



## *Trissolcus teretis* (Johnson, 1987) (Hymenoptera: Scelionidae) parasitism on *Euschistus heros* (Fabricius, 1798) and *Diceraeus melacanthus* Dallas, 1851 (Hemiptera: Pentatomidae) eggs at different temperatures

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### ABSTRACT

*Trissolcus teretis* has been recorded to parasitize eggs not only of *Euschistus heros* and *Diceraeus melacanthus* but also of other stink bug species in the most important soybean producing countries of South America such as Brazil, Argentina as well as other countries of the Neotropical region. Despite several studies relating to its natural incidence and parasitism, the impact of different temperatures on biology and parasitism capacity of *T. teretis* on eggs of *E. heros* and *D. melacanthus* is practically unknown. Considering that biological traits can be highly influenced by temperature, research on *T. teretis* parasitism at different temperatures and hosts is of theoretical and practical interest. We therefore evaluated *T. teretis* parasitism and development on eggs of *E. heros* and *D. melacanthus* at 15°C, 20°C, 25°C, and 30°C. Temperature had an impact on the parasitoid reared on eggs of both studied hosts. Although we recorded parasitism at an extreme temperature of 15°C, these conditions are unfavorable for *T. teretis* parasitism, impairing parasitoid biological traits, especially survival of larvae and adult parasitism. Therefore, for application in crop fields where temperatures of 15°C or lower are common, additional studies are necessary to investigate the possible need to increase parasitoid numbers during releases or to choose smaller intervals between multiple releases.

### Introduction

Among different pests that attack soybean in the field, stink bugs are notorious for feeding directly on pods, thereby not only reducing yield but also impairing physiological and sanitary quality of the seeds or grains (Corrêa-Ferreira and Azevedo, 2002; Bueno et al., 2020). At least 54 different stink bug species have been reported in soybean fields (Panizzi and Slansky, 1985). Among those species, the Neotropical brown stink bug *Euschistus heros* (Fabricius, 1798) (Hemiptera: Pentatomidae) is the most common and abundant species, especially in central Brazil between latitudes of 0° and 23°S (Panizzi and Corrêa-Ferreira, 1997; Bueno et al., 2015a). Recently, the green belly stink bug *Diceraeus melacanthus* Dallas, 1851 (Hemiptera: Pentatomidae) has also been gaining economic importance, especially in areas where soybean is succeeded by maize as a second crop (Bueno et al., 2015b; Gomes et al., 2020). This pest remains in the area after soybean harvest and attacks the sequentially grown maize, which makes it one of the most important maize pests (Smaniotto and Panizzi, 2015).

Synthetic insecticides are commonly preferred by most soybean and maize growers as a management tool against stink bugs (Song and Swinton, 2009; Panizzi, 2013; Bueno et al., 2020). However, excessive use of these chemicals triggers some negative side effects (Song and Swinton, 2009). The most important of these include selection of pests resistant to the used chemicals (Diez-Rodríguez and Omoto, 2001; Sosa-Gómez et al., 2001; Sosa-Gómez and Silva, 2010) and elimination of beneficial arthropods such as pollinators and natural biological control agents. These effects are even more prevalent when non-selective insecticides are used (Carmo et al., 2010; Van Lenteren and Bueno, 2003; Torres and Bueno, 2018).

In this scenario, it is crucial to develop and adopt a more sustainable and efficient pest management approach. One of the most environment-friendly strategies that have been increasingly applied worldwide is augmentative biological control (Van Lenteren et al., 2018). Among the agents used in augmentative biological control, egg parasitoids are the most important, since they are easily reared in the laboratory and are able to control pests at a stage of development (egg) preceding the occurrence of plant injuries (Koppel et al., 2009).

