J. Crop Prot. ***2018, 7 (3): 315-325***

Research Article

How does host quality affect oviposition rate and diapause in sexual and asexual *Trichogramma brassicae*?

Somayeh Rahimi-Kaldeh, Ahmad Ashouri* **and Alireza Bandani**

Department of Plant Protection, College of Agriculture and Natural Resources, University of Tehran, Karaj, Iran.

Abstract: The egg parasitoids of the genus *Trichogramma* have become one of the most important economic insects, for they are widely used in biological control of Lepidopteran key pests. For that reason, all aspects of their mass production including diapause have been considered over the last few years. In this study, the effect of host quality on the diapause induction of sexual and asexual *T. brassicae* Bezdenko (Hym: Trichogrammatidae) have been investigated at two temperatures. Maternal generation developed at two distinct temperatures (14 and 20 °C) and they oviposited on four different qualities of *Ephestia kuehniella* Zeller (Lep: Pyralidae) eggs including fresh eggs, frozen eggs, host eggs with developing embryo and low quality eggs. Data analysis revealed significant influence of temperature and host quality on diapause induction in both sexual and asexual strains. Maximum diapause happened in host eggs with developing embryo even though they were in fetal development. A higher level of diapause was observed in *T. brassicae* whose maternal generation had developed at 20 °C. The diapause induction in asexual *T. brassicae* was less than sexual wasps. The results imply that *Wolbachia* causes a disturbance in the diapause process. The outcomes of this study, which are new, indicate the complexity of diapause and the importance of factors such as host quality which have received less attention in diapause induction.

Keywords: Diapause, egg parasitoid, host quality, temperature, *Wolbachia*

Introduction

Trichogramma are minute polyphagous wasps which are the most widely used endoparasitoids of Lepidopteran pests (Andrade *et al*., 2011). These parasitoids often have two reproductive modes, arrhenotoky (sexual) and thelytoky (asexual). Arrhenotoky is common in most parasitoid wasps where males develop from unfertilized eggs and females from fertilized eggs. Thelytoky is another reproductive mode where unfertilized eggs develop into females (Stouthamer and Werren, 1993). The main reason for thelytoky in the *Trichogramma* genus is the presence of an obligatory endosymbiotic bacterium called *Wolbachia* (Pinto and Stouthamer, 1994). In spite of all the benefits of being infected by *Wolbachia* such as a higher population growth rate, no energy waste for the production of males and no time wasted on searching for mates, it is estimated that few species of *Trichogramma* wasps are infected by the bacterium in nature (Pinto and Stouthamer, 1994). Kishani Farahani *et al*. (2015) demonstrated that lower ability for determination of host quality in asexual *T. brassicae* could be the reason for scarcity of *Wolbachia* infected *Trichogramma* species in nature.

Handling Editor: Saeid Moharramipour

---

* **Corresponding author**, e-mail: ashouri@ut.ac.ir
Received: 18 October 2017 Accepted: 6 May 2018

[DOR: 20.1001.1.22519041.2018.7.3.5.2]

As the host is the only available nutritional source for immature parasitoid stages, consequently sufficient resources and a high quality host guarantees the survival and reduces the mortality rate of parasitoids (Visser *et al*., 1992). Host quality has an important role in foraging behavior, remaining time in the patch and foraging success of parasitoids (Outreman *et al*., 2005). Several studies have shown that parasitoids are able to estimate the quality of their hosts (Schmidt, 1994; Louapre *et al*., 2011). Sexual *T. brassicae* oviposited in high quality host while asexual ones oviposited regardless of host quality in order to increase their population (Kishani Farahani, 2014). Therefore, we could expect that host quality affects other properties of parasitoids such as the diapause induction in *Trichogramma* offspring.

Diapause happens in the prepupal stage in *Trichogramma* wasps, though in all life stages (embryonic to adult) they are sensitive to environmental abiotic factors such as temperature and photoperiod (Boivin, 1994). In these parasitoid wasps, photoperiodic conditions of pupal and adult development have maternal effects on diapause of their progeny (Ivanov and Reznik, 2008) and temperature is the key factor inducing the diapause in *Trichogramma* during embryonic and larval development of the progeny generation (Reznik *et al*., 2008). Most studies, have concentrated on the roles of indirect photoperiod and direct temperature on diapause induction of *Trichogramma* wasps (Reznik, 2011) while other environmental factors, such as host quality have not received attention. The reason may be due to the fact that host quality has been often shown to be a major factor inducing diapause for some insects such as *Hippodamia convergens* (Stewart *et al*., 1967), *Semiadalia undecimnotata* (Rolley *et al*., 1974), *Chilo zonellus* and *C. argyrolepia* (Scheltes, 1976) that undergo aestival rather than hibernal diapause (Tauber *et al*., 1986).

