the interaction being not significant, $F_{2,180} = 0.07$; $P = 0.94$).

3.4 Host preference and host acceptance at oviposition

In choice test, *T. dendrolimi* significantly preferred to parasitize unfertilized eggs over fertilized eggs ($t = 3.75$; $P < 0.05$). However, no significant differences in number eggs parasitized by *T. ostrinia* were found between fertilized and unfertilized eggs ($t = 1.67$; $P > 0.05$) (Fig. 3).

In the case of eggs attacked by *T. dendrolimi*, the proportion of unfertilized host eggs containing no wasp eggs was lower than on fertilized ones ($t = 2.85$; $P < 0.05$) (Fig. 4A). In contrast, the proportion of unfertilized host eggs containing one wasp egg was significantly higher than on fertilized ones ($t = 3.07$; $P < 0.05$). In the case of *T. ostrinia*, the proportion of unfertilized host eggs containing no wasp egg was slightly higher than on fertilized ones ($t = 2.85$; $P < 0.05$) (Fig. 4B), and there was no significant difference in the proportion of host eggs containing one wasp egg between the two kinds of host eggs ($t = 2.46$; $P > 0.05$). No significant differences were found in the proportion of host eggs containing two wasp eggs between fertilized and unfertilized host eggs for either *Trichogramma* species (*T. dendrolimi*: $t = 0.26$, $P = 0.80$; *T. ostrinia*: $t = 0.98$, $P = 0.38$).

Table 1. Emergence, female proportion, and developmental time of *Trichogramma* offspring on different host eggs

Parameters	Host eggs	<i>Trichogramma</i> species	
		<i>T. dendrolimi</i>	<i>T. ostrinia</i>
Emergence (%)	Fertilized	97.4±1.6 A a	96.2±1.6 A a
	UV/fertilized	95.5±2.1 A ab	96.2±1.7 A a
	Unfertilized	92.3±2.3 B b	96.7±2.3 A a
Female proportion (%)	Fertilized	80.5±2.8 A a	85.4±1.3 A a
	UV/fertilized	77.0±2.4 A a	85.4±0.7 A a
	Unfertilized	78.5±1.6 A a	83.0±2.3 A a
Developmental time (d)	Fertilized	9.60±0.02 B a	9.69±0.01 A a
	UV/fertilized	9.60±0.02 B a	9.69±0.01 A a
	Unfertilized	9.60±0.02 B a	9.69±0.01 A a

Data are means ± SEs. The uppercase letters indicated comparisons between the means in same row, and lowercase letters indicated comparison among the three host egg types under same parameters. Different letters indicate a significant difference (Tukey's test, $P < 0.05$)