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In soybean, stink bug eggs are efficiently parasitized by micro-hymenopterans of the family Scelionidae (Tillman, 2011). Among the different parasitoid species of this family, the genus *Trissolcus* includes some of the most important, due to high levels of parasitism (Yeargan, 1979; Jones, 1988; Foerster and Queiróz, 1990; Corrêa-Ferreira and Moscardi, 1995). There are several studies on the incidence and parasitism (Kobayashi and Cosenza, 1987; Medeiros et al., 1997; Medeiros et al., 1998), behavior (Borges et al., 2002; Sujii et al., 2002) and chemical ecology (Borges et al., 2003; Moraes et al., 2005; Cavalcante et al., 2006) of this genus. However, biology and parasitism capacity of *Trissolcus teretis* (Johnson, 1987) (Hymenoptera: Scelionidae) on eggs of *E. heros* and *D. melacanthus* is practically unknown. Therefore, considering that biological traits can be highly influenced by abiotic factors such as temperature (Noldus, 1989), the study of *T. teretis* parasitism at different temperatures and hosts can provide crucial information for the use of this biological control agent. As poikilothermic organisms, survival capacity and development of insects depend on environmental temperature (Wilson and Barnett, 1983). Temperature has a direct influence on parasitoid sex ratio and emergence rates as well as on other biological traits that are crucial to determine parasitoid field performance (Canto-Silva et al., 2005). Furthermore, parasitoids can be extremely sensitive to temperature changes since they depend on other insects as hosts. Parasitoids not only respond to direct effects of temperature change but also to indirect effects caused by variability in host population dynamics triggered by variations in temperature (Wu et al., 2016). Therefore, it is of great theoretical and practical interest to study the development and parasitism capacity of egg parasitoids at different temperatures prior to its use in the field. In this context, the objective of the present study was to evaluate *T. teretis* parasitism and development on eggs of *E. heros* and *D. melacanthus* at different temperatures.

## Material and methods

### Laboratory rearing of *Trissolcus teretis*, *Euschistus heros*, and *Diceraeus melacanthus*

The stink bugs and parasitoids used in the bioassays were obtained from insect colonies kept at Embrapa Soybean (one of the units of the Brazilian Agricultural Research Corporation), Londrina, State of Paraná, Brazil, according to methodologies described by Schaefer and Panizzi (2000) (stink bugs) and Peres and Corrêa-Ferreira (2004) (parasitoids). Colonies are reared inside Biochemical Oxygen Demand (BOD) climate chambers (ELETRoLab®, model EL 212, São Paulo, SP, Brazil) set at  $80 \pm 10\%$  humidity, a temperature of  $25 \pm 2^\circ\text{C}$ , and a photoperiod of 14:10 h (L:D).

Stink bug species were originally collected in soybean (*E. heros*) and maize (*D. melacanthus*) fields at Embrapa Soybean Experimental Farm, Londrina, State of Paraná, Brazil ( $23^\circ 11' 11.7''$  S and  $51^\circ 10' 46.1''$  W). The populations were kept in the laboratory for approximately 6 years under the previously described conditions. New field insects were introduced each year to maintain colony quality. Insects were kept in plastic boxes (20 x 20 x 24 cm) (Plasvale Ltda., Gaspar, State of Santa Catarina, Brazil), lined with filter paper and a piece of fabric (cotton) to serve as substrate for laying eggs. Insects were fed *ad libitum* with a mixture of beans (*Phaseolus vulgaris* L.; Fabaceae), soybeans (*Glycine max* L. Merr.; Fabaceae), peanuts (*Arachis hypogaea* L.; Fabaceae), sunflower seeds (*Helianthus annuus* L.; Asteraceae) and privet fruits (*Ligustrum lucidum* Aiton; Oleaceae). A Petri dish (diameter 9 cm) with a cotton wad soaked in distilled water was added to each cage. Cages were cleaned, food was replaced, and egg masses were collected on a daily basis. The eggs were then used for colony maintenance or stored

in liquid nitrogen ( $-196^\circ\text{C}$ ) for up to three months to be later used for experiments (Silva et al., 2008).

