



Parasitism performance of the parasitoid *Trichogramma dendrolimi* on the plum fruit moth *Grapholitha funebrana*

Yanyan Qu^{1,**}, Xu Chen^{1,2,**}, Lucie S. Monticelli³, Fan Zhang¹, Nicolas Desneux³,
Dai Huijie^{4,*}, Ricardo Ramirez-Romero⁵, and Su Wang^{1,*}

¹ Beijing Key Laboratory of Environment Friendly Management on Fruit Diseases and Pests in North China, Institute of Plant & Environment Protection, Beijing Academy of Agricultural and Forestry Sciences, Beijing, China

² College of Plant Protection, Jilin Agricultural University, Jilin, China

³ Université Côte d'Azur, INRAE, CNRS, UMR ISA, 06000 Nice, France

⁴ Weifang University of Science and Technology, Shandong, China

⁵ Biological Control Laboratory, Department of Agricultural Production, CUCBA, University of Guadalajara, Zapopan, Jalisco, Mexico

* Corresponding author: climsion@126.com; wangsu@ipepbaafs.cn

** Authors contributed the same to this article

With 6 figures

Abstract: The egg parasitoid *Trichogramma dendrolimi* Matsumura is one of the most widely used agents in sustainable crop protection to manage many lepidopteran pests in China, especially via inundative releases. It has been used as an important biocontrol agent in Integrated Pest Management (IPM) programs for the control of the plum fruit moth *Grapholitha funebrana* Tr. However, accurate knowledge of the parasitoid's biology and ecology is needed to optimize its practical application in pest management. In the current study, the effect of key factors on *T. dendrolimi* effectiveness as biocontrol agent, including host age, exposure time, parasitoid density and, host density was evaluated under laboratory conditions. The parasitoid showed a higher parasitism rate on younger over older *G. funebrana* eggs. When host egg density increased, the number of eggs parasitized by the parasitoid also increased, but parasitism rates decreased. The functional response of *T. dendrolimi* on *G. funebrana* eggs fitted the Holling type II Model ($N_t = 0.932N/(1+0.112N)$). When parasitoid density and exposure time of hosts to parasitoids increased, the parasitism rate of *T. dendrolimi* also increased. In addition, previous exposure of host eggs to ultraviolet (UV) light did not affect parasitism rate. All aforementioned factors did not influence the emergence rate of the parasitoid offspring. Our results would provide references for optimizing the application of *T. dendrolimi* inundative releases in large-scale management of *G. funebrana* in orchards.

Keywords: biological control, functional response, host age, orchard, Lepidoptera

1 Introduction

Trichogramma (Hymenoptera: Trichogrammatidae), a genus of egg parasitoids, is widely used to control lepidopteran pests in agricultural and forestry systems in many regions around the world (Smith 1996; Tabone et al. 2010; Helyer et al. 2014; Guo et al. 2019; Iqbal et al. 2019; Li et al. 2019). With the development of commercial mass-rearing of *Trichogramma dendrolimi* using silk moth eggs or artificial eggs in the 1970s, this parasitoid has been the most commonly used pest antagonist over the past half century in China for suppressing lepidopteran pests in several crops (Zhou et al. 2014; Li et al. 2016; Huang et al. 2018; Jin et al. 2019; Li et al. 2019; Zang

et al. 2021). For instance, augmentative release of *T. dendrolimi* in corn field resulted in 80% parasitism on eggs of the corn borer *Ostrinia furnacalis* (Lepidoptera: Crambidae) and reduced stalk-boring populations by 92.5% (Wang et al. 2005). In apple orchards the management of *Adoxophyes orana* (Lepidoptera: Tortricidae) using *T. dendrolimi* maintained parasitism rates of 81–99% after the massive release of this parasitoid, but it largely fluctuated in control orchards (Feng et al. 1989). Moreover, augmentative release of this biological control agent may provide more opportunities for managing more herbivorous pests such as *Grapholitha funebrana* (Lepidoptera: Tortricidae) (Helyer et al. 2014; Zhang et al. 2018).

The plum fruit moth *G. funebrana* Tr., native to Europe, has been one of the most destructive pests in fruit-growing regions of the Palearctic as it has two generations per year (Hári & Péntzes 2010; Rizzo et al. 2012; Negahban et al. 2016). The larvae of *G. funebrana* are polyphagous and can consume a variety of fruit plants, such as plum, apricot, cherry and peach (Hári & Péntzes 2010; Riolo et al. 2010). Severe damage by plum moths is caused by the trophic consumption of larvae inside the fruit, which can cause a yield loss up to 80% (Rizzo et al. 2012; Gavriiliță & Nastas 2017). Summer generation larvae feed on fruits and produce long-term damage from early summer until the harvest time (Stefanova et al. 2019). Infestation by *G. funebrana* not only produces color changes and boring holes in fruits but also results in early ripening and falling of fruits (Alford 1987; Rizzo et al. 2012). For a long time, the pest management of *G. funebrana* in fruit orchards mainly relied on chemical insecticides (Stefanova et al. 2019), but their extensive use is known to lead to serious issues, such as pesticide resistance in targeted pests, toxicity to human and non-target organisms, as well as environmental pollution (Weisenburger 1993; Desneux et al. 2007; Liu et al. 2017; Gul et al. 2019; Silva et al. 2019). With the global increasing concern on food and environmental safety, eco-friendly alternatives are urgently needed. Moreover, pesticide chemical treatments, sometimes are not efficient enough to control this pest because of the concealed lifestyle of *G. funebrana* larvae (Nastas et al. 2016).

As other egg parasitoids, *Trichogramma* females locate *G. funebrana* eggs via the kairomones produced and emitted by the hosts (Boo & Yang 2000; Helyer et al. 2014). Once a suitable host egg is found, the adult wasp drills into the host with its ovipositor and lays an egg inside the host (Helyer et al. 2014). The parasitoid larva develops and pupates inside the host egg, turning it black and killing it (Helyer et al. 2014), preventing *G. funebrana* eggs to develop into larvae (that are the main stage causing damage on fruits). Therefore, *Trichogramma* wasps could be preferentially selected to control *G. funebrana*, due to the mass rearing of the parasitoids and the effective control of the pest following egg parasitism (Nastas et al. 2016; Gavriiliță & Nastas 2017). In addition, the employment of *Trichogramma* parasitoids for pest control would contribute to improving the conservation of the beneficial organisms and biodiversity in nature, the biological control efficacy in the field, the yields, the food safety, and the reduction of the environmental pollution (Gavriiliță & Nastas 2017).

Parasitism performance of *Trichogramma* wasps can be affected by multiple abiotic and biotic factors, e.g. temperature and relative humidity, age and fertilization status of host eggs, host and parasitoid density, exposure time to parasitoids and, host suitability (Garcia et al. 2001; Rezniket al. 2011; Pizzolet al. 2010; 2012; Perveen & Sultan 2012; Moiroux et al. 2016; Du et al. 2018; Thiéry & Desneux 2018; Li et al. 2019). Therefore, prior to inundative releases

of *Trichogramma* parasitoids in the field, it is necessary to assess how these key factors affect the parasitoid's performance in the laboratory, which would be quite useful to understand and improve the parasitization efficiency of *Trichogramma* wasps in pest management programs (Paraiso et al. 2012; Pizzol et al. 2012).

On the basis of the above, in the present study, a series of experiments were conducted to evaluate the parasitism performance of *T. dendrolimi* parasitizing *G. funebrana* in laboratory conditions. Specifically, we assessed the effect of (1) host age, (2) exposure time of the host to the parasitoid, (3) parasitoid density and, (4) UV treatment of host eggs on parasitism performance. In addition, the functional response of *T. dendrolimi* on *G. funebrana* eggs was determined. These results can provide useful knowledge to optimize the employment of *T. dendrolimi* in the field (Pizzol et al. 2012) and better estimate the potential that *T. dendrolimi* could have as an effective biological control agent against *G. funebrana*.