This paper describes laboratory experiments designed to examine the maternal influence of host quality and maternal temperature on the facultative prepupal diapause of, on one side, the uninfected-sexual and, on the other, *Wolbachia*-infected asexual *T. brassicae* as the most abundant *Trichogramma* wasps in Iran (Poorjavad, 2011). The purpose of the present study was to assess the following predictions: (1) the proportion of prepupal stage of *T. brasiccae* entering diapause varies among different host qualities, (2) the mechanism by which host quality influences diapause induction is by influencing maternal generation developmental conditions relative to changes in temperature and reproductive mode, (3) the asexual strain may produce offspring with lower diapause ability through oviposition in low quality hosts, which may decrease even more in low temperatures as we have previously shown that asexual *T. brassicae* has less ability to overwinter (Rahimi *et al*., 2017a).

Materials and Methods

Insects

In this study, sexual and asexual *T. brassicae* strains kept in "Ecology and Behavior" laboratory of University of Tehran were used. Both strains were reared under laboratory conditions, 20 ± 1 °C, 16L: 8D photoperiod and 70 ± 5% RH on the *Ephestia kuehniella* eggs. The offspring of one female was used in this study to generate the highest genetic similarity. The genetic background of the two strains was previously determined by Kishani Farahani *et al*. (2015) based on the nuclear ribosomal DNA (nrDNA) internal transcribed spacer 2 (ITS2) region. Their results showed a close similarity between them as well as with other *T. brassicae* strains from the northern part of Iran, south of the Caspian Sea (Mazandaran and Guilan province).

Effect of host quality on the diapause percentage at two temperatures

The maternal generation of sexual and asexual *T. brassicae* was reared under 10L: 14D photoperiod (Rahimi *et al*., 2017b), 70 ± 5% RH and at two different temperatures (14 and 20 °C). The maternal generation was reared at

20 °C because higher maternal temperatures would inhibit diapause in *Trichogramma* offspring (Dr. S. Ya. Reznik, personal communication, Zoological Institute RAS, St. Petersburg) and at 14 °C which makes the life cycle of maternal generation longer (about 45-50 days). Therefore, maternal females are more likely to produce offspring with more ability to withstand low temperatures. Maternal females were developed under a short photoperiod because of the maternal influence of photoperiod on the diapause induction in *Trichogramma* wasps (Reznik *et al*., 2011; Rahimi *et al*., 2017b). One day after mass emergence of maternal generation (about 17-18 days at 20 °C and 45-50 days at 14 °C), 160 cardboard paper strips were exposed for 4 h to parasitization by 500 asexual and 1000 mated-sexual *T. brassicae* (both 24 h old) in transparent, plastic cylinders (approximately 18 cm tall × 8 cm in diameter) with an opening place covered with a mesh in order to allow for ventilation (Rahimi *et al*., 2017b).The 20% honey water was sprayed on the walls of cylinders to feed *T. brassicae* adults. Then, 50 *E. kuehniella* eggs were glued by non-toxic and water-soluble glue (Canco) on each cardboard paper strip (5cm × 1cm). The ovipositing females were provided with four different quality eggs of *E. kuehniella*, simultaneously. Those included host eggs with high quality which were less than 24 h old (high quality-fresh eggs), *E. kuehniella* eggs which were stored at □20 °C for 24h (frozen eggs, used usually as sterile eggs in the laboratories), *E. kuehniella* eggs which were stored at 4 °C for 40 days (low quality eggs, considered as low quality eggs by Kishani Farahani *et al*. (2015)) and *E. kuehniella* eggs which were stored at 14 °C for 10 days (eggs with developing embryo). The experiments were done with the aim to observe the effect of developing embryo of host eggs on the mean number of parasitized eggs/female and diapause induction in sexual and asexual *Trichogramma brassicae*. Eggs with different qualities were glued on separate cardboard paper strips (40 cardboard paper strips for each quality). Then the cards with parasitized host eggs were individually placed in glass tubes and incubated at 10 ± 1°C, 70 ± 5% RH and absolute darkness for two months (Rahimi *et al*., 2018). The parasitized host eggs were checked weekly.

At 10 °C, the darkening of parasitized eggs occurs after about one month but no emergence was observed at two months after parasitism whereas the darkening happens after about five days at 25 °C. We, therefore, considered these *T. brassicae* to be in diapause. All tubes were then transferred to 20 °C, L16: D8 and 70 ± 5% RH to break diapause and to facilitate the emergence of diapausing individuals. As *Trichogramma* females usually lay only one egg in each *E. kuehniella* egg (Garcia and Tavares, 2001), the number of diapausing individuals was estimated by counting the numbers of eggs with an emergence hole. The remaining eggs were then dissected to take into account the remaining living diapausing prepupae. The percentage of diapausing individuals was separately calculated for each card. We did not include cardboard paper strips with less than 10 parasitized *E. kuehniella* eggs in our experiments.

Statistical analysis

Chi-squared test was used to determine the influence of host quality on the oviposition rate (eggs/female) and the percentage of diapause induction in sexual and asexual *T. brassicae* at the two temperatures, separately with 40 replications. To determine which host quality differed from others in oviposition and diapause induction, we compared all pairwise combinations (six possible comparisons for four host qualities) using chi-squared test. The effect of *Wolbachia* infection (reproductive mode) and temperature on the oviposition rate and the diapause induction of *T. brassicae* were checked using *t*-test. All calculations were performed using SAS statistical software, version 9.2.