Parasitoids was originally collected in Brasília, DF, Brazil, and grown at the parasitoid rearing facilities of Embrapa Cenargen from where some specimens were transferred to Embrapa Soybean, Londrina, PR, Brazil, three years ago. From Londrina, some insects were sent to a specialist for taxonomic identification. The voucher specimen from IBCBE 003334 to IBCBE 003425 were deposited at the “Coleção de Insetos Entomófagos Oscar Monte”, Instituto Biológico de Campinas, Campinas, São Paulo, Brazil and insects were identified as *Trissolcus teretis* (Johnson, 1987) (Hymenoptera: Scelionidae).

*Trissolcus teretis* colony was kept in the laboratory for approximately three years on *E. heros* eggs under the previously described conditions. Eggs were glued to white cards (12 mm x 75 mm) and then exposed to parasitism. After 24 h, these cards were removed and placed in new plastic pots (2 L) (Plasvale Ltda., Gaspar, State of Santa Catarina, Brazil), containing droplets of honey on the walls for adult feeding as soon as they emerged. The pots were sealed with plastic film to prevent insects from escaping. The resulting adults were used for trials or colony maintenance.

### Bioassays

Four independent bioassays were carried out at  $15^\circ\text{C}$ ,  $20^\circ\text{C}$ ,  $25^\circ\text{C}$  and  $30^\circ\text{C} \pm 2^\circ\text{C}$  inside BOD chambers (ELETRoLab®, model EL 212, São Paulo, SP, Brazil) set at relative humidity  $80 \pm 10\%$ , and 14:10 h L:D photoperiod. Two bioassays evaluated the impact of the tested temperatures on parasitoid larval development reared on eggs of *E. heros* (bioassay 1) and *D. melacanthus* (bioassay 2). Two additional bioassays evaluated the impact of tested temperatures on adult parasitoid parasitism on eggs of *E. heros* (bioassay 3) and *D. melacanthus* (bioassay 4).

### Larval development of *Trissolcus teretis* on eggs of *Euschistus heros* (bioassay 1) and *Diceraeus melacanthus* (bioassay 2) at different temperatures

Bioassays were carried out in a completely randomized design with four treatments ( $15^\circ\text{C}$ ,  $20^\circ\text{C}$ ,  $25^\circ\text{C}$  and  $30^\circ\text{C} \pm 2^\circ\text{C}$ ) and seven replicates. Each replicate consisted of three individualized females (= 21 females per treatment). Data obtained from replicates, therefore, represent average measurements for three females. Rather than using a single female parasitoid per replicate, a group of females was used to increase representativeness. Egg parasitoids are small and fragile and thus vulnerable to tiny injuries during experimental manipulation, which could affect the results. Using a set of parasitoids for each replicate can partly mitigate this potentially negative effect of experimental manipulation (Queiroz et al., 2018).

Newly emerged *T. teretis* females ( $\leq 48$  h old, mated and with no previous parasitism experience) were individually placed in microtubes (12 mm in diameter and 75 mm in height) and fed with a honey droplet. Host eggs ( $n = 40$ ) were glued with white glue (Tenaz®) on a white card (10 mm x 70 mm), and labeled according to each treatment. Parasitism was allowed for 24 hours in BOD chambers ( $25 \pm 2^\circ\text{C}$ ). After this period, the eggs of each stink bug species were individualized into tubes (12 mm in diameter and 75 mm in height) and transferred to BOD chambers set at  $15^\circ\text{C}$ ,  $20^\circ\text{C}$ ,  $25^\circ\text{C}$  or  $30^\circ\text{C} \pm 2^\circ\text{C}$ , according to each treatment. The following biological traits were evaluated: egg-to-adult period (days), emergence (%) calculated as the number of parasitized eggs with emergence holes/number of total parasitized eggs x 100, and sex ratio calculated as the number of emerged females/(number of emerged females + number of emerged males). To determine egg-

to-adult periods (days), emergence of *T. teretis* was observed daily. The evaluation of parasitoid emergence was carried out under a stereomicroscope, counting the eggs of the host that had an exit hole through which adults had emerged. The number of parasitized eggs was calculated as the number of emerged parasitoids plus the number of adult parasitoids completely developed but dead inside the host (observed by means of dissection).