2 Materials and methods

2.1 Insects

The procedures for rearing insects were similar to those described in detail by Hou et al. (2018). Here below, these procedures are briefly described. All insect rearing and bioassays were conducted at 25 °C, 65% RH, 16L:8D and 600 lux of light intensity at the insectaries in the Institute of Plant and Environment Protection, Beijing Academy of Agricultural and Forestry Sciences, Haidian, Beijing, China.

2.1.1 *Trichogramma dendrolimi*

Over 20,000 *T. dendrolimi* individuals were collected from maize fields in Jilin province, China during May 2019. These wasps were brought to the insectaries and reared there. Taxonomical identification of founder individuals was performed following Lin (1994). The parasitoids were reproduced using eggs of the alternative host *Antherea penyi* Guerin-Meneville (Lepidoptera: Saturniidae) (Geng et al. 2005). Newly emerged female and male adults of *T. dendrolimi* were respectively collected and maintained in plastic boxes (8.0 × 8.0 × 4.0 cm, 200–250 females per box). Some virginal females copulated with male adults for pursuing the colony. The other female wasps were employed in the following experiments when they were 2-day old (Pak et al. 1986).

2.1.2 *Grapholitha funebrana*

A total of 300 peach branches with mature larvae of *G. funebrana* were cut from trees and maintained in the same insectaries as mentioned above. About 250 newly emerged adult moths were recovered from branches. Male and female adults were isolated in separated boxes (15.0 × 15.0 × 10.0 cm, 15 adults per box) until sexual maturity, which occurred after 3–4 days (Wang et al. 2019). Taxonomical identification

of founder individuals was performed following Zhang & Xu (2000). One pair of virgin and sexually matured adults of *G. funebrana* (3-day old) was placed into a plastic Petri dish (9 cm diameter which sealed by fabric net [40 mesh]). After 12h, the male was removed from the Petri dish and one sphere-shape filter paper (8.5 cm diameter) with one fresh peach leaf (6.0–6.5 cm²) was placed inside the Petri dish as an oviposition substrate. After a 12h oviposition period for each female, newly laid eggs on the peach leaves were collected for experiments or colonies.

2.2 Effect of host age on *T. dendrolimi* parasitism performance

A peach leaf bearing fifty (Hou et al. 2018) 1-day-old *G. funebrana* eggs (the eggs were selected after 23–25h of being oviposited by female moths) was placed into a small plastic Petri dish (4.5 cm diameter). Subsequently, one 2-day old *T. dendrolimi* female adult (F₀) was introduced into the Petri dish along with the *G. funebrana* eggs. After 24h of exposure (Du et al. 2018; Hou et al. 2018), the parasitoid was removed and the host eggs were kept in the same Petri dish until turning black (confirming parasitism). All black eggs were maintained until new parasitoid (F₁) emerged. The number of black eggs and emerged parasitoids were both recorded. The parasitism rate and emergence rate were estimated as follows: Parasitism rate = the number of black eggs/ the total number of eggs in each treatment. Emergence rate = the number of emerged parasitoids/ the number of all black eggs. Two other treatments with different host ages, namely 2- and 3-day-old *G. funebrana* eggs (fifty eggs per age), were also tested following the same procedure as that for treatment with 1-day-old eggs. Each treatment was replicated 15 times.

2.3 Effect of exposure time of the host to *T. dendrolimi* on parasitism

One 2-day old *T. dendrolimi* female adult and fifty 1-day old *G. funebrana* eggs on a patch leaf were introduced together into a Petri dish (D = 4.5 cm) that was covered by a fabric net. After the parasitoid and the host eggs were placed in the Petri dish, different exposure times of the host to the parasitoid were established. Then, exposure times of 12h, 24h, 36h, 48h, and 60h were set up. When those exposure times finished, the parasitoids were removed from the Petri dishes and host eggs in Petri dishes were daily supervised to record the number of parasitized eggs and the number of emerged parasitoids in each treatment. Each exposure time of the host to the parasitoid was considered as a treatment. Each treatment was replicated 15 times.

2.4 Effect of *T. dendrolimi* density on its parasitism performance

Different densities of 2-day old *T. dendrolimi* females were tested. Then, 1, 3, 5, 7, and 9 parasitoid females were respec-

tively introduced into a Petri dish (D = 9.0 cm) containing a leaf bearing two hundred 1-day old *G. funebrana* eggs per Petri dish. Parasitoids and the host eggs were confined together in the Petri dish for 24h. Then, parasitoids were removed and eggs in Petri dishes were daily supervised to record the total number of parasitized eggs (black eggs) and the number of emerged parasitoids. Here the parasitism rate per female was calculated (= parasitism rate / number of female wasps). Each treatment (i.e. parasitoid density) was replicated 15 times.

2.5 Effect of host eggs exposure to ultraviolet (UV) light on *T. dendrolimi* parasitism

One peach leaf bearing fifty 1-day old *G. funebrana* eggs was placed in a plastic Petri dish (D = 4.5 cm). Afterwards, the eggs in the Petri dish were exposed to 800 lux of UV light (230 nm) for 24h to kill egg embryo activity (Takada et al. 2001). After the 24h UV exposure, one 2-day old *T. dendrolimi* female was introduced into the Petri dish which was covered with mesh fabric net. Subsequently, the parasitoid was allowed to oviposit for 24h and then it was removed from the Petri dish. The host eggs were kept in the Petri dish and were daily observed to record the number of parasitized eggs and of newly emerged parasitoids. In addition to the UV-exposed group, a control group was also set up. This control group consisted of fifty 1-d old *G. funebrana* eggs in a Petri dish that followed the same experimental procedure than that for the UV-exposed group but were not treated with UV light. Both, control and UV-exposed groups were replicated 15 times.

2.6 Functional response of *T. dendrolimi* to *G. funebrana*

A peach leaf infested with different densities (15, 30, 45, 60 and 75 eggs per treatment) of 1-day old *G. funebrana* eggs was respectively placed in a Petri dish (D = 4.5 cm). One 2-day old *T. dendrolimi* female was introduced into each Petri dish that was then covered by a fabric net. After 24h of exposure, the female parasitoid was removed from the Petri dish. Afterwards, the exposed eggs were monitored to daily record the number of black eggs and emerged wasps as described above. Each treatment was replicated 15 times.

The functional response of *T. dendrolimi* parasitizing *G. funebrana* eggs was tested to fit the Holling II model (Holling 1959)

$$N_t = \frac{a'NT}{1 - a'T_h N} \quad (1)$$

Where N is the host egg density; T is the given holding duration (in the present study $T = 1$ day = 24h); N_t is the number of parasitized host eggs under each host egg density; “ a' ”

is the instantaneous attack rate, which means the theoretic parasitizing frequency (parasitized number) per given holding duration; “ T_h ” is the handling duration, which indicates the time needed to parasitize each host egg.

2.7 Statistical analysis

Parasitism, including parasitism rate per female in section 2.4, and emergence rates at each experiment were checked for normal distribution using Kolmogorov-Smirnov test prior to the analysis of variance. Parasitism and emergence rates at all experiments were transformed by arcsine square root to normalize data distribution and homogenize the variances. After transformation, they were analyzed using univariate analysis of variance (ANOVA) with a linear model followed by a Tukey’s HSD test for multiple comparisons (Zar 1998). In that way, the effect of the host age, host density, parasitoid density and exposure time on the parasitism and emergence rate of *T. dendrolimi* were tested. In addition, the correlation between parasitism rate and the host age was analyzed using the Pearson test. The effect of UV treatment of *G. funebrana* eggs on the parasitism and the emergence rate of *T. dendrolimi* was tested by independent t test at $P = 0.05$ level as data fitted normality and homoscedasticity assumptions. All statistical analyses were performed using SPSS 22.0 (SPSS Inc, Chicago, USA). The fitting regression of the *T. dendrolimi* parasitization performance to the Holling type II model was performed using Matlab r2019b(2019).