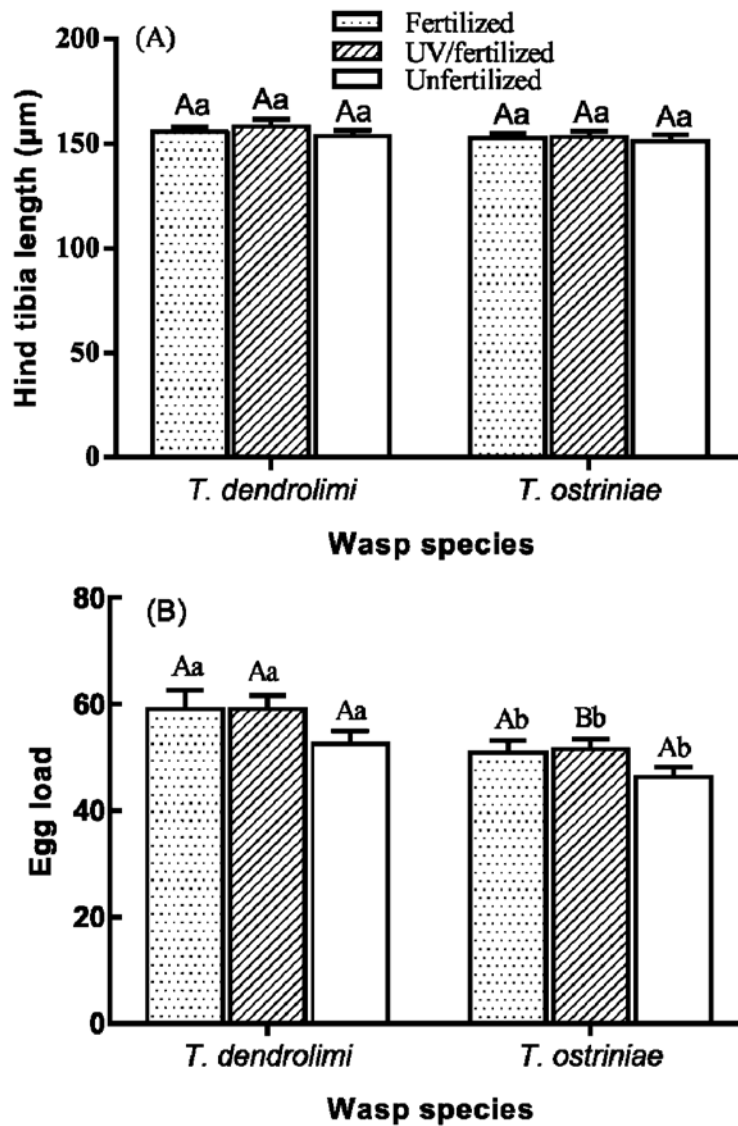


Fig. 2. Hind tibia length **(A)** and egg load **(B)** (mean + SE) of *Trichogramma* female offspring emerged from eggs of *Ostrinia furnacalis* in no-choice tests. The uppercase letters above the histograms indicated comparisons among the three types of host eggs, and the lowercase letters indicated comparisons between the two *Trichogramma* species emerged from corresponding host eggs. Different letters indicated significant differences (Tukey's test, $P < 0.05$).

4 Discussion

Our study showed that the preference of female wasps toward fertilized and unfertilized *O. furnacalis* eggs differed between the parasitoids *T. dendrolimi* and *T. ostriniae*. The difference observed in host acceptance by the parasitoid females of the two *Trichogramma* species did translate to actual differences in parasitism of *O. furnacalis* eggs. However, after the parasitoid eggs were laid in host eggs, the development of offspring of both *Trichogramma*

species was not affected by the fertilization status of the host eggs.

The *Trichogramma* females can estimate the fertilization status of host eggs (Yang et al. 2016; Du et al. 2018) and egg parasitoids are known to have enough handling time to evaluate the quality of putative host eggs. Therefore the number of host eggs effectively parasitized by a *Trichogramma* female may reflect the actual suitability of a given host for effective offspring development (Li & Liu 2015). In the present study, both the PIR and the number of hosts parasitized

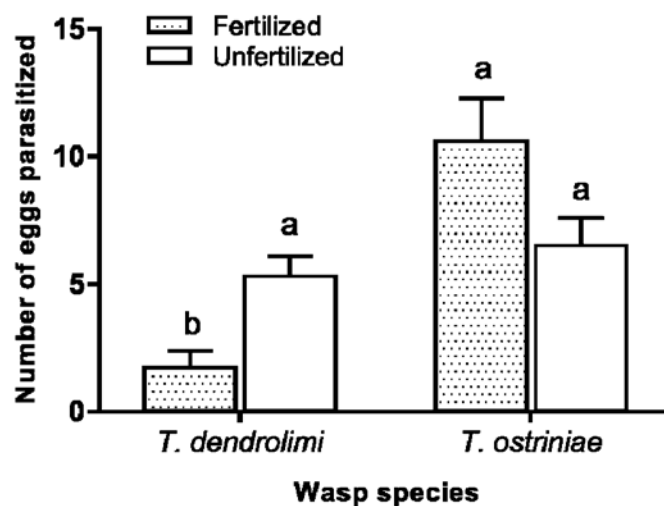


Fig. 3. Number (mean + SE) of *Ostrinia furnacalis* eggs parasitized by *Trichogramma* in choice tests. Different lowercase letters indicated significant differences between fertilized and unfertilized host eggs exposed to same *Trichogramma* species (Paired *t*-test, $P < 0.05$).

were different between fertilized and unfertilized *O. furnacalis* eggs (although only marginally significant in one of the choice test assay) indicating that the females of the two *Trichogramma* species were able detecting the fertilization status of host eggs.

The host preference and the PIR still differed between the two *Trichogramma* species, with *T. ostrinae* preferring parasitizing fertilized eggs and *T. dendrolimi* preferring parasitizing unfertilized eggs. This result is consistent with multiple previous studies reporting that the preference of *Trichogramma* between fertilized and unfertilized could vary among *Trichogramma*-host combinations. Several *Trichogramma* species, including *T. chilonis*, *T. dendrolimi*, *T. japonicum*, and *T. leucaniae* Pang & Chen, parasitized more fertilized than unfertilized eggs in a *Trichogramma*-host combination with eggs of *C. cephalonica* or *Chilo suppressalis* Walker (Lep.: Crambidae) (Xu et al. 2016, Du et al. 2018). However, no preference was found in *T. pretiosum* and *T. nerudai* (Cagnotti et al. 2016) and another egg parasitoid *Gonatocerus morrilli* Howard (Hym.: Mymaridae) (Krugner, 2014). In contrast, higher preference toward unfertilized host eggs was reported in *T. principium* Sug. Et Sor. when parasitizing *Cydia pomonella* L. (Lep.: Tortricidae) (Makee 2006). These results hinted that difference in parasitoid preference between fertilized and unfertilized host eggs could be different not only among *Trichogramma* – host combinations but also among different taxa and guilds of egg parasitoids.