#### *Trissolcus teretis* parasitism capacity on eggs of *Euschistus heros* (bioassay 3) and *Diceraeus melacanthus* (bioassay 4) at different temperatures

Bioassays were carried out in a completely randomized design, with four treatments (15°C, 20°C, 25°C and 30°C ± 2°C) and seven replicates composed of three individualized females as previously explained, for each host species (21 insects per treatment). Newly emerged *T. teretis* females (≤48 h old, mated and with no previous parasitism experience) were individualized into tubes (12 mm in diameter and 75 mm in height) with cards (8 mm x 50 mm) containing approximately 40 stink bug eggs (*E. heros* or *D. melacanthus* according to each treatment) and placed inside BODs at the designated temperature of each treatment. Eggs were replaced by new ones on a daily basis until the death of females. After 24 h of parasitism, eggs were stored in plastic bags (40 mm x 230 mm), and kept in a BOD chamber (25 ± 2°C) until adult emergence. The biological traits evaluated were: longevity of parental females (days), lifetime parasitism (total number of parasitized eggs per female), daily parasitism (number of eggs parasitized per day), cumulative parasitism (%), progeny emergence (%) and progeny sex ratio.

#### Data analysis

The results were submitted to exploratory analyses to evaluate the assumptions of normality of the residuals (Shapiro and Wilk, 1965), and homogeneity of variance among treatments (Burr and Foster, 1972) for ANOVA, followed by a Tukey test ( $p \leq 0.05$ ). When the data did not follow a normal distribution, the Kruskal-Wallis test, a non-parametric analysis of variance, was used, followed by Chi-Square ( $\chi^2$ ) mean comparisons ( $p \leq 0.05$ ) (SAS Institute, 2001).

## Results

#### Larval development of *Trissolcus teretis* on eggs of *Euschistus heros* (bioassay 1) and *Diceraeus melacanthus* (bioassay 2) at different temperatures

We found a significant influence of temperature on the egg-to-adult period (days) of *T. teretis* developing on the eggs of either host species (*E. heros* and *D. melacanthus*). A significant increase in development

rate, resulting in a reduced egg-to-adult period was observed with increasing temperature. The egg-to-adult period of *T. teretis* on *E. heros* and *D. melacanthus* eggs was 9.9 and 9.6 days at 30°C and 50.4 and 45.0 days at 15°C, respectively. Thus, the increase in temperature from 15°C to 30°C resulted in a reduction of the egg-to-adult period of *T. teretis* by 40.5 and 35.4 days on *E. heros* and *D. melacanthus* eggs, respectively (Table 1).

Similarly, the studied temperatures in which larvae were reared also influenced the emergence (%) of *T. teretis* from eggs of either host species (*E. heros* and *D. melacanthus*). When *T. teretis* developed on *E. heros* eggs, the highest emergence was observed at 25°C (93.1%) followed by 20°C and 30°C (71.8% and 75.6%, respectively). At 15°C, *T. teretis* emergence from *E. heros* eggs was only 24.6%. When *T. teretis* developed on *D. melacanthus* eggs, the highest emergence occurred at 20°C and 25°C (90.9% and 89.9%, respectively) followed by the emergence recorded at 30°C (70.8%). The lowest emergence of *T. teretis* from *D. melacanthus* eggs also occurred at 15°C (39.7%) (Table 1).

Sex ratio was also influenced by the temperature in which larvae were reared. Higher values were recorded for parasitoids developing at 15°C on both *E. heros* (0.87) and *D. melacanthus* (0.75) eggs. It is noteworthy that the *T. teretis* sex ratio observed at 15°C (0.75) on *D. melacanthus* eggs did not differ from that observed at 20°C (0.69) (Table 1).