Results and Discussion

The results showed that differences in oviposition rate among host qualities were more obvious and statistically significant at 20 °C ($\chi^2 = 524.83$, df =

3, P ≤ 0.0001) than at 14 °C (χ^2 = 65.89, df = 3, P ≤ 0.0001) in asexual strain. Six pairwise comparisons among the four qualities resulted in three and five significant differences among qualities at 14 and 20 °C, respectively (Table 1), with lower levels of oviposition in frozen eggs than the other three qualities (Fig. 1A, B). Host quality influenced the oviposition rate of sexual strain more significantly at 14 °C (χ^2 = 936.25, df = 3, P ≤ 0.0001) than 20 °C (χ^2 = 368.33, df = 3, P ≤ 0.0001). Six and five of six pairwise comparisons among host qualities were significant after applying chi square test at 14 and 20 °C, respectively (Table 2). No significant difference was observed between fresh and eggs with developing embryo at 20 °C (Table 2). The lowest oviposition rate was shown on low host quality at both temperatures (Fig. 1A, B). According to the results, sexual females oviposited more on host eggs with developing embryo and high quality eggs at both temperatures. The number of parasitized eggs/female by asexual females on the high and low quality eggs was similar at 14 °C (Fig. 1A) while it was completely different at 20 °C with maximum oviposition on eggs with developing embryo followed by high quality eggs (Fig. 1B). As a result, temperature could affect the oviposition of asexual females but not sexual ones which could be related to *Wolbachia* infection. As seen in Fig. 1B, the oviposition rate of asexual *T. brassicae* on all the host qualities (except for frozen eggs) was greater than that of sexual wasps at 20 °C, while the oviposition rate of sexual strain in all the host qualities except low quality host was greater than that of asexual one at 14 °C (Fig. 1A). Our results confirm the importance of temperature in changing the oviposition behavior of *Trichogramma* wasps which is controlled by *Wolbachia* as the results showed that asexual wasps have lower oviposition rate in comparison to sexual ones at 14 °C while something completely different happened at 20 °C.

The results showed that differences in diapause percentage among host qualities were more obvious and statistically significant at 20 °C (χ^2 = 289.75, df = 3, P ≤ 0.0001) than 14 °C (χ^2 = 42.69, df = 3, P ≤ 0.0001) in asexual strain. Six pairwise comparisons among the four qualities resulted in five and six significant differences among qualities at 14 °C and 20 °C, respectively (Table 3), with lower levels of diapause induction in low host quality than the other three qualities. A significant difference was not observed between fresh and frozen eggs at 14 °C whereas it was observed at 20 °C in asexual strain (Table 3). Host quality influenced the percentage of prepupal diapause at both 14 °C (χ^2 = 232.37, df = 3, P ≤ 0.0001) and 20 °C (χ^2 = 107.86, df = 3, P ≤ 0.0001) in sexual strain. Five and three of six pairwise comparisons among host qualities were significant after applying chi square test at 14 °C and 20 °C, respectively (Table 4). A significant difference was not observed between fresh eggs and eggs with developing embryo at both 14 °C and 20 °C whereas the significant difference was not observed either between fresh and frozen eggs and frozen and eggs with developing embryo at 20 °C in sexual strain (Table 4). The lowest percentage of diapause was shown on low host quality. These results suggest that nutritional quality significantly influences the induction of diapause in both sexual and asexual strains.

Table 1 Results of pairwise comparisons of oviposition (mean eggs/female) in asexual *Trichogramma brassicae* among four host qualities at 14 °C and 20 °C.

Comparison	14 °C			20 °C		
	χ^2	P	Significant	χ^2	P	Significant
Fresh vs. frozen eggs	59.57	< 0.0001	yes	250.96	< 0.0001	yes
Fresh vs. low quality eggs	0.04	0.8379	no	303.19	< 0.0001	yes
Fresh vs. eggs with developing embryo	0.00	1.0000	no	1.56	0.2108	no
Frozen vs. low quality eggs	56.89	< 0.0001	yes	9.00	0.0027	yes
Frozen vs. eggs with developing embryo	59.57	< 0.0001	yes	220.16	< 0.0001	yes
Low quality vs. eggs with developing embryo	0.04	0.8379	no	271.41	< 0.0001	yes

Each comparison represents a chi-square approximation with df = 1.

[DOR: 20.1001.1.22519041.2018.7.3.5.2]

