Bulletin of Insectology ***76*** *(1): 95-100, 2023*
ISSN 1721-8861 eISSN 2283-0332

Evaluation of the maternal photoperiodic effect as a storage method on *Trichogramma nerudai*

Mariana M. Viscarret, Cynthia L. Cagnotti, Silvia N. López
Instituto Nacional de Tecnología Agropecuaria (INTA), Instituto de Microbiología y Zoología Agrícola, Castelar, Buenos Aires, Argentina

Abstract

Maternal photoperiodic effect on *Trichogramma nerudai* Pintureau et Gerding (Hymenoptera Trichogrammatidae) was evaluated to test its possible exploitation to store the parasitoid. Freshly parasitized eggs of *Sitotroga cerealella* (Olivier) (Lepidoptera Gelechiidae) were randomly assigned to one of the following light (L)/dark (D) cycles (hours) (treatments): 3L:21D, 6L:18D, 9L:15D and 12L:12D. This was the maternal generation (P1). Once the P1 emerged, they were exposed for 24 hours to fresh eggs of *S. cerealella.* The resulting parasitized eggs (F1 generation) were maintained under a moderately low temperature (11 ± 2 °C) and complete darkness. All the variables registered on the F1 were affected by light/dark cycles. A longer time of emergence was registered for treatments 3L:21D and 12L:12D (94 and 92 days, respectively). The lowest times of emergence, were for 6L:18D and 9L:15D treatments (68 and 55 days, respectively). Treatment 3L:21D (80.20 ± 2.46%) presented the highest value of emergence following for 12L:12D (69.85 ± 3.10%), 6L:18D (62.70 ± 2.87%) and finally 9L:15D (25.90 ± 3.25%). About the female proportion, treatment 3L: 21D had the highest value (0.61 ± 0.02), followed by treatment 12L:12D (0.51 ± 0.02). The female proportion was similar for treatments 9L:15D (0.41 ± 0.03), and 6L:18D (0.43 ± 0.02). The non-emerged and dissected material showed a high proportion of prepupal diapausing stage on 12L:12D treatment. However, other treatments presented a high proportion of pupal and adult non-emerged showing other quiescent stages for this parasitoid. Treatment 3L:21D on P1 generation keeping the F1 on a relative low temperature showed the best combination to obtain *ca* 90 days of storage, with high values of adult emergence and female parasitoid proportion.

Key words: *Trichogramma nerudai*, maternal effect, dormancy, storage.

Introduction

Dormancy is a term used to define a combination of strategies that allows insects to survive under different environmental conditions. Although its definition has been subjected to many discussions, it is widely accepted that dormancy corresponds to “any state of suppressed development (developmental arrest), which is adaptive (that is ecologically or evolutionarily meaningful and not just artificially induced), and usually accompanied with metabolic suppression.” (Košťál, 2006). The induction of dormancy in response to different conditions has been studied across many species, not just to understand dormancy in depth, but also to improve the rearing and stockpiling of beneficial insects and as a tool for the management and control of insect pests. The ability to store natural enemies produced in continuous culture could be a valuable tool to provide flexible and efficient mass production, to allow good synchronicity between the host and the parasitod/predator, to facilitate the long distance transport of insects, and to keep the genetic background of the population in dormancy (Rossi, 1997; van Lenteren and Tommasini, 2003).

Among wasps in the genus *Trichogramma*, the induction of dormancy has been studied in several species. It was found that the main driver of prepupal diapause is temperature (Rossi, 1997; Ventura García *et al*., 2002; Reznik *et al*., 2003; Reznik and Kats, 2004). However, the induction of prepupal diapause on F1 generation is also possible through a maternal effect. Prepupal diapause occurs when the maternal generation is exposed to specific photoperiodic conditions and the F1 is kept under storage conditions near threshold temperatures (Reznik, 2011; Reznik *et al*., 2003). From an ecological point of view, this approach could be useful to differentiate, for example, days with low temperature and a short light period in winter from those with low temperature but a longer light period in early spring (Reznik, 2011).

The maternal effect on diapause has been studied in multiple different species of insects (Denlinger, 1998; Saunders *et al*., 2002; Danks, 2007). In the case of *Trichogramma* species, several authors have established that this effect is mainly determinated by the photoperiod condition of the pupal stage of maternal females (Ivanov and Reznik, 2008; Reznik, 2011; Reznik *et al*., 2011; Vaghina *et al*., 2011).