#### *Trissolcus teretis* parasitism capacity on eggs of *Euschistus heros* (bioassay 3) and *Diceraeus melacanthus* (bioassay 4) at different temperatures

Adults of *T. teretis* were clearly affected by temperature while exposed to eggs of either of the studied hosts (*E. heros* and *D. melacanthus*) (Table 2 and Figures 1 and 2). Longevity of parental females of *T. teretis* was inversely proportional to the increase in temperature on both hosts. When reared on *E. heros* eggs, the maximum longevity of *T. teretis* parental females was 104.1 days at 15°C. Lower values of 70.1, 34.5 and 24.7 days were recorded at 20°C, 25°C and 30°C, respectively. Similarly, when reared on *D. melacanthus* eggs, the maximum longevity of *T. teretis* was 112.9 days at 15°C followed by 60.1, 39.0 and 23.0 days at 20°C, 25°C and 30°C, respectively (Table 2).

Lifetime parasitism varied with temperature on both host species. Overall, *T. teretis* parasitized higher numbers of eggs of *D. melacanthus* than of *E. heros*. When *T. teretis* was reared on *E. heros* eggs, the number of parasitized eggs was higher at 30°C (29.2) than at 15°C (16.8), 20°C (15.8) and 25°C (22.2), with no significant difference between the latter three values. In contrast, when *T. teretis* was reared on *D. melacanthus* eggs, the highest number of parasitized eggs was recorded at 20°C (54.1) and 25°C (55.1), while the lowest parasitism was recorded at the lowest studied temperature of 15°C (36.6) (Table 2).

It is important to emphasize that in bioassays 1 and 2 parasitism occurred at 25°C and larval development and adult emergence (%) was

**Table 1**

Larval development of *Trissolcus teretis* on *Euschistus heros* (bioassay 1) and *Diceraeus melacanthus* (bioassay 2) eggs at different temperatures.

Host	Temperature (°C)	Egg-to-adult period (days)	Emergence (%)	Sex ratio
<i>E. heros</i>	15	50.4 ± 1.0 a <sup>a</sup>	24.6 ± 4.9 c <sup>a</sup>	0.87 ± 0.06 a <sup>a</sup>
	20	21.5 ± 0.2 b	71.8 ± 1.8 b	0.63 ± 0.05 b
	25	13.2 ± 0.2 c	93.1 ± 1.9 a	0.66 ± 0.04 b
	30	9.9 ± 0.1 d	75.6 ± 2.1 b	0.55 ± 0.06 b
<i>D. melacanthus</i>	15	45.0 ± 0.5 a <sup>a</sup>	39.7 ± 1.9 c <sup>b</sup>	0.75 ± 0.03 a <sup>b</sup>
	20	20.4 ± 0.2 b	90.9 ± 1.0 a	0.69 ± 0.01 ab
	25	12.5 ± 0.2 c	89.9 ± 2.1 a	0.66 ± 0.01 b
	30	9.6 ± 0.2 d	70.8 ± 3.4 b	0.66 ± 0.02 b

<sup>a</sup>Means ± SEM followed by the same letter within a column for each host species did not differ statistically (Kruskal-Wallis ANOVA, test  $\chi^2$  test  $p > 0.05$ ). <sup>b</sup>Means ± SEM followed by the same letter within a column for each host species did not differ statistically (ANOVA, Tukey test  $p > 0.05$ ).

measured at different temperatures (temperature impact on larval development was measured). Differently, in bioassays 3 and 4 parasitism occurred at different temperatures, and their offspring (parasitized eggs) was immediately transferred to a constant temperature of 25°C (temperature impact on adult parasitism was measured). Consequently, no differences were observed in progeny emergence (%) from either *E. heros* (bioassay 3) or *D. melacanthus* (bioassay 4), which had values above 85% (Table 2).