3 Results

3.1 Effect of host age on *T. dendrolimi* parasitism

The parasitism rate of *T. dendrolimi* significantly decreased with the increasing age of *G. funebrana* eggs from one to three days old ($F_{2,57} = 15.639$, $P < 0.05$). Additionally, the parasitism rate of *T. dendrolimi* was negatively correlated with the age of host eggs ($y = 26.65x + 8.633$, $R^2 = 0.98$, $P < 0.05$). However, when the emergence rate of F₁ wasps was compared among different ages of host eggs, no difference was found ($F_{2,57} = 1.392$, $P = 0.087$, Fig. 1).

3.2 Effect of exposure time of the host to *T. dendrolimi* on parasitism

The parasitism rate of *T. dendrolimi* positively increased with the exposure time of *G. funebrana* eggs exposure to the parasitoid ($F_{4,70} = 15.215$, $P < 0.01$), but emergence rate of F₁ offspring of the parasitoid was not affected by the exposure time ($F_{4,70} = 0.925$, $P = 0.135$, Fig. 2).

3.3 Effect of *T. dendrolimi* density on its parasitism performance

As shown in Fig. 3, the parasitism rate of *T. dendrolimi* on *G. funebrana* eggs significantly increased with the parasitoid density ($F_{4,70} = 116.395$, $P < 0.01$). However, parasitism rate per *T. dendrolimi* female was significantly reduced as parasitoid density increased ($F_{4,70} = 17.132$, $P < 0.01$). The para-

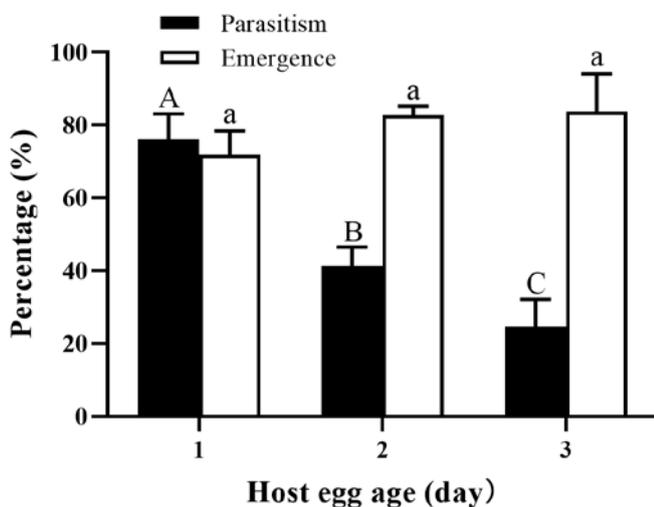


Fig. 1. Mean percentage (\pm SEM) of differently-aged *G. funebrana* eggs parasitized by *T. dendrolimi* female in 24h, and mean emergence percentage (\pm SEM) of F₁ offspring of the parasitoid. Histograms bearing different letters are significantly different ($P < 0.05$, ANOVA followed by a Tukey’s post hoc test).

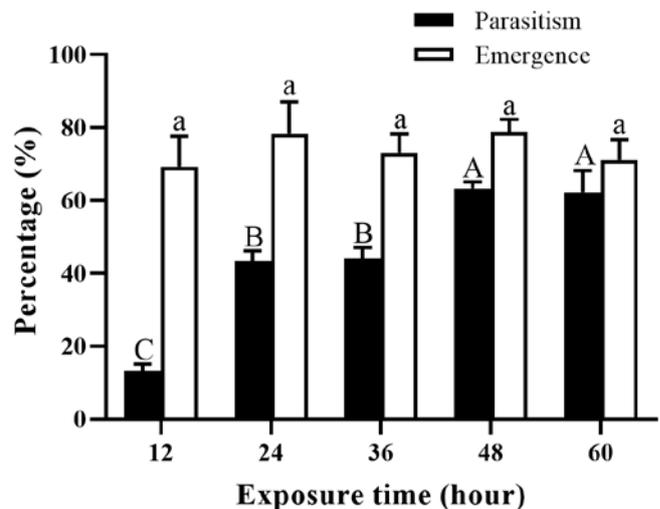


Fig. 2. Mean percentage (\pm SEM) of parasitized *G. funebrana* eggs exposed to *T. dendrolimi* female for different time and the resultant mean emergence percentage (\pm SEM) of F₁ *T. dendrolimi*. Histograms bearing different letters are significantly different ($P < 0.05$, ANOVA followed by a Tukey’s post hoc test).

sitism rate per female was similar when parasitoid densities were 1, 3 or 5 adult females, but was significantly reduced when parasitoid densities were 7 or 9 female adults (Fig. 3). The emergence rate of the F₁ parasitoid offspring was not significantly modified by the parasitoid density ($F_{4,70} = 2.505$, $P = 0.065$).

3.4 Effect of host eggs exposure to ultraviolet (UV) light on *T. dendrolimi* parasitism

As shown in Fig. 4, exposure of *G. funebrana* eggs to UV light did not affect parasitism rate of *T. dendrolimi* ($t = 4.477$, $d.f. = 29$, $P = 0.073$) nor the emergence rate ($t = 1.001$, $d.f. = 27$, $P = 0.092$) of F₁ parasitoids.

3.5 Functional response of *T. dendrolimi* to *G. funebrana*

The functional response of *T. dendrolimi* fitted well into the Holling type II Model with an equation of $N_t = 0.932N / (1 + 0.112N)$ ($R^2 = 0.932$, $P < 0.05$, Fig. 5). In a 24h period, the instantaneous attack rate (a') was 0.039 for single *T. dendrolimi* female and the handling duration time (T_h) was 0.287 h. As the density of *G. funebrana* eggs increased, the number of host eggs parasitized by *T. dendrolimi* significantly increased ($F_{4,70} = 14.091$, $P < 0.01$, Fig. 5), while the percentage of parasitism by the wasps significantly decreased ($F_{4,70} = 8.046$, $P < 0.01$, Fig. 6). However, the emergence rate of the F₁ parasitoid *T. dendrolimi* was not significantly affected by the density of host eggs ($F_{4,70} = 1.391$, $P = 0.088$, Fig. 6).

4 Discussion

Our results demonstrated that parasitism rate of *T. dendrolimi* significantly decreased as *G. funebrana* eggs aged (Fig. 1). This result is in line with previous results reported with *Trichogramma* parasitoids (Reznik & Umarova 1990; Ruberson & Kring 1993; Tunçbilek & Ayvaz 2003; Makey 2005; Reznik et al. 2011; Zhang et al. 2014; Du et al. 2018). For instance, it was documented that five *Trichogramma* species, *T. dendrolimi*, *T. chilonis*, *T. ostrinae*, *T. leucaniae* and *T. japonicum*, parasitizing *Mythimna separata* (Lepidoptera: Noctuidae), showed preference toward younger host eggs (Hou et al. 2018). Particularly, the parasitism rate of *T. dendrolimi* on 0- and 1-day-old *M. separata* eggs was significantly higher than that on 2- and 3-day-old eggs (Hou et al. 2018). Together, that results and those of the present study, indicate that parasitism performance of *T. dendrolimi* will be higher on younger than older host eggs (Fig. 1). A possible explanation for this finding includes the possibility that the host's defensive capacities increase with age (Mattiacci & Dicke 1995). Future experiments analyzing the immune response of this host along its age would be helpful to test this hypothesis (Contreras-Garduño et al. 2016). Other possibility includes a potential variation of host nutritional properties along its age and the ability of the wasp to discriminate that quality (Velasco-Hernández et al. 2017), future research to explore this possibility is warranted. From an applied point of view, this result suggests that special attention must

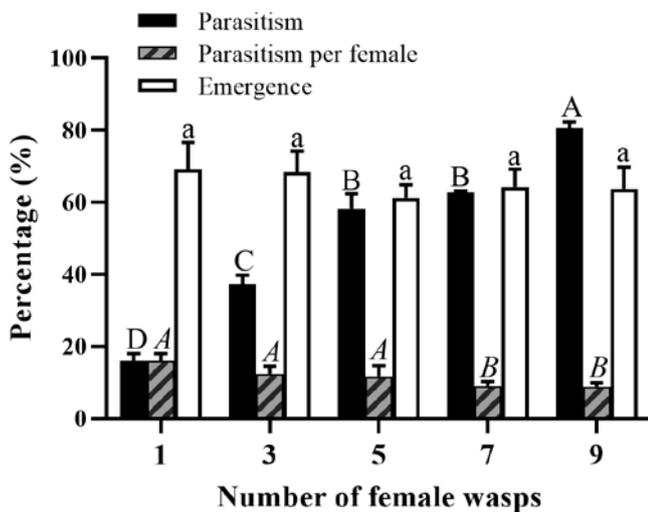


Fig. 3. Total and per female parasitism percentage of different densities of *T. dendrolimi* on *G. funebrana* eggs in 24h as well as emergence percentage of F₁ *T. dendrolimi* in parasitized eggs. Histograms (values are present by mean \pm SEM) bearing different letters are significantly different ($P < 0.05$, ANOVA followed by a Tukey's post hoc test).