Trichogramma nerudai Pintureau et Gerding (Hymenoptera Trichogrammatidae) is an egg parasitoid, mainly of lepidopteran species as *Cydia pomonella* (L.) (Lepidoptera Tortricidae) and *Tuta absoluta* (Meyrick) (Lepidotera Gelechiidae). It has been studied as a natural enemy in several biological control programs (Botto *et al*., 2005; Argerich and López, 2007; Botto and Glaz, 2010; Desneux *et al*., 2010; Do Thi Khanh *et al*., 2012; Luna *et al*., 2012; van Lenteren, 2012). Previous research has studied the effects of cold storage on pupal and prepupal stage of *T. nerudai* (Tezze and Botto, 2004; Cagnotti *et al*., 2018). These studies evaluated different temperatures of cold storage including acclimation periods. However, no maternal effect studies were performed to use these effects as an approach to store this parasitoid species. Developing effective methods to store natural enemies without affecting their fitness is crucial to use them in biological control strategies (Leopold, 1998; Morales Ramos *et al*., 2022). The goal of the present work is therefore to evaluate the maternal photoperiodic effect in *T. nerudai* as approach to use it as storage method.

Materials and methods

The research was carried out at the Insectario de Investigaciones para Lucha Biológica (IILB) IMYZA-INTA Castelar, Buenos Aires, Argentina. *T. nerudai* and its host *Sitotroga cerealella* (Olivier) (Lepidoptera Gelechiidae) were obtained from colonies reared at this laboratory. This parasitoid has been reared since 1997 on UV irradiated eggs of *S. cerealella* in accordance with standardized production procedures (modified from Hassan, 1997) at 25 ± 2 °C, 40-65% RH and 12L:12D photoperiod. During the period of the rearing, quality controls in accordance with standardized procedures of the IOBC for other *Trichogramma* spp. have been performed (van Lenteren, 2003). According to these quality control guidelines, specific biological variables (fecundity, longevity, sex ratio, natural host parasitism) have to be compared to the accepted reference values.

To obtain the maternal generation (P1), fresh eggs of *S. cereallela* stuck in a sheet of cardboard (ca 12 × 17 cm) and previously treated with ultraviolet light, were placed within a glass jar (3 litres volume) for 24 hours to be parasitized by newly emerged parasitoid females at 25 ± 2 °C, 40-65% RH and 12L:12D hours. Each jar contained around 40000 females and the proportion ♀:eggs was 1:2.3.

Then, the cardboard was cut into pieces holding about 600 parasitized *S. cerealella* eggs each. Parasitized eggs could be clearly recognizable by their change in colour from orange to black (chorion melanisation) 4 days after the female parasitoid oviposition, under the assay conditions. These pieces contained the immature parasitoid individuals defined as the maternal generation (P1) in this experiment. Each piece of cardboard was individually placed in a glass tube (height 10 cm, diameter 1.5 cm, covered with film). Twenty tubes (replicates) with freshly parasitized eggs were randomly assigned to one of the following light/dark cycles (treatments): 12L:12D (control, as in the routine rearing); 9L:15D, 6L:18D and 3L:21D. To obtain the offspring generation (F1), when adults of the maternal generation emerged in each replicate (<24 hours old; ca 400-500 individuals by tube; female proportion 0.5), they were exposed for 24 hours (under light regime: 12L:12D) to fresh eggs of *S. cerealella* (ca 600 eggs) stuck in a sheet of cardboard and previously treated with UV light. Twenty replicates (tubes) were carried out per treatment (photoperiod of maternal generation). After exposure, the resulting parasitized eggs (F1 offspring generation) were maintained under a moderately low temperature (11 ± 2 °C) and complete darkness. These conditions were chosen because several studies dealing with *Trichogramma* species have demonstrated that under these conditions the percentage of diapausing insects depends on the maternal photoperiodic settings (Zaslavski and Umarova, 1990; Reznik *et al*., 2002; 2012).