The number of host eggs parasitized per day by *T. teretis* females (daily parasitism) decreased constantly in both host species over the parasitoid lifespan, especially at temperatures of 20°C, 25°C and 30°C (Figures 1 and 2). At 15°C, daily parasitism varied in the first days of parasitism, peaking at day 13 for *E. heros* (Figure 1A) and day 17 for *D. melacanthus* (Figure 2A) eggs. Cumulative parasitism (%) of *E. heros*

eggs reached 80% on days 18, 16, 16 and 12 when adults were kept at temperatures of 15°C, 20°C, 25°C and 30°C, respectively (Figure 1). In *D. melacanthus* eggs, 80% of cumulative parasitism reached 80% of lifespan parasitism at 21, 18, 14 and 9 days of parasitism at temperatures of 15°C, 20°C, 25°C and 30°C, respectively (Figure 2).

## Discussion

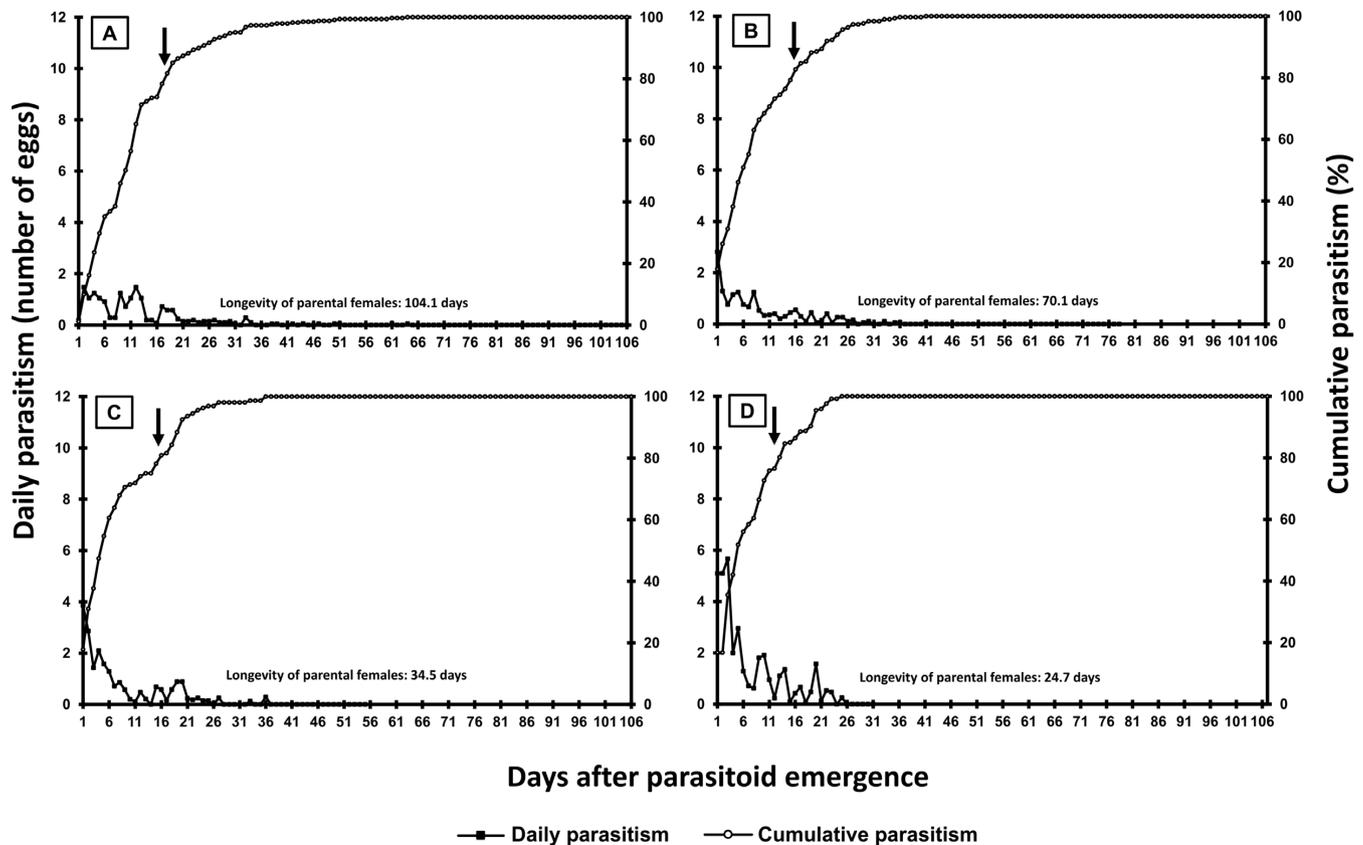
The data in this study contribute to a better understanding of not only parasitism capacity of *T. teretis* on *E. heros* and *D. melacanthus* eggs at different temperatures but also of the impact of temperature on the development of young stages of the parasitoid. Such information is of theoretical and practical interest in order to successfully use this