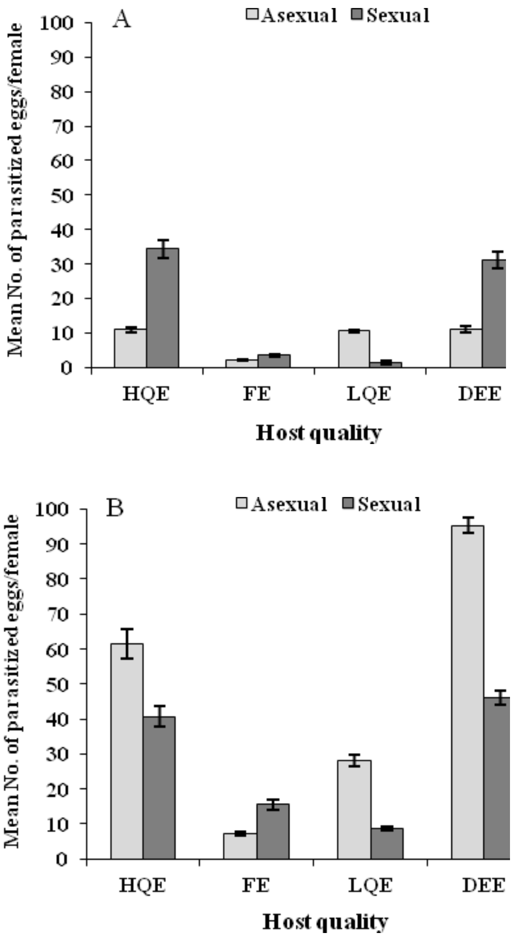

Figure 1 The mean number of parasitized eggs/female in sexual and asexual *Trichogramma brassicae* on four different host qualities, (HQE)-*Ephestia kuehniella* eggs which were 24 h old, (FE)-*E. kuehniella* eggs which were stored at −20 °C for 24 h, (LQE)- *E. kuehniella eggs* which were stored at 4 °C for 40 days, (DEE)-*E. kuehniella* eggs which were stored at 14 °C for 10 days. The maternal generation developed at (A) 14 °C and (B) 20 °C. Chi-square test was used to determine the influence of host quality on the mean number of parasitized eggs/female in sexual and asexual *T. brassicae*.

Maximum diapause happened on *E. kuehniella* eggs with developing embryo, which was followed by fresh, frozen and low quality eggs, respectively, in asexual strain whose maternal generation had developed at 14 and 20 °C, and in sexual strain whose maternal generation had developed at 14 °C. As expected, these results were in good agreement with the result of Hu *et al.* (1999). They stated that freezing may cause damage to the egg structure through a reduction in the host quality resulting from the denaturation of the large proteins naturally induced by freezing which directly impact the development of the parasitoid. Unlikely as it may be, the highest percentage of diapause was observed on frozen eggs in sexual strain whose maternal generation had developed at 20 °C. The lowest diapause percentage was observed in low quality eggs in all the treatments. Our results revealed that the mortality of individuals increased during the diapause process as a result of host quality reduction. Similarly, Ozder (2004) showed that the quality of *E. kuehniella* eggs kept at 0, 4 and 8 °C decreased as storage time increased.

Based on the results of this research, the question arises as to whether the concept of host quality for *Trichogramma* females is the same as our definition for host quality? We had expected higher diapause percentage in *E. kuehniella* eggs which were 24 h old (high quality-fresh eggs), but the results showed that *E. kuehniella* eggs which were stored at 14 °C for 10 days (eggs with developing embryo) had a higher diapause percentage. It is likely that host eggs with developing embryo attract more ovipositing females or they may have more nutrients in comparison with other host qualities. Similarly, Hunter and Mcneil (1997) have shown that the proportion of larvae entering diapause was two times higher on the low- than on the high-quality artificial diet under constant environmental conditions. Brodeur and Boivin (2004) revealed the fact that chemical components in insect eggs change from semi-liquid to solid in texture and this phenomenon can have negative effects on host acceptance and suitability, parasitism, sex ratio and mortality of parasitoid offspring. Exposure to 14 °C for 10 days will certainly cause fetal development of *E. kuehniella*. Jacob and Cox (1977) indicated that fetal development of *E. kuehniella* takes 14 days at 15 °C and 70% RH. Consequently, embryonic development was not completed after 10 days in our experiment. It seems that embryonic development of *E. kuehniella* eggs turns them to a better host for oviposition and diapause induction.

[DOR: 20.1001.1.22519041.2018.7.3.5.2]

Table 2 Results of pairwise comparisons of oviposition (mean eggs/female) in sexual *Trichogramma brassicae* among four host qualities at 14 °C and 20 °C.

Comparison	14 °C			20 °C		
	χ^2	P	Significant	χ^2	P	Significant
Fresh vs. frozen eggs	429.47	< 0.0001	yes	112.99	< 0.0001	yes
Fresh vs. low quality eggs	124.17	< 0.0001	yes	209.01	< 0.0001	yes
Fresh vs. eggs with developing embryo	73.82	< 0.0001	yes	3.36	0.0668	no
Frozen vs. low quality eggs	124.45	< 0.0001	yes	89.75	< 0.0001	yes
Frozen vs. eggs with developing embryo	759.69	< 0.0001	yes	152.01	< 0.0001	yes
Low quality vs. eggs with developing embryo	367.34	< 0.0001	yes	257.08	< 0.0001	yes

Each comparison represents a chi-square approximation with df = 1.

Table 3 Results of pairwise comparisons of diapause induction in asexual *Trichogramma brassicae* among four host qualities at 14 °C and 20 °C.