The samples were daily checked until the massive emergence of the adults (about 55-94 days). At this point, two circular subsamples were selected from each sample (piece of cardboard containing exposed eggs). For this purpose, an acetate template with two circles of 0.5 cm diameter each was superimposed, and the following variables for the offspring generation (F1) were recorded in these two subsamples per replicate: adult emergence time (from egg to adult), adult emergence percentage [(emerged adults / total parasitized eggs) × 100] and female proportion (number of females / total emerged individuals). The non-emerged material remained under the conditions of the test (10-11 °C and total darkness) for another week. No new emergences were recorded during this period. After this week, other two circular subsamples (diameter 0.5 cm) in each replicate were examined. Parasitized eggs from which no adult parasitoid emerged were dissected to determine if parasitoids were alive (turgid and/or mobile) or dead (dry and/or immobile) and their stage (prepupa, pupa, or adult). The percentage of non-emerged alive parasitoids corresponding to each stage was estimated as (number of non-emerged alive parasitoids in X stage / total number of non-emerged alive parasitoids) × 100.

Adult emergence (F1), sex ratio (F1) and pupae, prepupae and adult proportion in non-emerged parasitized eggs (F1) were analysed as binary responses using logistic regression (logit link function) with photoperiod treatment as categorical factor. The model fit was checked by deviance and means were separated using LSD Fisher multiple comparison test. All statistical analyses were performed using Infostat (Di Rienzo *et al*., 2020). Data in results and figures are presented as mean ± SE. The level of significance of the parameters considered was 0.05.

Results

All the individuals (F1) in each treatment emerged at the same time. A descriptive analysis showed a longer time of emergence for treatments 3L:21D and 12L:12D and the emergence time was shorter for parasitoids under the treatments 6L:18D and 9L:15D (figure 1a).

The percentage of emerged adults from the F1 generation was significantly affected by the photoperiodic treatments ($\chi^2 = 1434.5$; df = 3; $p < 0.0001$). The treatment 3L:21D presented the highest value of emergence followed by 12L:12D treatment, 6L:18D treatment and finally, with the lowest value of adults emerged, the treatment 9L:15D (figure 1b).

The proportion of females in the offspring generation (F1) was affected by the light/dark cycle to which their mothers were exposed ($\chi^2 = 87.94$; df = 3; $p < 0.0001$). The treatment 3L:21D had the highest proportion of females, followed by the proportion of females at 12L:12D. On treatments 9L:15D and 6L:18D the female proportion was intermediate and similar (figure 1c).

The percentage of non-emerged alive prepupae was negligible for the treatments 3L:21D, 6L:18D and 9L:15D. However, the percentage of non- emerged alive prepupae was high for the treatment 12L:12D ($\chi^2 = 513.82$; DF= 3; $p<0.0001$) (figure 2a).

Different treatments significantly affected the percentage of non-emerged alive pupae ($\chi^2 = 333.82$; df = 3; $p < 0.0001$). The treatment 3L:21D showed the highest value of non-emerged pupae. On the other hand, there were no differences between treatments 6L:18D, 9L:15D and 12L:12D (figure 2b).