**Table 2**

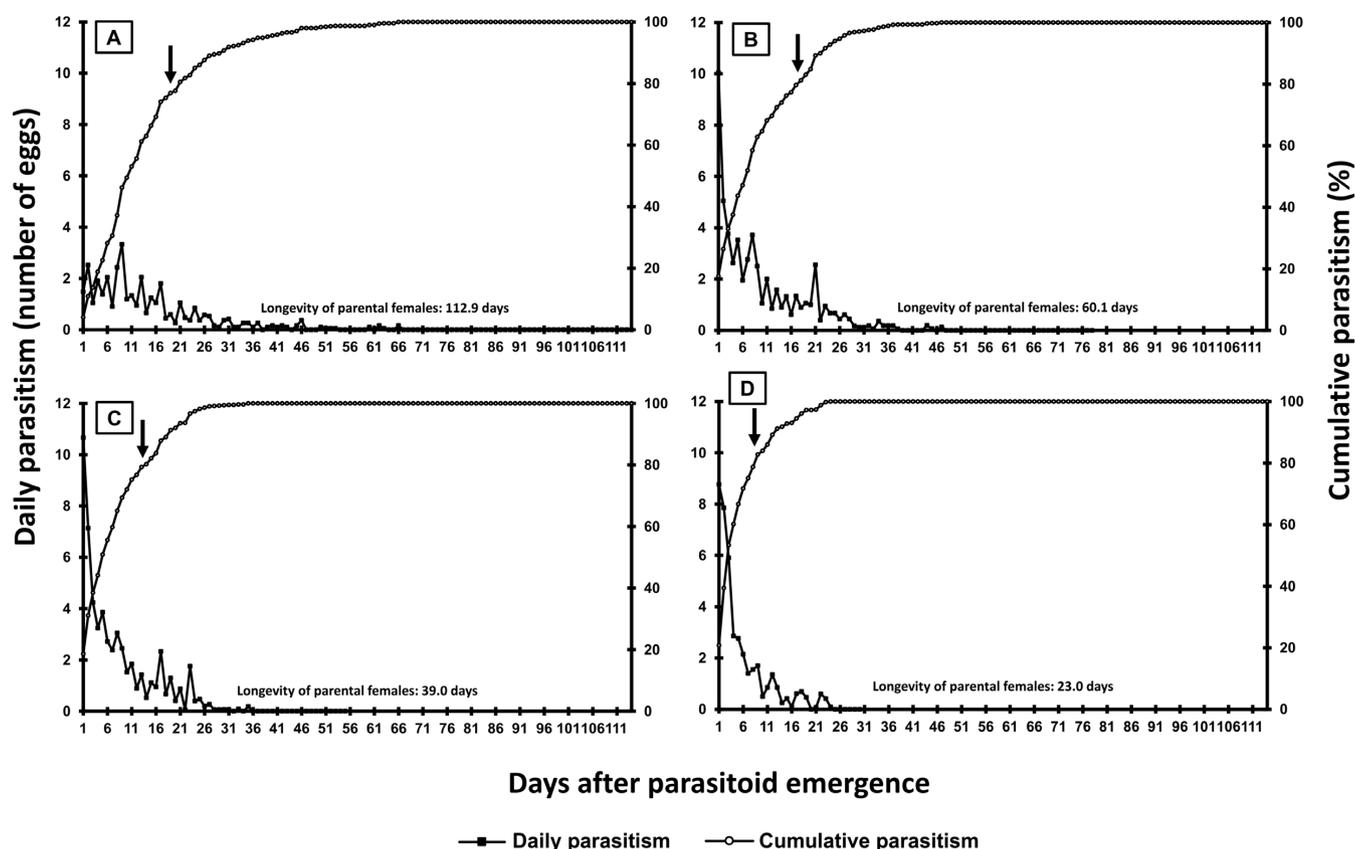
Parasitism capacity of *Trissolcus teretis* on *Euschistus heros* (bioassay 3) and *Diceraeus melacanthus* (bioassay 4) eggs at different temperatures.