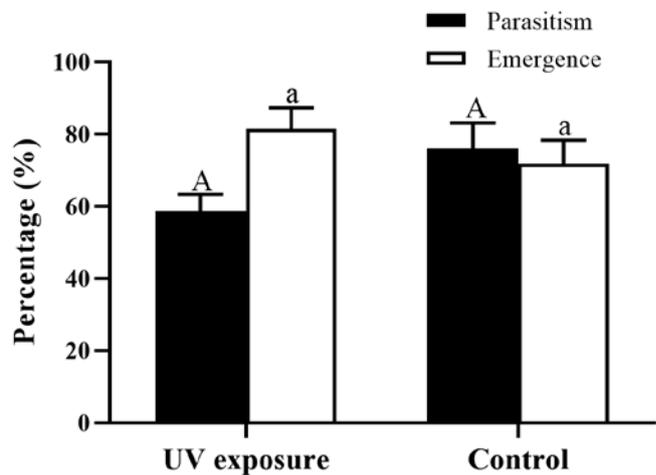


Fig. 4. Mean parasitism and emergence percentage (\pm SEM) of *T. dendrolimi* on UV-exposed and unexposed (control) *G. funebrana* eggs. Histograms bearing the same letter are not significantly different ($P > 0.05$, independent *t* test)

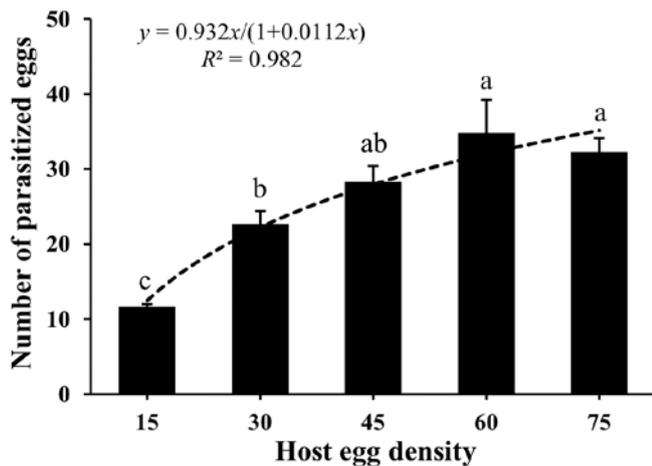


Fig. 5. Functional response of *T. dendrolimi* to the increasing *G. funebrana* egg density. Functional response curve is fitting into the Holling type II equation ($y = 0.932x / (1 + 0.0112x)$, $R^2 = 0.982$). Histograms (values are present by mean \pm SEM) bearing different letters are significantly different ($P < 0.05$, ANOVA followed by a Tukey's post hoc test).

be paid to the time-point release of the wasps. It is likely that a better parasitism effectiveness would be obtained if parasitoid releases have place at the beginning of the reproductive period of *G. funebrana* moths. Regarding the effect of exposure time of the host to *T. dendrolimi*, our results show that parasitism increases as exposure time increases (Fig. 2). This result is in agreement with a previous study by Laurentis et al. (2019) where the parasitism of *Trichogramma pretiosum* on *Corcyra cephalonica* eggs significantly increased over the time of exposure. More specifically, parasitism rate was significantly higher after 48 h of host exposure, compared to 24 h of exposure (Laurentis et al. 2019). The increased parasitism rate over the time exposure may be directly related to the greater window of availability of the hosts for the parasitoid. It is important to note that parasitism after 24h of exposure was almost three times that of parasitism at 12h and, in subsequent exposure periods, parasitism did not increase as much (Fig. 2). The foregoing suggests that the wasp of this species could be able to integrate processes of learning to optimize foraging and parasitism mainly during the first 24 hours (Guiunti et al. 2015). Subsequent studies to analyze this possibility are needed.

As for the effect of parasitoid density on its parasitism performance, our results show that with an increase of the parasitoid density, their total parasitism rate increases (Fig. 3). However, when parasitism per female was analyzed, it was found a significant reduction in parasitism per female (Fig. 3). As intra and interspecific interactions can modulate prey-predator interactions (Perez-Valencia et al. 2019), the observed reduction is probably due to intraspecific competition among female wasps for the hosts at the

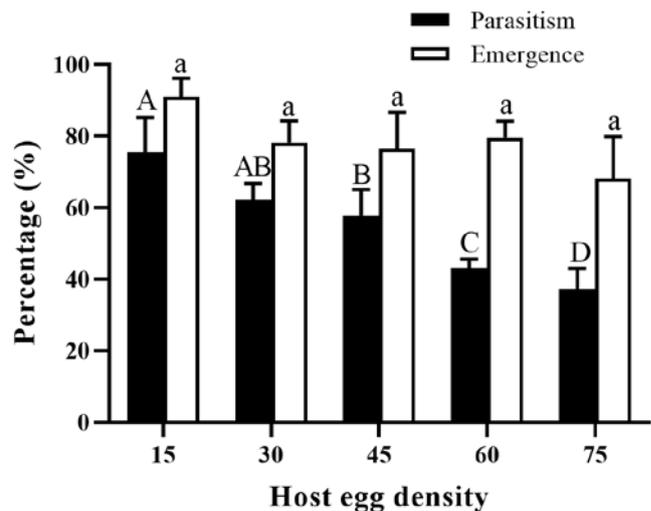


Fig. 6. Mean parasitism percentage (\pm SEM) of *T. dendrolimi* female on different densities of *G. funebrana* eggs in 24 h, and mean emergence percentage (\pm SEM) of F1 *T. dendrolimi*. Histograms bearing different letters are significantly different ($P < 0.05$, ANOVA followed by a Tukey's post hoc test).

higher parasitoid densities (7 and 9 *T. dendrolimi* females / 200 *G. funebrana* eggs). Besides, the mutual interference among parasitoids could also occur with an increase of parasitoid density, leading to a lower parasitism rate per female (Hassell & Varley, 1969; Hassell 1978). Nonetheless, the ultimate biocontrol effectiveness to the pests, represented by the parasitism rate, was dramatically accelerated as the density of parasitoids increased (i.e. near to 80% of eggs were parasitized when 9 parasitoid females were released, Fig. 3). This indicates that although intraspecific competition and/or mutual interference could have place, affecting the individual parasitism (i.e. parasitism rate per female), the overall parasitism performance of this wasp (i.e. parasitism rate) increased with a higher number of released females (Fig. 3).

In this study we were also interested to assess the potential effect of host eggs exposure to ultraviolet (UV) light on *T. dendrolimi* parasitism. This is of particular interest because UV irradiation has been frequently used to sterilize host eggs in numerous *Trichogramma* parasitism studies (Hoffmann et al. 2001; St-Onge et al. 2016; Takada et al. 2000; 2001). Then, it was important to assess whether host eggs sterilization using UV light could affect parasitism performance (St-Onge et al. 2014). On this regard, our results showed that the exposure of host eggs to UV light does not modify the parasitism rate of *T. dendrolimi* (Fig. 4). This indicates that the sterilization of host eggs using UV light during mass production of the biological agent *T. dendrolimi* does not affect its parasitism performance. *Trichogramma* could develop and emerge normally even when the host eggs were killed by UV irradiation (St-Onge et al. 2014).