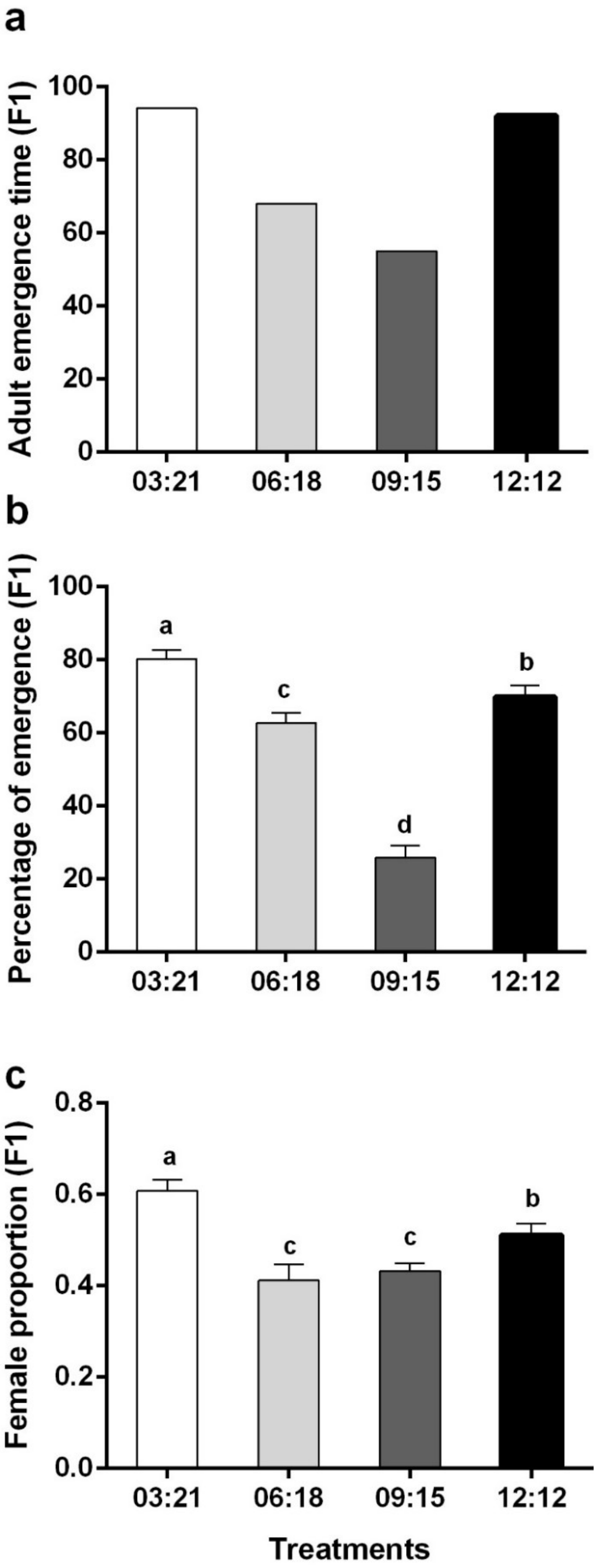

Figure 1. (**a**) Adult emergence time (F1), (**b**) percentage of emergence (F1), (**c**) female proportion (F1) of *T. nerudai*. Different letters show significant differences between treatments ($p < 0.0001$). Except for graphic a, data are presented as means ± standard error.