Although the preference of *T. dendrolimi* was affected by the fertilization status of host eggs, there was no major difference in proportion of female offspring (sex ratio), developmental time, and size and egg load (in female offspring) between fertilized and unfertilized host eggs; only

emergence rate was observed to be reduced on unfertilized eggs. This was also reported in other egg parasitoids, e.g. *Trissolcus japonicus* (Ashmead) (Hym.: Scelionidae) for which the emergence rate from unfertilized eggs of *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae) was higher than that from fertilized ones (Yang et al. 2018). Previous studies indicated that *T. dendrolimi* parasitized less *O. furnacalis* eggs than *T. ostrinae* in fields (Zhang et al. 1979; Zhang et al. 1990; Feng 1996) and under laboratory condition (Li et al. 2002; Zhu et al. 2014). Furthermore, when the *O. furnacalis* eggs age increased from < 6 h to > 18 h, the PIR and parasitism decreased by $> 50\%$ (Liu et al. 1998). It hinted that *O. furnacalis* eggs may be a suboptimal host for *T. dendrolimi*. However, we found no significant difference in main traits investigated (female proportion, developmental time of offspring, and size and egg load of female offspring) between fertilized and unfertilized host eggs for both of the *Trichogramma* species. One possible reason to explain this inconsistency is that the emerged *Trichogramma* offspring have been selected at the egg stage; although *T. dendrolimi* eggs were laid into fertilized *O. furnacalis* eggs, some of them could not develop to larvae (early mortality). Those host eggs did not turn to grey color and thus could not be counted as parasitized ones. Previous experiments did find that some fertilized *O. furnacalis* eggs that got stung by *Trichogramma* parasitoids can stay as non-parasitized status for a long time and with no parasitoid individual coming out (Li et al. 2002; Zhu et al. 2014). In overall, the nutritional quality of either fertilized or unfertilized *O. furnacalis* eggs proved to be suitable for the development of the *Trichogramma* embryo which survived the competition with host embryo.