The functional response is a very valuable tool to identify the optimal ratio of host population and the natural enemies, especially for those to be massively produced under laboratory conditions and it's also a necessary parameter for the experimental evaluation on the performance of biological control agents (Berryman 1999; Bernstein 2000; Fernández-Arhex & Corley 2003; Zang et al. 2011). Holling II model is a customary type of functional response that is generally associated with the invertebrate parasitoids and predators (Holling 1959; Hassell et al. 1977; Desneux et al. 2005; Liu et al. 2011; Yao et al. 2015). According to the results of this study, the functional response of *T. dendrolimi* when confronted to increasing densities of *G. funebrana* eggs fitted the Holling II model (Fig. 5). As seen in Fig. 5 and Fig. 6, the Holling type II functional response, is an asymptotic curve that decelerated gradually as the density of *G. funebrana* eggs increased due to the handling time needed by the parasitoid to manipulate the host. Therefore, the capacity of parasitization (the number of parasitized host eggs) would increase with the increasing host density until the maximum capacity of parasitization by the natural enemy (Li et al. 2011; Luo et al. 2013). Theoretically, the maximum number of hosts parasitized per female and day is the ratio (T/T_h) between exposure time and handling time (Chen et al., 2006). Consequently, a maximum of 83.6 *G. funebrana* eggs per day could be parasitized by a single *T. dendrolimi* female, under the current experimental condition (calculated by the parameters in Section 3.5). The baseline information obtained from the laboratory functional response could be useful to establish the quality control standards in mass-rearing projects of this biological control agent *T. dendrolimi* (Allahyari et al. 2004). Although Holling type II model has been used to evaluate the functional response of parasitoids to pest hosts in many researches, it may be more suitable to evaluate predators rather parasitoids because the Holling model fitness may be influenced by predation or parasitism (Fernández-arhex & Corley 2003; Zamani et al. 2006). Mostly, we considered the parasitizing as another kind of Lotka-Volterra model (Margiotta et al. 2017; Mills & Getz 1996). Besides, for the purposes of functional response assessment, parasitoids may be regarded as similar than predators because parasitized host eggs would no longer affect the pest population growth. In addition, a more suitable ecological model between hosts and parasitoids will be further explored and developed in future studies.

Overall, these results suggest that a better parasitism performance of *T. dendrolimi* on *G. funebrana* could be obtained paying attention to the *T. dendrolimi* time-point release (as a higher parasitism is obtained with younger host eggs, Fig. 1), releasing higher densities of the wasp (Fig. 3) and considering the host eggs densities (Fig. 5). Augmentative release of *Trichogramma* parasitoids to manage the plum fruit moth *G. funebrana* and other lepidopteran pests is one of the key IPM components in various fruit orchards in China (Feng et al. 1989; Li et al. 2014, 2016; Zhou et al. 2014). Nevertheless,

due to the sensitivity of parasitoids to numerous biotic and abiotic factors in the inundative biological control program, potential integration with other control tactics may contribute to preventing yield and economic losses. For instance, environmentally friendly insecticides or biopesticides could be used as supplementary treatments to control the surviving caterpillars that were not killed as moth eggs (Rizzo et al. 2012; Zhou et al. 2014). In addition, more biological agents, including predatory or larval parasitoids and other strategies such as the use of pheromone traps, can be integrated in the system to achieve a higher efficiency of the plum fruit moth control (Zhou et al. 2014; Nastas et al. 2016; Negahban et al. 2016)

5 Conclusions

Improvement of augmentative biological control of lepidopteran fruit pests using *Trichogramma* parasitoids in large-scale orchards will be an important part of organic agriculture development in China. In the laboratory, the parasitism rate of *T. dendrolimi* was studied regarding the effect of *G. funebrana* egg ages. This parasitoid parasitized significantly more younger than older host eggs. In addition, the density of *T. dendrolimi* female adults and the exposure time between *G. funebrana* eggs and *T. dendrolimi* adults both positively impacted the parasitism rate of *T. dendrolimi*. Treatment with UV irradiation on the host eggs did not change the parasitism rate of the parasitoid. Moreover, functional response of *T. dendrolimi* to *G. funebrana* eggs fitted the Holling II Model. All factors above did not influence the emergence rate of F_1 parasitoids. Field application of *T. dendrolimi* should be done in future studies to validate and optimize the biological control efficiency of this parasitoid on the plum fruit pest.

Authors Contributions: X.C., F.Z., L.Z. and S.W. designed the experiment; X.C. conducted the experiment; X.C., F.Z., L.S.M., and S.W. carried out the data analysis; Y.Q., R.R-R, N.D. and S.W. wrote and revised the manuscript; all authors read and approved the final version of manuscript.

Conflict of Interest: The authors have declared that they have no conflict of interest.

Ethics approval: This article does not contain any studies with human participants or animals performed by any of the authors.

Data Availability: All data analyzed during this study are included in this published article.

Acknowledgements: This work was financially supported by Beijing Key Laboratory of Environment-Friendly Management on Fruit Diseases and Pests in North China, Grant/Award

Number: BZ0432; National Key Research and Development Program of China, Grant/Award Number: 2017YFD0201000; Beijing Science and Technology Program, Grant/Award Number: D171100001617003. RRR thanks Dr. Jorge Contreras-Garduño (ENES-UNAM, Morelia, Mexico) for providing optimal conditions to work on this study during his sabbatical stay, as well as the CONAcYt sabbatical scholarship N° 740591.