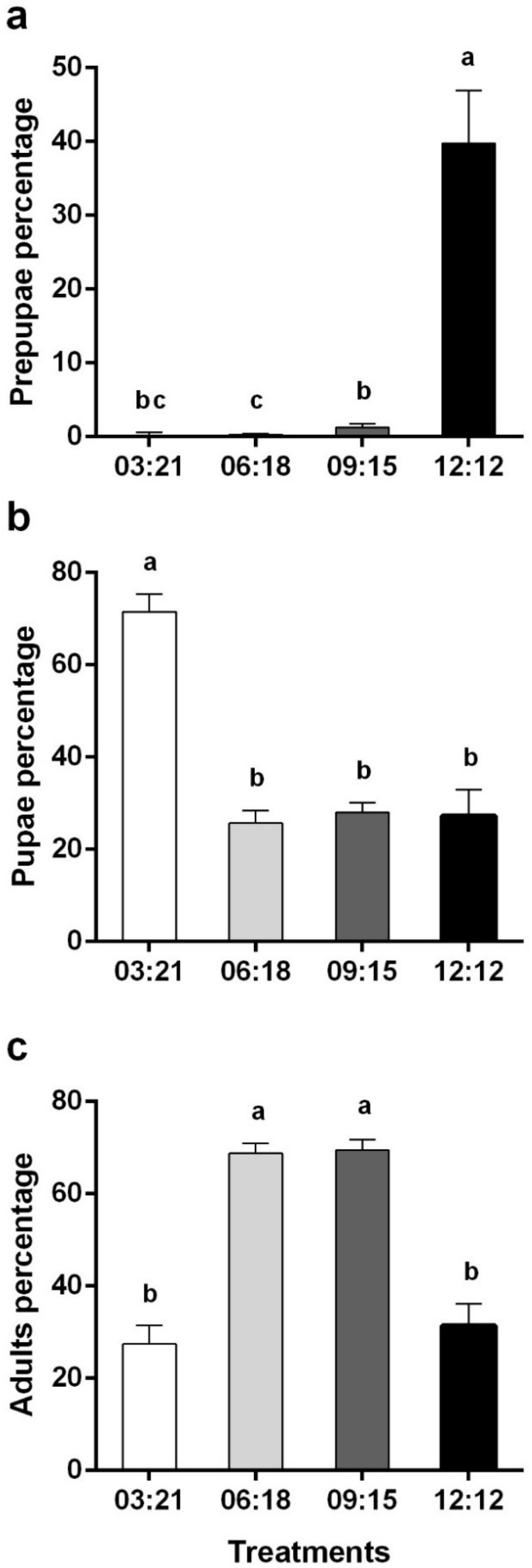

Figure 2. (**a**) Prepupae percentage registered in non-emerged and dissected eggs, (**b**) pupa percentage registered on non-emerged and dissected eggs, (**c**) adult percentage registered on non-emerged and dissected eggs. Different letters show significant differences between treatments ($p < 0.0001$). Data are presented as means ± standard error. The mean number of eggs dissected by treatment were: 3L:21D: 19.75 ± 1.86, 6L:18D: 49.74 ± 4.10, 9L:15D: 64.2 ± 4.26 and 12L:12D: 1215 ± 1.61.

The percentage of alive parasitoids in the adult stage that did not emerge differed significantly among the treatments ($\chi^2 = 414.78$; df = 3; $p < 0.0001$). It was similar between treatments 6L:18D and 9L:15D, and between treatments 3L:21D and 12L:12D (figure 2c).

Discussion

According to Mousseau and Fox (1998) in many insects several variables as photoperiod, temperature and host availability experienced by an ovipositing female determine the probability of diapausing on her offspring. In general, females that experience short photoperiods, cool temperatures or few potential hosts (i.e. cues that predict declining environmental conditions) tend to produce a high proportion of diapausing offspring.

In *Trichogramma* one of the mechanisms reported behind the maternal effect is the direct photoperiodic reaction in embryos through the abdominal cuticle of their mother (Volkoff and Daumal, 1994; Saunders *et al.*, 2002). Other mechanisms involve transmission of cytoplasmatic factors and environment induced epigenetic changes (Uller, 2008; Bossdorf *et al.*, 2008; Ghosh and Ballal, 2018). In all these cases, the factors affecting the mother can have an impact on the development of her offspring.

According to other authors, in moderate climates, all the *Trichogramma* species studied diapause in the prepupal stage (Zaslavski and Umarova, 1990; Boivin, 1994; Reznik, 2011; Voinovich *et al.*, 2015). Reznik (2011) found that the maximal proportion of diapausing progeny in *Trichogramma* species was induced by a short day light (10-12 hours) on the maternal generation. Also, Voinovich *et al.* (2003) and Ivanov and Reznik (2008) found a maximum proportion of diapausing progeny of *Trichogramma embryophagum* (Hartig) induced by short day light duration (ca 12 hours) and a low proportion of diapausing prepupae with long day light (>15 hours of light, right threshold) and short day light (<9 hours of light, left threshold) durations. Zaslavski and Umarova (1990) found similar effects on *Trichogramma pintoi* Voegele. Meanwhile the right threshold has ecological importance, because it occurs in nature and can affect the seasonal activity, the left threshold only can be experienced by the parasitoids of temperate zones under laboratory conditions (Voinivich *et al.*, 2003). In our study, the treatment 12L:12D showed that of non-emerged F1 the highest value consists of prepupae (39.75%) even though it was lower than those registered for other *Trichogramma* spp. (by between 60 and 100%) (Voinovich *et al.*, 2003; Reznik *et al.*, 2011; Vaghina *et al.*, 2011). This low value compared to other studies could be a consequence of a possible artificial selection since the laboratory colony is maintained under the photoperiod 12L:12D, and only the non-diapausing individuals are laying descendants. On the other hand, we observed that shorter periods of light did not show a greater number of diapausing prepupae but very low values (≤1%). The longest day light period here evaluated for *T. nerudai* was 12 hours, and 3 to 9 hours of light could be considered the “left threshold” of the photophase for this species. Further research considering light periods longer than 12 hours in a new established colony is required to determine the effect of longer photoperiods on the percentage of diapausing offspring.