Comparison	14 °C			20 °C		
	χ^2	P	Significant	χ^2	P	Significant
Fresh vs. frozen eggs	0.31	0.5760	no	32.21	< 0.0001	yes
Fresh vs. low quality eggs	11.78	0.0006	yes	143.55	< 0.0001	yes
Fresh vs. eggs with developing embryo	9.39	0.0022	yes	19.31	< 0.0001	yes
Frozen vs. low quality eggs	8.29	0.0040	yes	42.40	< 0.0001	yes
Frozen vs. eggs with developing embryo	13.08	0.0003	yes	99.76	< 0.0001	yes
Low quality vs. eggs with developing embryo	41.33	< 0.0001	yes	258.12	< 0.0001	yes

Each comparison represents a chi-square approximation with df = 1.

Table 4 Results of pairwise comparisons of diapause induction in sexual *Trichogramma brassicae* among four host qualities at 14 °C and 20 °C.

Comparison	14 °C			20 °C		
	χ^2	P	Significant	χ^2	P	Significant
Fresh vs. frozen eggs	6.06	0.0138	yes	0.83	0.3615	no
Fresh vs. low quality eggs	176.59	< 0.0001	yes	75.24	< 0.0001	yes
Fresh vs. eggs with developing embryo	3.61	0.0575	no	0.01	0.9449	no
Frozen vs. low quality eggs	120.78	< 0.0001	yes	91.44	< 0.0001	yes
Frozen vs. eggs with developing embryo	18.96	< 0.0001	yes	0.71	0.3990	no
Low quality vs. eggs with developing embryo	226.02	< 0.0001	yes	76.41	< 0.0001	yes

Each comparison represents a chi-square approximation with df = 1.

The oviposition rate of *T. brassicae* showed a statistically significant difference between two temperatures in both sexual ($t = -2.69$, $P = 0.009$) and asexual ($t = -7.09$, $P \leq 0.001$) strains. Similarly, the induction of diapause showed significant difference between the two temperatures in both sexual ($t = -2.39$, $P = 0.019$) and asexual ($t = -6.96$, $P \leq 0.001$) strains. The oviposition rate of both strains decreased at 14 °C compared to 20 °C, which was followed by reduction in diapause induction (Fig. 1, 2) while the pattern of diapause was the same at two temperatures (Fig. 2A,B). Similar result was obtained by Zaslavski and Umarova (1990), and they indicated that the induction of diapause increased by increasing maternal temperature from 15 to 25 °C.

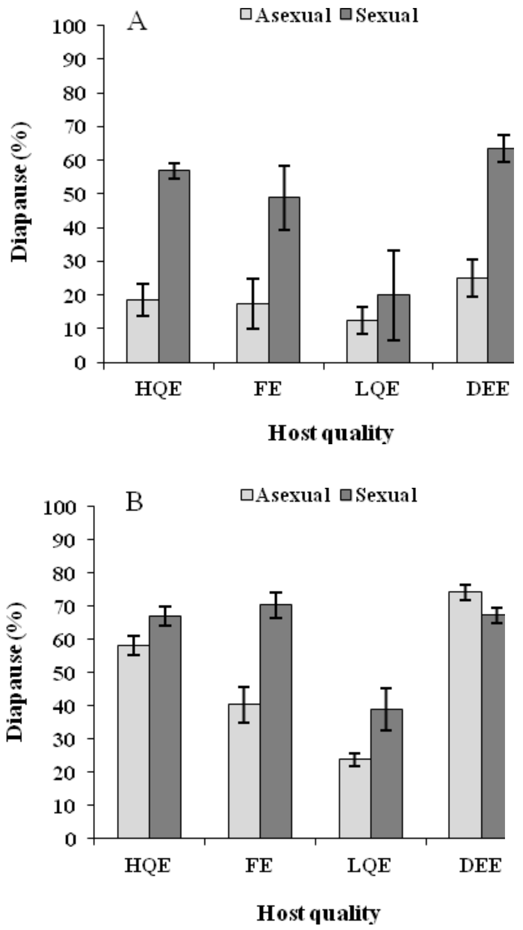

Figure 2 The induction of diapause in sexual and asexual *Trichogramma brassicae* on four different host qualities, (HQE)- *Ephestia kuehniella* eggs which were 24 h old, (FE)- *E. kuehniella* eggs which were stored at □20 °C for 24 h, (LQE)- *E. kuehniella* eggs which were stored at 4 °C for 40 days, (DEE)- *E. kuehniella* eggs which were stored at 14 °C for 10 days. The maternal generation developed at (A) 14 °C and (B) 20 °C. Chi-square test was used to determine the influence of host quality on the induction of diapause in sexual and asexual *T. brassicae.*