References

- Alford, D. V. (1987). *Farbatlas der Obstschädlinge*. Stuttgart: Thieme.
- Allahyari, H., Fard, P. A., & Nozari, J. (2004). Effects of host on functional response of offspring in two populations of *Trissolcus grandis* on the sunn pest. *Journal of Applied Entomology*, 128(1), 39–43. <https://doi.org/10.1046/j.1439-0418.2003.00804.x>
- Bernstein, C. (2000). Host-parasitoid models: the story of a successful failure. In M. E. Hochberg & A. R. Ives (Eds.), *Parasitoid population biology* (pp. 41–57). Princeton: University Press.
- Berryman, A. A. (1999). The theoretical foundations of biological control. In B. A. Hawkins & H. V. Cornell (Eds.), *Theoretical approaches to biological control* (pp. 3–21). Cambridge: Cambridge University Press. <https://doi.org/10.1017/CBO9780511542077.003>
- Boo, K. S., & Yang, J. P. (2000). Kairomones used by *Trichogramma chilonis* to find *Helicoverpa assulta* eggs. *Journal of Chemical Ecology*, 26(2), 359–375. <https://doi.org/10.1023/A:1005453220792>
- Chen, W. L., Leopold, R. A., & Harris, M. O. (2006). Parasitism of the glassy-winged sharpshooter, *Homalodisca coagulata* (Homoptera: Cicadellidae): Functional response and superparasitism by *Gonatocerus ashmeadi* (Hymenoptera: Mymaridae). *Biological Control*, 37(1), 119–129. <https://doi.org/10.1016/j.biocontrol.2005.10.011>
- Contreras-Garduño, J., Lanz-Mendoza, H., Franco, B., Nava, A., Pedraza-Reyes, M., & Canales-Lazcano, J. (2016). Insect immune priming: Ecology and experimental evidences. *Ecological Entomology*, 41(4), 351–366. <https://doi.org/10.1111/een.12300>
- Desneux, N., Fauvergue, X., Dechaume-Moncharmont, F. X., Kerhoas, L., Ballanger, Y., & Kaiser, L. (2005). *Diaeretiella rapae* limits *Myzus persicae* populations following applications of deltamethrin in oilseed rape. *Journal of Economic Entomology*, 98(1), 9–17. <https://doi.org/10.1093/jee/98.1.9>
- Desneux, N., Decourtye, A., & Delpuech, J. M. (2007). The sublethal effects of pesticides on beneficial arthropods. *Annual Review of Entomology*, 52(1), 81–106. <https://doi.org/10.1146/annurev.ento.52.110405.091440>
- Du, W. M., Xu, J., Hou, Y. Y., Lin, Y., Zang, L. S., Yang, X., ... Desneux, N. (2018). *Trichogramma* parasitoids can distinguish between fertilized and unfertilized host eggs. *Journal of Pest Science*, 91(2), 771–780. <https://doi.org/10.1007/s10340-017-0919-z>
- Feng, J. G., Zhang, Y., Tao, X., Wang, Y. S., & Xu, Z. G. (1989). Release of *Trichogramma dendrolimi* [Hym.: Trichogrammatidae] to control *Adoxophyes orana* [Lep.: Tortricidae] in apple orchards. *Zhongguo Shengwu Fangzhi Xuebao*, 5, 56–59.
- Fernández-Arhex, V., & Corley, J. C. (2003). The functional response of parasitoids and its implications for biological control. *Biocontrol Science and Technology*, 13(4), 403–413. <https://doi.org/10.1080/0958315031000104523>
- García, P., Wajnberg, E., Oliveira, L., & Tavares, J. (2001). Is the parasitization capacity of *Trichogramma cordubensis* influenced by the age females? *Entomologia Experimentalis et Applicata*, 98(2), 219–224. <https://doi.org/10.1046/j.1570-7458.2001.00777.x>
- Gavriliță, L., & Nastas, T. (2017). Reduction of *Grapholita funebrana* Hb. pest density at plum culture. In *Conservation of Plant Diversity* pp. 131.
- Geng, J., Shen, Z., Li, Z., & Zhang, F. (2005). Optimal stage and temperature for cold storage of *Trichogramma dendrolimi* reared on *Antheraea pernyi* eggs. *Acta Entomologica Sinica*, 48, 903.
- Giunti, G., Canale, A., Messing, R. H., Donati, E., Stefanini, C., Michaud, J. P., & Benelli, G. (2015). Parasitoid learning: Current knowledge and implications for biological control. *Biological Control*, 90, 208–219. <https://doi.org/10.1016/j.biocontrol.2015.06.007>
- Gul, H., Ullah, F., Biondi, A., Desneux, N., Qian, D., Gao, X., & Song, D. (2019). Resistance against clothianidin and associated fitness costs in the chive maggot, *Bradysia odoriphaga*. *Entomologia Generalis*, 39(2), 81–92. <https://doi.org/10.1127/entomologia/2019/0861>
- Guo, X. J., Di, N., Chen, X., Zhu, Z., Zhang, F., Tang, B., ... Wang, S. (2019). Performance of *Trichogramma pintoi* when parasitizing eggs of the oriental fruit moth *Grapholita molesta*. *Entomologia Generalis*, 39(3-4), 239–249. <https://doi.org/10.1127/entomologia/2019/0853>
- Hári, K., & Péntzes, B. (2010). Selectivity of the oriental fruit moth sex pheromone trap in peach and apricot orchards. *International Journal of Horticultural Science*, 16(2), 17–20. <https://doi.org/10.31421/IJHS/16/2/878>
- Hassell, M. P. (1978). *The dynamics of arthropod predator-prey systems*. Princeton: Princeton University Press.
- Hassell, M. P., Lawton, J. H., & Beddington, J. R. (1977). Sigmoid functional responses by invertebrate predators and parasitoids. *Journal of Animal Ecology*, 46(1), 249–262. <https://doi.org/10.2307/3959>
- Hassell, M. P., & Varley, G. C. (1969). New inductive population model for insect parasites and its bearing on biological control. *Nature*, 223(5211), 1133–1137. <https://doi.org/10.1038/2231133a0>
- Helyer, N., Cattlin, N. D., & Brown, K. C. (2014). *Biological control in plant protection: a colour handbook*. Boca Raton: CRC Press. <https://doi.org/10.1201/b16042>
- Hoffmann, M. P., Ode, P. R., Walker, D. L., Gardner, J., van Nouhuys, S., & Shelton, A. M. (2001). Performance of *Trichogramma ostrinae* (Hymenoptera: Trichogrammatidae) reared on factitious hosts, including the target host, *Ostrinia nubilalis* (Lepidoptera: Crambidae). *Biological Control*, 21(1), 1–10. <https://doi.org/10.1006/bcon.2000.0912>
- Holling, C. S. (1959). Some characteristics of simple types of predation and parasitism. *Canadian Entomologist*, 91(7), 385–398. <https://doi.org/10.4039/Ent91385-7>
- Hou, Y. Y., Yang, X., Zang, L. S., Zhang, C., Monticelli, L. S., & Desneux, N. (2018). Effect of oriental armyworm *Mythimna separata* egg age on the parasitism and host suitability for five