It is important to note that the percentage of pupae that did not emerge in the course of our 100 day observation period was higher in the treatment 3L:21D (71.47%) than in the other treatments (25-28%). Besides, the percentage of adults that did not emerge was higher particularly for the treatments of 6L:18D and 9L:15D (67-68%). Therefore, our results suggest that other phases of development could be in a stage of quiescence under the described experimental conditions. In the present study, once the massive emergence of parasitoids occurred, the non-emerged material remained under the relatively low temperature conditions of the test (10-11 °C and total darkness) for another week. No new emergences were recorded during this period. After that, the material was dissected to verify the development stages of those non-emerged individuals. For this reason, it was not possible to register new emergences in this experiment after 100 days. However, in more recent studies on the maternal effect on *Trichogramma pretiosum* Riley (Viscarret, unpublished data), after the massive emergence of the parasitoids, part of the material was dissected and another part was kept under rearing conditions. In this case, it was observed that there was one well-marked period of emergence after the initial massive emergence. Although no material of *T. nerudai* was kept under rearing conditions after the first massive emergence, the observations in the *T. pretiosum* case suggests that a second period of emergence might occur for *T. nerudai* as well. This would explain, in particular in the treatments of 6L:18D and 9L:15D, the high percentages of non-emerged adults. Future studies keeping material under rearing condition are necessary in order to test this hypothesis.

In order to store pupal stage of *T. nerudai*, Tezze and Botto (2004) reported that the adult emergence and mobility of individuals kept at 4 °C were similar to those of the control not subjected to cold conditions, provided that the storage was not longer than 50 days. In addition, Cagnotti *et al.* (2018), in an experiment storing prepupal stage, recorded that the adult emergence and fecundity of individuals stored during 70 days (50 days at 5.4 °C after 20 days at an acclimation at 12 °C) were similar to those of the control at rearing conditions. In the present study, the maternal exposition at 3L:21D and 12L:12D treatments allowed to keep the filial generation for 90 days at an intermediate temperature increasing the storage period obtained by these authors. Similarly, Ghosh and Ballal (2018) were able to increase the period of storage of *Trichogramma chilonis* Ishii up to 125 days by controlling thermal and photoperiod outcome on the maternal generation.

To conclude, in this study we found that by keeping the maternal generation (P1) under conditions (3L:21D) and storing the offspring (F1) in egg stage under moderate low temperatures, it is possible to store the parasitoids during ca 90 days with an adult emergence rate of 82% and a 61% female proportion. The advantage of this approach is that it allows to store the parasitoids for longer periods without affecting their basic biological parameters, making them available to use in different strategies of pest control. The evaluation of the biological parameters of the F2 generation, sexual proportion, fecundity and longevity, must be evaluated in future studied in order to check the quality of insects obtained.

Acknowledgements

This research received financial support from research contract INTA-IAEA (International Atomic Energy Agency, number 18289) and the INTA Project PNPV 1135033. The authors thank Sergey Reznik and Ana López for their valuable and critical comments and suggestions.

References

Argerich C. A., López S., 2007.- Liberación de *Trichogramma nerudai* (Hymenoptera: Trichogrammatidae) para el control de la polilla del tomate *Tuta absoluta* (Lepidoptera: Gelechidae) en cultivo de tomate a campo en Mendoza, p. 54. In: *XXX congreso Argentino de horticultura*, 25-28 September 2007, La Plata, Buenos Aires, Argentina.

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

Bossdorf O., Richards C. L., Pigliucci M., 2008.- Epigenetics for ecologists.- *Ecology Letters*, 11: 106-115.

Botto E., Glaz P., 2010.- Potential for controlling codling moth *Cydia pomonella* (Linnaeus) (Lepidoptera: Tortricidae) in Argentina using the sterile insect technique and egg parasitoids.- *Journal of Applied Entomology*, 134: 251-260.

Botto E. N., Garrido S., Saez T., Hernández C., Lafalce C., Cichón L., Fernández D., 2005.- Evaluación de *Trichogramma* spp. (Hymenoptera: Trichogrammatidae) para el control biológico de *Cydia pomonella* (L.) (Lepidoptera: Tortricidae) en Alto Valle de Río Negro, Argentina, p. 44. In: *XXVII congreso nacional entomología*, 23-25 November 2005, Valdivia, Chile.

Cáceres S., Almonacid R. C., Aguirre M. R. A., López S. N., Botto E. N., 2007.- Evaluación de liberaciones de *Trichogramma nerudai* y *Trichogrammatoidea bactrae* para el control de huevos de la polilla del tomate *Tuta absoluta* en Corrientes, p. 70. In: *XXX congreso Argentino de horticultura*, 25-28 September 2007, La Plata, Buenos Aires, Argentina.