The oviposition rate of *T. brassicae* showed a statistically significant difference between two strains at both 14 °C (t = -3.34, P ≤ 0.001) and 20 °C (t = 3.29, P = 0.002). Similarly, the induction of diapause showed significant difference between two strains at both 14 °C (t = -5.13, P ≤ 0.001) and 20 °C (t = -2.63, P = 0.01). Although both strains showed the same pattern of diapause in response to host quality yet the diapause percentage decreased by *Wolbachia* infection. Many studies have shown negative effects of *Wolbachia* infection on biological characteristics of parasitoids such as fecundity, survival, parasitism rate and body size (Grenier and De Clercq, 2003). For example, *Wolbachia* infection caused shorter longevity in *Aedes aegypti* (Moreira *et al*., 2009). Also, asexual *T. kaykai* showed a lower parasitism rate, emergence rate and longevity in comparison with sexual ones (Hohmann *et al*., 2001; Miura and Tagami, 2004). Moreover, asexual *T. cacoeciae* and *T. evanescens* indicated a higher mortality rate in the embryonic stage than sexual individuals (Tagami *et al*., 2001). Kishani Farahani *et al*. (2015) have also stated that asexual *T. brassicae* have a higher mortality rate in comparison with sexual individuals, which would reduce the fitness and number of asexual offspring. Our previous results also showed that *Wolbachia* infection has a negative effect on the overwintering of *T. brassicae* under outdoor conditions (Rahimi *et al*., 2017a) and long term storage of *T. brassicae* under laboratory conditions (Rahimi *et al*., 2017b) through disturbance of the clock gene expression (Rahimi *et al*., 2017c). As a result, it seems that even if some of the parasitoid characteristics were not affected by the *Wolbachia* infection; the fitness of parasitoids was reduced by it which could be the reason for scarcity of asexual strain in comparison with the sexual one in nature.

Kishani Farahani *et al*. (2015) showed that sexual *T. brassicae* which were reared on high quality host were larger than those reared on low quality host. Body size is directly related to the amount of lipid reserves, therefore larger insects will have more lipid reserves (Candy *et al*., 1997). It has been shown that larger individuals are generally more resistant to stresses such as cold temperatures in comparison with smaller ones (Rivero and West, 2002; Arnett and Gotelli, 2003). This could indicate greater ability of sexual wasps to survive at low temperatures.

Consequently, results of this study demonstrate that there is a direct effect of host quality on diapause induction of *T. brassicae* that is dependent on temperature and reproductive mode. It has also been shown that greater diapause induction occurred at higher temperature and sexual strain which indicates negative effects of *Wolbachia* infection on the diapause induction of *T. brassicae*. It is hoped that the results of the present study will encourage further work in this area.

Acknowledgements

The authors sincerely thank Dr. Nafiseh Poorjavad (Isfahan University of Technology, Isfahan, Iran) for the molecular and morphological identification of asexual and sexual *T. brassicae* and Petra Pribicevic (Faculty of Philology, University of Belgrade, Serbia) for her proofreading.

References

Andrade, G. S., Pratissoli, D., Dalvi, L. P., Desneux, N. and Goncalves, H. J. 2011. Performance of four *Trichogramma* species (Hymenoptera: Trichogrammatidae) as biocontrol agents of *Heliothis virescens* (Lepidoptera: Noctuidae) under various temperature regimes. Journal of Pest Science, 84: 313-320.

Arnett, A. E. and Gotelli, N. J. 2003. Bergmann's rule in larval ant lions: testing the starvation resistance hypothesis. Ecological Entomology, 28: 645-650.

Boivin, G. 1994. Overwintering strategies of egg parasitoids. In: Wajnberg, E. and Hassan, S. A. (Eds.) Biological control with egg parasitoids. CAB International, Wallingford, pp. 219-244.

Brodeur, J. and Boivin, G. 2004. Functional ecology of immature parasitoids. Annual Review of Entomology, 49: 27-49.

Candy, D.J., Becker, A. and Wegener, G. 1997. Coordination and integration of metabolism in insect flight. Comparative Biochemistry & Physiology, 117: 497-512.

Garcia, P. and Tavares, J. 2001. Effect of host viability on *Trichogramma cordubensis* (Insecta: Hymenoptera) reproductive strategies. Arquipelago Life and Marine Sciences Supplement, 2:43-49.

Grenier, S. and De Clercq, P. 2003. Comparison of artificially vs. naturally reared natural enemies and their potential for use in biological control. In: van Lenteren, J. C. (Ed.) Quality control and production of biological control agents theory and testing procedures. CABI Publishing, Wallingford Oxon, UK. pp. 115-131.

Hohmann, C. L., Luck, R.F. J. C. and Stouthamer, R. 2001. Effect of *Wolbachia* on the survival and reproduction of *Trichogramma kaykai* Pinto & Stouthamer (Hymenoptera: Trichogrammatidae). Neotropical Entomology, 30: 607-612.

Hu, J. S., Gelman, D. B. and Bell, R. A. 1999. Effects of selected physical and chemical treatments of Colorado potato beetle eggs on host acceptance and development of the parasitic wasp, *Edovum puttleri*. Entomologia Experimentalis et Applicata, 90: 237-245.

Hunter, M. D. and Mcneil, J. N. 1997. Host-plant quality influences diapause and voltinism in a polyphagous insect herbivore. Ecology, 78: 977-986.

Ivanov, M. F. and Reznik, S. Ya. 2008. Photoperiodic regulation of the diapause of the progeny in *Trichogramma embryophagum* Htg. (Hymenoptera, Trichogrammatidae): dynamics of sensitivity to photoperiod at immature stages of maternal females. Entomological Review, 88: 261-268.