- Trichogramma* species. *Journal of Pest Science*, 91(4), 1181–1189. <https://doi.org/10.1007/s10340-018-0980-2>
- Huang, J., Hua, H. Q., Zhang, F., & Li, Y. X. (2018). Suitability assessment of three *Trichogramma* species in the control of *Mythimna separata* (Lepidoptera: Noctuidae). *Journal of Applied Entomology*, 142(1-2), 131–140. <https://doi.org/10.1111/jen.12414>
- Iqbal, A., Chen, Y. M., Hou, Y. Y., Zhang, L., Desneux, N., & Zang, L. S. (2019). Factitious host species impact on the outcome of multiparasitism between egg parasitoids. *Journal of Pest Science*, 92(3), 1261–1269. <https://doi.org/10.1007/s10340-019-01122-8>
- Jin, T., Lin, Y., Han, S., Ma, G., Wen, H., & Peng, Z. (2019). Host performance of *Trichogramma* species on *Opisina arenosella*, and evaluation of their biological control efficacy. *Journal of Asia-Pacific Entomology*, 22(3), 990–996. <https://doi.org/10.1016/j.aspen.2019.06.010>
- Laurentis, V. L., Ramalho, D. G., Santos, N. A., Carvalho, V. F. P., Vacari, A. M., De Bortoli, S. A., ... Dami, B. G. (2019). Performance of *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae) on eggs of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). *Scientific Reports*, 9(1), 1156. <https://doi.org/10.1038/s41598-018-37797-9>
- Li, X. Y., Lei, Q., Hua, H. Q., Song, H. F., Wang, S., Ramirez-Romero, R., ... Li, Y. X. (2019). Impact of host suitability on oviposition preference toward fertilized and unfertilized host eggs in two *Trichogramma* parasitoid species. *Entomologia Generalis*, 39(3-4), 313–323. <https://doi.org/10.1127/entomologia/2019/0857>
- Li, D. S., Liao, C., Zhang, B. X., & Song, Z. W. (2014). Biological control of insect pests in litchi orchards in China. *Biological Control*, 68, 23–36. <https://doi.org/10.1016/j.biocontrol.2013.06.003>
- Li, J., Zhao, L., Li, Y., Zhao, Z., & Ma, R. (2016). Inoculative releases of *Trichogramma dendrolimi* for suppressing the oriental fruit moth (*Grapholita molesta*) in peach orchard in China. *Fruits*, 71(2), 123–128. <https://doi.org/10.1051/fruits/2015054>
- Lin, N. Q. (1994). *The Trichogramma Taxa in China (Hymenoptera: Trichogramma)*. Fuzhou, China: Fujian Science and Technology Publishing House.
- Liu, S., Wang, S., Liu, B., Zhou, C., & Zhang, F. (2011). The predation function response and predatory behavior observation of *Chrysopa pallens* larva to *Bemisia tabaci*. *Zhongguo Nong Ye Ke Xue*, 44, 1136–1145.
- Liu, X. L., Tang, Q. L., Li, Y. D., Campos, M. R., Liang, P., & Gao, X. W. (2017). Widespread resistance of the aphid *Myzus persicae* to pirimicarb across China, and insights on ace2 mutation frequency in this species. *Entomologia Generalis*, 36(4), 285–299. <https://doi.org/10.1127/entomologia/2017/0480>
- Lu, Q. G. (1992). A laboratory study on the functional response of *Trichogramma* sp (Hymenoptera: Trichogrammatidae) in Kenya. *Zhongguo Shengwu Fangzhi Xuebao*, 8, 151–154.
- Luo, S., Li, H., Lu, Y., Zhang, F., Haye, T., Kuhlmann, U., & Wu, K. (2014). Functional response and mutual interference of *Peristenus spretus* (Hymenoptera: Braconidae), a parasitoid of *Apolygus lucorum* (Heteroptera: Miridae). *Biocontrol Science and Technology*, 24(3), 247–256. <https://doi.org/10.1080/09583157.2013.855703>
- Makee, H. (2005). Factors influencing the parasitism of codling moth eggs by *Trichogramma cacoeciae* March. and *T. principium* Sug. et Sor. (Hymen. Trichogrammatidae). *Journal of Pest Science*, 78(1), 31–39. <https://doi.org/10.1007/s10340-004-0064-3>
- Margiotta, M., Bella, S., Buffa, F., Caleca, V., Floris, I., ... Tortorici, F. (2017). Modeling environmental influences in the *Psyllaephagus bliteus* (Hymenoptera: Encyrtidae) – *Glycaspis brimblecombei* (Hemiptera: Aphalaridae) parasitoid-host system. *Journal of Economic Entomology*, 110, 491–501.
- MathWorks (2019). *Statistics and Machine Learning Toolbox™ User's Guide R2019b*.
- Mattiacci, L., & Dicke, M. (1995). The parasitoid *Cotesia glomerata* (Hymenoptera: Braconidae) discriminates between first and fifth larval instars of its host *Pieris brassicae*, on the basis of contact cues from frass, silk, and herbivore-damaged leaf tissue. *Journal of Insect Behavior*, 8(4), 485–498. <https://doi.org/10.1007/BF01995321>
- Mills, N. J., & Getz, W. M. (1996). Modelling the biological control of insect pests: A review of host-parasitoid models. *Ecological Modelling*, 92(2-3), 121–143. [https://doi.org/10.1016/0304-3800\(95\)00177-8](https://doi.org/10.1016/0304-3800(95)00177-8)
- Moiroux, J., Abram, P. K., Louâpre, P., Barrette, M., Brodeur, J., & Boivin, G. (2016). Influence of temperature on patch residence time in parasitoids: Physiological and behavioural mechanisms. *Naturwissenschaften*, 103(3–4), 32. <https://doi.org/10.1007/s00114-016-1357-0>
- Nastas, T., Gavrilita, L., Bradowsky, N., & Elisovetcaia, D. (2016). The influence of the biological agents on the density suppression of *Grapholita funebrana* Tr. population in plum crop. *Biologie*, 25, 11–15.
- Negahban, M., Sedaratian-Jahromi, A., Ghancee-Jahromi, M., & Haghani, M. (2016). Monitoring of an Iranian population of *Grapholita funebrana* Treitschke, 1835 (Lepidoptera: Tortricidae) using sex pheromone traps: an applicable procedure for sustainable management. *Entomofauna Zeitschrift für Entomologie*, 37, 241–252.
- Pak, G. A., Buis, H. C. E. M., Heck, I. C. C., & Hermans, M. L. G. (1986). Behavioural variations among strains of *Trichogramma* spp.: Host-age selection. *Entomologia Experimentalis et Applicata*, 40(3), 247–258. <https://doi.org/10.1111/j.1570-7458.1986.tb00508.x>
- Paraiso, O., Hight, S. D., Kairo, M. T., Bloem, S., Carpenter, J. E., & Reitz, S. (2012). Laboratory biological parameters of *Trichogramma fuentesi* (Hymenoptera: Trichogrammatidae), an egg parasitoid of *Cactoblastis cactorum* (Lepidoptera: Pyralidae). *The Florida Entomologist*, 95(1), 1–7. <https://doi.org/10.1653/024.095.0101>
- Pérez-Valencia, L. I., Camorlinga-Cortés, P., Carrillo-Arámbula, L. C., Palmeros-Suárez, P. A., & Ramirez-Romero, R. (2019). Why can a predator increase its consumption of prey when it is released along with a parasitoid? *Entomologia Generalis*, 39(3-4), 205–219. <https://doi.org/10.1127/entomologia/2019/0810>
- Perveen, F., & Sultan, R. (2012). Effects of the host and parasitoid densities on the quality production of *Trichogramma chilonis* on lepidopterous (*Sitotroga cerealella* and *Corcyra cephalonica*) eggs. *Arthropods*, 1, 63.
- Pizzol, J., Pintureau, B., Khoualdia, O., & Desneux, N. (2010). Temperature-dependent differences in biological traits between two strains of *Trichogramma cacoeciae* (Hymenoptera: Trichogrammatidae). *Journal of Pest Science*, 83(4), 447–452. <https://doi.org/10.1007/s10340-010-0327-0>
- Pizzol, J., Desneux, N., Wajnberg, E., & Thiéry, D. (2012). Parasitoid and host egg ages have independent impact on vari-