Cagnotti C. L., Lois M., López S. N., Botto E. N., Viscarret M. M., 2018.- Cold storage of *Trichogramma nerudai* using an acclimation period.- *BioControl*, 63: 565-573.

Danks H. V., 2007.- The elements of seasonal adaptations in insects.- *Canadian Entomology*, 139: 1-44.

Denlinger D. L., 1998.- Maternal control of fly diapause, pp. 275-287. In: *Maternal effects as adaptations* (Mosseau T. A., Fox C. W., Eds).- Oxford University Press, NY, USA.

Desneux N., Wajnberg E., Wyckhuys K. A. G., Burgio G., Arpaia S., Narváez-Vasquez C. A., González-Cabrera J., Catalán Ruescas D., Tabone R., Frandon J., Pizzol J., Poncet C., Cabello T., Urbaneja A., 2010.- Biological invasion of european tomato crops by *Tuta absoluta*: ecology, geographic expansion and prospects for biological control.- *Journal of Pest Science*, 83: 197-215.

Di Rienzo J. A., Casanoves F., Balzarini M. G., González L., Tablada M., Robledo C. W., 2020.- *InfoStat. Centro de Transferencia InfoStat*, FCA, Universidad Nacional de Córdoba, Argentina [online] URL: http://www.infostat.com.ar

Do Thi Khanh H., Chailleux A., Tiradon M., Desneux N., Colombel E., Tabone E., 2012.- Using new egg parasitoids (*Trichogramma* spp.) to improve integrated management against *Tuta absoluta*.- *Bulletin OEPP/EPPO*, 4: 249-254.

Ghosh E., Ballal C. R., 2018.- Maternal influence on diapause induction: an approach to improve long-term storage of *Trichogramma chilonis*.- *Phytoparasitica*, 46: 383-389.

Hassan S. A., 1997.- Criaçao da traça do milho, *Sitotroga cerealella*, para a produçao massal de *Trichogramma*, pp. 173-182. In: *Trichogramma e controle biológico aplicado* (Parra R. A. P., Zucchi R. A., Eds).- FEALQ, Piracicaba, Brazil.

Hernández C. M., Garrido S., Viscarret M. M., Botto E. N., Cichón L., Lago J., 2015.- Control biológico del gusano de la pera y la manzana, pp. 103-105. In: *Plagas cuarentenarias de frutales de la República Argentina* (Rossini M., Agostini J., Dummel D., Eds).- Ediciones INTA, Buenos Aires, Argentina.

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

Košťál V., 2006.- Eco-physiological phases of insect diapause.- *Journal of Insect Physiology*, 52: 113-127.

Leopold R. A., 1998.- Cold storage of insects for integrated pest management, pp. 235-267. In: *Temperature sensitivity in insects and application in integrated pest management* (Hallman G. J., Denlinger D. L., Eds).- Westview Press, Boulder, CO, USA.

Luna M. G., Sánchez N. E., Pereyra P. C., Nieves E., Savino V., Luft E., Virla E., Speranza S., 2012.- Biological control of *Tuta absoluta* in Argentina and Italy: evaluation of indigenous insects as natural enemies.- *Bulletin OEPP/EPPO*, 42: 260-267.

Morales Ramos J., Goolsby J. A., Geden C., Rojas M. G., García Cancino M. D., Rodríguez Vélez B., Arredondo Bernal H., Ciomper M. A., Simmons G. S., Gould J. R., Hoelmer K. A., 2022.- Production of hymenopteran parasitoid. Chapter 5, p 101-156. In: *Mass production of beneficial organisms invertebrates and entomopathogens*, 2nd edition (Morales-Ramos J. A., Guadalupe Rojas M., Shapiro-Ilan D. I., Eds).- Academic Press, London, UK.

Mousseau T. A., Fox C. W., 1998.- The adaptive significance of maternal effects.- *Trends in Ecology & Evolution*, 13: 403-407.

Reznik S. Y., 2011.- Ecological and evolutionary aspects of photothermal regulation of diapause in Trichogrammatidae.- *Journal of Evolutionary Biochemistry and Physiology*, 47: 512-523.

Reznik S.Y., Kats T. S., 2004.- Exogenous and endogenous factors inducing diapauses in *Trichogramma principium* Sug. Et Sor. (Hymenoptera: Trichogrammatidae).- *Entomological Review*, 84: 963-970.