Jacob, T. A. and Cox, P. D. 1977. The influence of temperature and humidity on the life cycle of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae). Journal of Stored Products Research, 13: 107-118.

Jones, K. E. and MacLarnon, A. M. 2004. Affording larger brains: Testing hypotheses of mammalian brain evolution on bats. American Naturalist, 164: 20-31.

Kishani Farahani, H. 2014. A survey on learning ability and memory duration of *Trichogramma brassicae*. PhD Thesis, University of Tehran, Iran.

[DOR: 20.1001.1.22519041.2018.7.3.5.2]

Kishani Farahani, H., Ashouri, A., Goldansaz, S. H., Farrokhi, S., Ainouche, A. and van Baaren, J. 2015.Does *Wolbachia* infection affect decision-making in a parasitic wasp? Entomologia Experimentalis et Applicata, 155: 102-116.

Louapre, P., van Baaren, J., Pierre, J. S. and van Alphen, J. J. M. 2011. Information gleaned and former patch quality determines foraging behavior of parasitic wasps. Behavioral Ecology, 22: 1064-1069.

Miura, K. and Tagami, Y. 2004. Comparison of life history characters of sexual and *Wolbachia*-associated asexual *Trichogramma kaykai* (Hymenoptera: Trichogrammatidae). Annals of the Entomological Society of America, 97: 765-769.

Moreira, L. A., Saig, E., Turley, A. P., Ribeiro, J. M. C., O'Neill, S. L. and McGraw, E. A. 2009. Human probing behavior of *Aedes aegypti* when infected with a life-shortening strain of *Wolbachia*. PLoS Neglected Tropical Diseases, 3: e568.

Outreman, Y., LeRalec, A., Wajnberg, E. and Pierre, J. S. 2005. Effects of within and among-patch experiences on the patch-leaving decision rules in an insect parasitoid. Behavioral Ecology and Sociobiology, 58: 208-217.

Ozder, N. 2004. Effect of different cold storage periods on parasitization performance of *Trichogramma cacoeciae* (Hymenoptera, Trichogrammatidae) on eggs of *Ephestia kuehniella* (Lepidoptera, Pyralidae). Biocontrol Science and Technology, 14: 441-447.

Pinto, J. D. and Stouthamer, R. 1994. Systematic of the Trichogrammatidae with emphasis on *Trichogramma*. In: Wajnberg, E. and Hassan, S. A. (Eds.) Biological control with egg parasitoids. Wallingford, CABI. pp. 1-36.

Poorjavad, N. 2011. Morphological, molecular and reproductive compatibility studies on the systematic of the genus *Trichogramma* Westwood (Hymenoptera: Trichogrammatidae) in Tehran and Mazandaran province (Iran). PhD Thesis, University of Tehran, Iran.

Rahimi-Kaldeh, S., Ashouri, A. and Bandani, A. R. 2017a. Does *Wolbachia* infection change the overwintering ability of *Trichogramma brassicae* (Hymenoptera: Trichogrammatidae)? Neotropical Entomology, https://doi:10.1007/s13744-017-0549-4.

Rahimi-Kaldeh, S., Ashouri, A. and Bandani, A. R. 2017b. Long-term storage of sexual and asexual *Trichogramma brassicae* (Hymenoptera: Trichogrammatidae). Biocontrol Science and Technology, 27 (11): 1339-1347. https://doi.org/10.1080/09583157.2017.1397599.

Rahimi-Kaldeh, S., Ashouri, A., Bandani, A. R. and Modarres Hasani, S. A. 2018. Maternal age influence on diapause induction in sexual and asexual *Trichogramma brassicae*. International Journal of Pest Management, https://doi.org/10.1080/09670874.2017.1422569.

Rahimi-Kaldeh, S., Ashouri, A., Bandani, A. R. and Tomioka, K. 2017c. The effect of *Wolbachia* on diapause, fecundity, and clock gene expression in *Trichogramma brassicae* (Hymenoptera: Trichogrammatidae). Development Genes and Evolution, 227: 401-410.

Reznik, S. Y., Vaghina, N. P., and Voinovich, N. D. 2008. Diapause induction in *Trichogramma embryophagum* Htg. (Hymenoptera, Trichogrammatidae): the dynamics of thermosensitivity. Journal of Applied Entomology, 132: 502-509.

Reznik, S. Ya., Voinovich, N. D. and Vaghina, N. P. 2011. Maternal influence on diapause induction in *Trichogramma* (Hymenoptera, Trichogrammatidae): the dynamics of photosensitivity. Journal of Applied Entomology, 135: 438-445.

Reznik, S. Ya. 2011. Ecological and evolutionary aspects of photo-thermal regulation of diapause in Trichogrammatidae. Journal of Evolutionary Biochemistry and Physiology, 47: 512-523.

Rivero, A. and West, S. A. 2002. The physiological costs of being small in a

[DOR: 20.1001.1.22519041.2018.7.3.5.2]

parasitic wasp. Evolutionary Ecology Research, 4: 407-420.