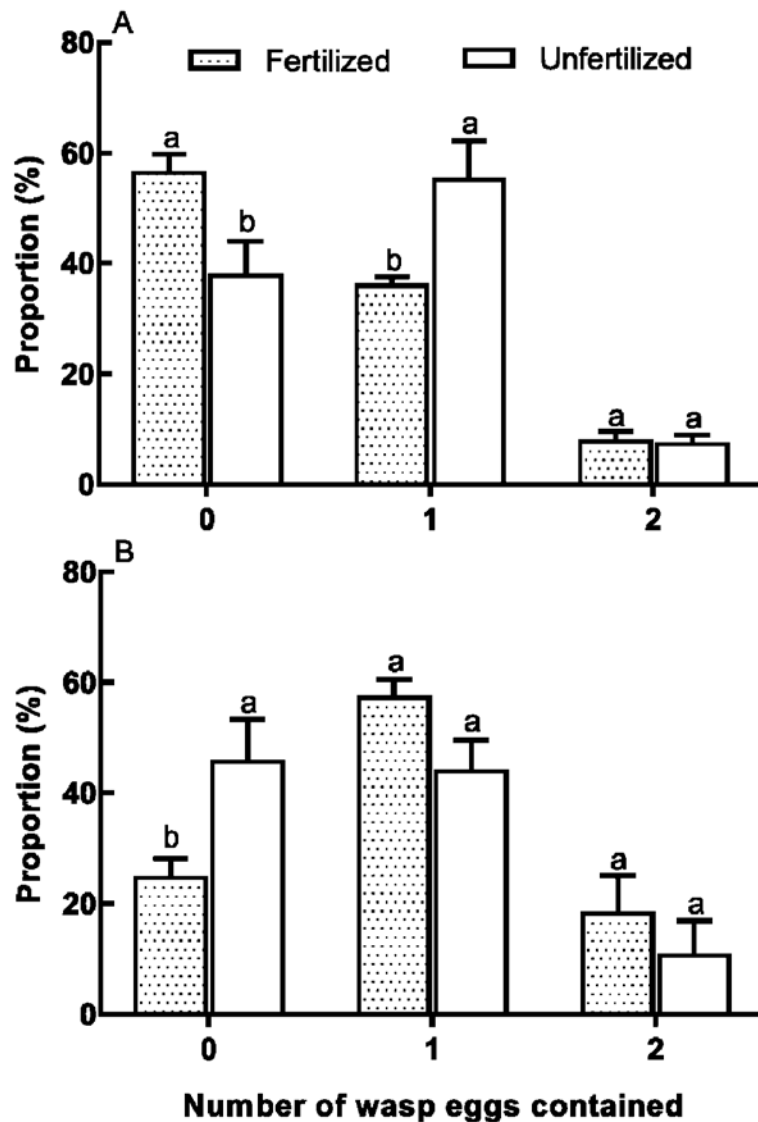


Fig. 4. Proportion (mean + SE) of host eggs with a certain number of wasp eggs after one attack by a *Trichogramma* female. **(A)** *Trichogramma dendrolimi*; **(B)** *Trichogramma ostrinae*. Different lowercase letters indicated significant differences between fertilized and unfertilized host eggs containing same number wasp eggs (*t*-test, $P < 0.05$).

Although host eggs may be suitable for the development of *Trichogramma*, they may not always be considered as suitable by *Trichogramma* females at the time of oviposition decision (Wu & Qin 1982; Honda & Luck 2000; Dias et al. 2010). It has been reported that the decision of *Trichogramma* females could be affected by both abiotic and biotic factors, such as amino acid concentration (Wu & Qin 1982; Barrett & Schmidt 1991; Dias et al. 2010) or the status of host embryo developing in the eggs (Ruberson & Kring 1993; Olson 1998; Honda & Luck 2000). In the present study, many stung host eggs, including both fertilized and unfertilized ones, contained actually no parasitoid

egg when they were dissected. The result is consistent for *T. dendrolimi* because *O. furnacalis* may be a suboptimal host, and females may decide to not lay eggs at the time of the oviposition step (40–60% of host eggs contained no parasitoid eggs). However, it remains unclear why 20–40% of host eggs did not contain *T. ostrinae* eggs, especially since this host is suitable for this parasitoid species. Considering the decreased parasitism rate related to the increasing embryo age of host egg (Liu et al. 1998), and the contrasted results on the numbers of *T. dendrolimi* eggs laid in fertilized and unfertilized *O. furnacalis* eggs, there might be factors related to host embryo development that actually impacted the host

acceptance of the *Trichogramma* females. More unfertilized than fertilized eggs contained one *T. dendrolimi* eggs and it implied that *T. dendrolimi* preferred to parasitize unfertilized *O. furnacalis* eggs; this was consistent with the results in choice test conditions. It is still unclear what mechanism(s) induced the rejection of oviposition after the insertion of the ovipositor into fertilized eggs for *T. dendrolimi*. Further research on the composition and nutritional differences inside the two kinds of eggs would shed light on the mechanism(s) that caused the difference observed in host acceptance.

The ideal result of integrated pest management comes from the integrated application of various multiple complementary methods (Kogan 1998; Desneux et al. 2007; Ragsdale et al. 2011; Lu et al. 2012; Guedes et al. 2016; Gurr et al. 2017; Biondi et al. 2018; Mohammed et al. 2018; Jaworski et al. 2019). Sex pheromone (mainly attracting male adults) and sterile insect techniques have been used in the control of agricultural and forest insect pests (Botto & Glaz 2010; Witzgall et al. 2010). When many male adults are trapped (or sterilized), some females produce unfertilized eggs (owing to a lack of mating opportunities or fertilization). Unfertilized eggs provide a longer vulnerable window for potential parasitism by egg parasitoids if compared with fertilized eggs (e.g. in the case of *T. dendrolimi*), from which host larvae would emerge within a couple of days (Vinson 1998). Furthermore, our results hinted that unfertilized eggs could be preferred over fertilized ones by egg parasitoids when they face suboptimal hosts. Therefore any potential methods leading to increase in number of unfertilized eggs available (e.g. resulting from more males being killed by sex pheromone traps) may increase parasitism rate by a variety of egg parasitoids, notably those lacking finding suitable fertilized host eggs.

Acknowledgements: This study was supported by the National Key R&D Program of China (Grant No. 2017YFD0201000) from the Ministry of Agriculture of the People's Republic of China, Jiangsu Agriculture Science and Technology Innovation Fund (Grant No. CX-18-1003), and the Youth Scientific Research funds of Beijing Academy of Agricultural and Forestry sciences (QNJJ201725). RRR thanks CONACyT sabbatical scholarship n°740591. We thank two anonymous reviewers and the editor for helpful comments on the manuscript.

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Manuscript received: 26 August 2019

Revisions requested: 18 September 2019

Modified version received: 3 October 2019

Accepted: 24 October 2019