Reznik S. Y., Kats T. S., Umarova T. Y., Voinovich N. D., 2002.- Maternal age and endogenous variation in maternal influence on photoperiodic response in the progeny diapause in *Trichogramma embryophagum* (Hymenoptera: Trichogrammatidae).- *European Journal of Entomology*, 99: 175-179.

Reznik S. Y., Umarova T. Y., Voinovich N. D., 2003.- Egg retention in *Trichogramma* (Hymenoptera: Chalcidoidea: Trichogrammatidae): learning or diapauses?- *Acta Societatis Zoologicae Bohemicae*, 67: 25-33.

Reznik S. Y., Voinovich N. D., Vaghina N. P., 2011.- Maternal regulation of *Trichogramma embryophagum* Htg. (Hymenoptera: Trichogrammatidae) diapause: photoperiodic sensitivity of adult females.- *Biological Control*, 57: 158-162.

Reznik S. Y., Vaghina N. P., Voinovich N. D., 2012.- Multigenerational maternal effect on diapause induction in *Trichogramma* species (Hymenoptera: Trichogrammatidae).- *Biocontrol Science and Technology*, 22: 429-445.

Rossi M. M., 1997.- As interruoçoes de desenvolvimento em *Trichogramma*, pp. 151-172. In: *Trichogramma e controle biológico aplicado* (Parra R. A. P., Zucchi R. A., Eds).- FEALQ, Piracicaba, Brazil.

Saunders D. S., Steel C. G. H., Vafopoulou X., Lewis R. D., 2002.- *Insect clocks*. 3rd edition.- Elsevier Science, Amsterdam, The Netherlands.

Tezze A. A., Botto E. N., 2004.- Effect of cold storage on the quality of *Trichogramma nerudai* (Hymenoptera: Trichogrammatidae).- *Biological Control*, 30: 11-16.

Uller T., 2008.- Developmental plasticity and the evolution of parental effects.- *Trends in Ecology and Evolution*, 23: 432-438.

Vaghina N. P., Reznik S. Y., Voinovich N. D., 2011.- Photoperiodic responses of pupa and adult determining maternal influence on progeny diapause in two species of the genus *Trichogramma* (Hymenoptera: Trichogrammatidae).- *Entomological Review*, 93: 1-8.

van Lenteren J. C., 2003.- *Quality control and production of biological control agents: theory and testing procedures*.- CABI Publishing, Wallingford, UK.

van Lenteren J. C., 2012.- The state of commercial augmentative biological control: plenty of natural enemies, but a frustrating lack of uptake.- *BioControl*, 57: 1-20.

van Lenteren J. C., Tommasini M. G., 2003.- Mass production, storage, shipment and release of natural enemies, pp. 181-190. In: *Quality control and production of biological control agents: theory and testing procedures* (van Lenteren J. C., Ed.).- CABI, Wallingford, UK.

Ventura García P., Wajnberg E., Pizzol J., Oliveira M. L. M., 2002.- Diapause in the egg parasitoid *Trichogramma cordubensis*: role of temperature.- *Journal of Insect Physiology*, 48: 349-355.

Voinovich N. D., Umarova T. Y., Kats T. S., Resnik S. Y., 2003.- Variation of photoperiodic reaction in *Trichogramma embryophagum* Htg. (Hymenoptera: Trichogrammatidae).- *Entomological Review*, 83: 779-782.

Voinovich N. D., Reznik S. Y., Vaghina N. P., 2015.- Maternal thermal effect on diapause in *Trichogramma* species (Hymenoptera: Trichogrammatidae).- *Journal of Applied Entomology*, 139: 783-790.

Volkoff A. N., Daumal J., 1994.- Ovarian cycle in immature and adult stages of *Trichogramma cacoeciae* and *T. brassicae* (Hym.: Trichogrammatidae).- *Entomophaga*, 39: 303-312.

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

Authors' addresses: Mariana M. Viscarret (corresponding author: viscarret.mariana@inta.gob.ar), Cynthia L. Cagnotti, Silvia N. López, Instituto Nacional de Tecnología Agropecuaria (INTA), Instituto de Microbiología y Zoología Agrícola, Las Cabañas y De los Reseros s/n. C.C.25. 1712, Ituzaingó, Buenos Aires, Argentina.

Received July 7, 2022. Accepted January 23, 2023.