Rolley, F., Hodek, I. and Iperti, G. 1974. Influence de la nourriture aphidienne (selon l'age de la plante-hote a partir de laquelle les pucerons se multiplient) sur l'induction de la dormance chez *Semiadalia undecimnotata* Schn. (Coleop., Coccinellidae). Annales Zoologiques, 6: 53-60.

Scheltes, P. 1976. The role of Graminaceous host-plants in the induction of aestivation-diapause in the larvae of *Chilo zonellus* Swinhoe and *Chilo argyrolepia* Hamps. Symposia Biologica Hungary, 16: 247-253.

Schmidt, J. M. 1994. Host recognition and acceptance by *Trichogramma*. In: Wajnberg, E. and Hassan, S. A. (Eds.) Biological control with egg parasitoids. CABI, Oxon, pp: 165-200.

Stewart, J. W., Whitcomb, W. H. and Bell, K. O. 1967. Estivation studies of the convergent lady beetle in Arkansas. Journal of Economic Entomology, 60: 1730-1735.

Stouthamer, R. and Werren, J. R. 1993. Microbes associated with parthenogenesis in wasps of the genus *Trichogramma*. Journal of Invertebrate Pathology, 61: 6-9.

Tagami, Y., Miura, K. and Stouthamer, R. 2001. How does infection with parthenogenesis inducing *Wolbachia* reduce the fitness of *Trichogramma*? Journal of Invertebrate Pathology, 78: 267-271.

Tauber, M. J., Tauber, C. A. and Masaki, S. 1986. Seasonal adaptations of insects. Oxford University Press, New York, USA, 411 pp.

Visser, M. E., van Alphen, J. J. M. and Nell, H. W. 1992. Adaptive superparasitism and patch time allocation in solitary parasitoids: the influence of pre-patch experience. Behavioral Ecology and Sociobiology, 31: 163-171.

Zaslavski, V. A. and Umarova, T. Ya. 1990. Environmental and endogenous control of diapause in *Trichogramma* species. Entomophaga, 35: 23-29.

[DOR: 20.1001.1.22519041.2018.7.3.5.2]

چگونگی اثر کیفیت میزبان بر میزان تخم‌گذاری و دیاپوز زنبورهای دوجنسی و تک‌جنسی *Trichogramma brassicae*

سمیه رحیمی کلده، احمد عاشوری* و علیرضا بندانی

گروه گیاه‌پزشکی، پردیس کشاورزی و منابع طبیعی، دانشگاه تهران، کرج، ایران.
* پست الکترونیکی نویسنده مسئول مکاتبه: ashouri@ut.ac.ir

دریافت: ۲۶ مهر ۱۳۹۶؛ پذیرش: ۱۶ اردیبهشت ۱۳۹۷

چکیده: کاربرد گسترده زنبورهای پارازیتویید *Trichogramma* در کنترل بیولوژیک آفات مهم بال‌پولکدار، آن‌ها را به یکی از مهم‌ترین حشرات اقتصادی تبدیل کرده است. بر این اساس، جنبه‌های مختلف تولید انبوه این زنبورها در سراسر دنیا مورد توجه قرار گرفته است. مطالعه همه جانبه دیاپوز در زنبورهای جنس *Trichogramma* می‌تواند کمک شایانی در اقتصادی کردن پرورش انبوه این حشرات مفید داشته باشد. در این پژوهش، اثر کیفیت میزبان بر درصد دیاپوز زنبورهای تک‌جنسی (آلوده به ولباکیا) و دوجنسی (غیرآلوده) *T. brassicae* Bezdenko در دو دمای۱۴ و ۲۰ درجه سلسیوس مورد مطالعه قرار گرفت. نسل مادری در دو دمای فوق پرورش یافتند و روی چهار کیفیت متفاوت میزبان شامل تخم‌های باکیفیت، تخم‌های منجمد شده، تخم‌های حاوی جنین رشد یافته و تخم‌های بی‌کیفیت *Ephestia kuehniella* Zeller تخم‌گذاری کردند. نتایج نشان داد که کیفیت میزبان دارای اثر معنی‌داری بر درصد دیاپوز هر دو استرین در هر دو دما است. بیش‌ترین درصد دیاپوز در تخم‌های حاوی جنین رشد یافته مشاهده شد. هم‌چنین نتایج نشان داد، میزان دیاپوز در نتاجی که نسل مادری آن‌ها در دمای ۲۰ درجه سلسیوس پرورش یافتند بیش از نتاجی بود که نسل مادری آن‌ها در دمای ۱۴ درجه سلسیوس پرورش یافتند. درصد دیاپوز در زنبورهای تک‌جنسی کم‌تر از دوجنسی بود. این نتیجه بیانگر ایجاد اختلال در روند دیاپوز زنبور توسط باکتری *Wolbachia* است. نتایج این پژوهش، حاکی از پیچیدگی فرایند دیاپوز و تحت تأثیر قرار گرفتن آن توسط عواملی (کیفیت میزبان) است که تاکنون کم‌تر مورد توجه بوده‌اند.

واژگان کلیدی: دیاپوز، پارازیتویید تخم، کیفیت میزبان، دما، *Wolbachia*

[DOR: 20.1001.1.22519041.2018.7.3.5.2]