- ous biological traits in a *Trichogramma* species. *Journal of Pest Science*, 85(4), 489–496. <https://doi.org/10.1007/s10340-012-0434-1>
- Reznik, S. Y., & Umarova, T. Y. (1990). The influence of host's age on the selectivity of parasitism and fecundity of *Trichogramma*. *Entomophaga*, 35(1), 31–37. <https://doi.org/10.1007/BF02374298>
- Reznik, S. Y., Vaghina, N. P., & Voinovich, N. D. (2011). Effects of previous experience and age-related changes on host eggs parasitization by *Trichogramma buesi* Voegelé (Hymenoptera, Trichogrammatidae) females. *Entomological Review*, 91(3), 281–291. <https://doi.org/10.1134/S0013873811030018>
- Riolo, P., Bruni, R., Cappella, L., Rama, F., & Isidoro, N. (2010). Control of the plum fruit moth, *Grapholita funebrana* (Treitsch.) (Lepidoptera, Tortricidae), by false-trail following. In *Integrated Fruit Protection in Fruit Crops. IOBC/WPRS Bulletin*, 54, 401–404.
- Rizzo, R., Lo Verde, G., & Lombardo, A. (2012). Effectiveness of spinosad and mineral oil for control of *Grapholita funebrana* Treitschke in organic plum orchards. *New Medit*, 11, 70–72.
- Ruberson, J. R., & Kring, T. J. (1993). Parasitism of developing eggs by *Trichogramma pretiosum* (Hymenoptera: Trichogrammatidae): host age preference and suitability. *Biological Control*, 3(1), 39–46. <https://doi.org/10.1006/bcon.1993.1007>
- Silva, J. E., Ribeiro, L. M. D., Vinasco, N., Guedes, R. N. C., & Siqueira, H. A. A. (2019). Field-evolved resistance to chlorantraniliprole in the tomato pinworm *Tuta absoluta*: Inheritance, cross-resistance profile, and metabolism. *Journal of Pest Science*, 92(4), 1421–1431. <https://doi.org/10.1007/s10340-018-1064-z>
- Smith, S. M. (1996). Biological control with *Trichogramma*: Advances, successes, and potential of their use. *Annual Review of Entomology*, 41(1), 375–406. <https://doi.org/10.1146/annurev.en.41.010196.002111>
- St-Onge, M., Cormier, D., Todorova, S., & Lucas, É. (2014). Comparison of *Ephesttia kuehniella* eggs sterilization methods for *Trichogramma* rearing. *Biological Control*, 70, 73–77. <https://doi.org/10.1016/j.biocontrol.2013.12.006>
- St-Onge, M., Cormier, D., Todorova, S., & Lucas, É. (2016). Conservation of *Ephesttia kuehniella* eggs as hosts for *Trichogramma ostrinae*. *Journal of Applied Entomology*, 140(3), 218–222. <https://doi.org/10.1111/jen.12227>
- Stefanova, D. R., Kutinkova, H. Y., Savov, P. V., Andreev, R. A., Palagacheva, N. G., & Tityanov, M. G. (2019). Control of plum fruit moth, *Grapholita funebrana* Tr., by ISOMATE®-OFM TT dispensers in plum orchards of Bulgaria. In *Pheromones and Other Semiochemicals in Integrated Production and Integrated Protection of Fruit Crops. IOBC/WPRS Bulletin*, 146, 64–68.
- Subchev, M., Toshova, T., Koshio, C., Franke, S., Tröger, A., Twele, R., ... Woodcock, C. M. (2009). Identification and biological activity of sex pheromone components from females of the plum moth *Illiberis rotundata* Jordan (Lepidoptera: Zygaenidae: Procrudinae). *Chemoecology*, 19(1), 47–54. <https://doi.org/10.1007/s00049-009-0008-8>
- Tabone, T., Bardon, C., Desneux, N., & Wajnberg, E. (2010). Parasitism of different *Trichogramma* species and strains on *Plutella xylostella* L. on greenhouse cauliflower. *Journal of Pest Science*, 83, 251–256. <https://doi.org/10.1007/s10340-010-0292-7>
- Takada, Y., Kawamura, S., & Tanaka, T. (2000). Biological characteristics: growth and development of the egg parasitoid *Trichogramma dendrolimi* (Hymenoptera: Trichogrammatidae) on the cabbage armyworm *Mamestra brassicae* (Lepidoptera: Noctuidae). *Applied Entomology and Zoology*, 35(3), 369–379. <https://doi.org/10.1303/aez.2000.369>
- Takada, Y., Kawamura, S., & Tanaka, T. (2001). Host preference of *Trichogramma dendrolimi* (Hymenoptera: Trichogrammatidae) on its native host, *Mamestra brassicae* (Lepidoptera: Noctuidae) after 12 continuous generations on a factitious host. *Applied Entomology and Zoology*, 36(2), 213–218. <https://doi.org/10.1303/aez.2001.213>
- Thiéry, D., & Desneux, N. (2018). Host plants of the polyphagous grapevine moth *Lobesia botrana* during larval stage modulate moth egg quality and subsequent parasitism by the parasitoid *Trichogramma cacoeciae*. *Entomologia Generalis*, 38(1), 47–59. <https://doi.org/10.1127/entomologia/2018/0675>
- Tunçbilek, A. Ş., & Ayvaz, A. (2003). Influences of host age, sex ratio, population density, and photoperiod on parasitism by *Trichogramma evanescens* Westw. (Hym., Trichogrammatidae). *Journal of Pest Science*, 76(6), 176–180. <https://doi.org/10.1007/s10340-003-0018-1>
- Velasco-Hernández, M. C., Desneux, N., Ramírez-Martínez, M. M., Cicero, L., & Ramírez-Romero, R. (2017). Host species suitability and instar preference of *Aphidius ervi* and *Aphelinus abdominalis*. *Entomologia Generalis*, 36(4), 347–367. <https://doi.org/10.1127/entomologia/2017/0500>
- Wang, C. L., Zhang, J., & Huo, S. T. (1998). Study, reproduction and utilization of *Trichogramma*. In J.Z. Bao & D.X. Gu (eds), *Biological Control in China. Chapter 1, Section 2*. (pp. 67–123). Taiyuan: Shanxi Science & Technology Press.
- Wang, Z. Y., He, K., & Yan, S. (2005). Large-scale augmentative biological control of Asian corn borer using *Trichogramma* in China: A success story. In *Second International Symposium on Biological Control of Arthropods*, Davos, Switzerland, 1216, 487–494.
- Wang, Y., Kong, W. N., Guo, Y. F., Chai, X. H., Li, J., & Ma, R. Y. (2019). Effect of pupal exposure to different photoperiods on emergence, mating and reproduction of *Grapholita molesta* (Lepidoptera, Tortricidae). *Yingyong Kunchong Xuebao*, 56, 307–315.
- Wang, Y., Xiang, M., Hou, Y. Y., Yang, X., Dai, H. J., Li, J., & Zang, L. S. (2019). Impact of egg deposition period on the timing of adult emergence in *Trichogramma* parasitoids. *Entomologia Generalis*, 39(3-4), 339–346. <https://doi.org/10.1127/entomologia/2019/0896>
- Weisenburger, D. D. (1993). Human health effects of agricultural use. *Human Pathology*, 24(6), 571–576. [https://doi.org/10.1016/0046-8177\(93\)90234-8](https://doi.org/10.1016/0046-8177(93)90234-8)
- Xu, H. Q. (2014). The acute toxicity and safety evaluation of 16 insecticides used in forestry to *Trichogramma dendrolimi*. *Forest Science and Technology*, 2, 5.
- Yao, F. L., Zheng, Y., Zhao, J. W., Desneux, N., He, Y. X., & Weng, Q. Y. (2015). Lethal and sublethal effects of thiamethoxam on the whitefly predator *Serangium japonicum* (Coleoptera: Coccinellidae) through different exposure routes. *Chemosphere*, 128, 49–55. <https://doi.org/10.1016/j.chemosphere.2015.01.010>
- Zamani, A., Talebi, A., Fathipour, Y., & Baniamiri, V. (2006). Temperature-dependent functional response of two aphid parasitoids, *Aphidius colemani* and *Aphidius matricariae* (Hymenoptera: Aphidiidae), on the cotton aphid. *Journal of Pest Science*, 79(4), 183–188. <https://doi.org/10.1007/s10340-006-0132-y>

- Zar, J. H. (1998). *Biostatistical Analysis*. Upper Saddle River, NJ: Prentice Hall.
- Zang, L. S., Liu, T. X., Zhang, F., Shi, S. S., & Wan, F. H. (2011). Mating and host density affect host feeding and parasitism in two species of whitefly parasitoids. *Insect Science*, *18*(1), 78–83. <https://doi.org/10.1111/j.1744-7917.2010.01382.x>
- Zang, L. S., Wang, S., Zhang, F., & Desneux, N. (2021). Biological control with *Trichogramma* in China: History, present status and perspectives. *Annual Review of Entomology*. <https://doi.org/10.1146/annurev-ento-060120-091620>
- Zhang, F., Li, Y. H., Sun, T., Sun, G. Z., Cui, J. A., ... Li, S. H. (1993). An evaluation of the efficacy of releasing *Trichogramma dendrolimi* composed of mixed development stages for the control of the Asian corn corer. *Jilin Nongye Daxue Xuebao*, *15*, 11–15.
- Zhang, J., & Xu, J. (2000). The geographic distribution and identification of *Grapholitha molesta* and other several fruit borers. *Plant Protection*, *26*, 40–41.
- Zhang, J. J., Ren, B. Z., Yuan, X. H., Zang, L. S., Ruan, C. C., Sun, G.-Z., & Shao, X. W. (2014). Effects of host-egg ages on host selection and suitability of four Chinese *Trichogramma* species, egg parasitoids of the rice striped stem borer, *Chilo suppressalis*. *BioControl*, *59*(2), 159–166. <https://doi.org/10.1007/s10526-013-9557-4>
- Zhang, J. J., Zhang, X., Zang, L. S., Du, W. M., Hou, Y. Y., Ruan, C.-C., & Desneux, N. (2018). Advantages of diapause in *Trichogramma dendrolimi* mass production on eggs of the Chinese silkworm, *Antheraea pernyi*. *Pest Management Science*, *74*(4), 959–965. <https://doi.org/10.1002/ps.4795>
- Zhou, H., Yu, Y., Tan, X., Chen, A., & Feng, J. (2014). Biological control of insect pests in apple orchards in China. *Biological Control*, *68*, 47–56. <https://doi.org/10.1016/j.biocontrol.2013.06.009>

Manuscript received: 20 March 2020

Revisions requested: 12 May 2020

Modified version received: 22 June 2020

Accepted: 14 August 2020