Host	Temperature (°C)	Longevity of parental females (days)	Lifetime parasitism	Progeny emergence (%)	Progeny sex ratio
<i>E. heros</i>	15	104.1 ± 3.8 a <sup>a</sup>	16.8 ± 1.3 b <sup>b</sup>	94.5 ± 1.1 <sup>ns</sup>	0.49 ± 0.06 b <sup>b</sup>
	20	70.1 ± 5.3 b	15.8 ± 1.1 b	91.9 ± 1.7	0.73 ± 0.02 a
	25	34.5 ± 5.0 c	22.2 ± 2.1 b	94.1 ± 1.3	0.51 ± 0.08 b
	30	24.7 ± 1.4 c	29.2 ± 2.2 a	95.0 ± 1.1	0.63 ± 0.03 ab
<i>D. melacanthus</i>	15	112.9 ± 2.9 a <sup>a</sup>	36.6 ± 2.7 c <sup>b</sup>	88.2 ± 1.6 <sup>ns</sup>	0.66 ± 0.03 <sup>ns</sup>
	20	60.1 ± 3.7 b	54.1 ± 3.9 ab	86.2 ± 1.2	0.72 ± 0.02
	25	39.0 ± 2.1 c	55.1 ± 4.4 a	88.5 ± 1.6	0.71 ± 0.03
	30	23.0 ± 0.9 d	41.0 ± 2.5 bc	91.1 ± 2.2	0.72 ± 0.03

<sup>a</sup>Means ± SEM followed by the same letter within a column for each host species did not differ statistically (Kruskal-Wallis ANOVA, test  $\chi^2$  test  $p > 0.05$ ). <sup>b</sup>Means ± SEM followed by the same letter within a column for each host species did not differ statistically (ANOVA, Tukey test  $p > 0.05$ ). <sup>ns</sup>ANOVA not significant.



**Figure 1** Daily and cumulative parasitism of *Trissolcus teretis* on *Euschistus heros* eggs at 15°C (A), 20°C (B), 25°C (C), 30°C (D) ± 2°C, RH 70% ± 10% and photoperiod of 14/10h (Light/Dark). The arrow indicates 80% parasitism.



**Figure 2** Daily and cumulative parasitism of *Trissolcus teretis* on *Diceræus melacanthus* eggs at 15°C (A), 20°C (B), 25°C (C), 30°C (D)  $\pm$  2°C, RH 70%  $\pm$  10% and photoperiod of 14/10h (Light/Dark). The arrow indicates 80% parasitism.

biological control agent to manage the stink bug species *E. heros* and *D. melacanthus* in the field in future augmentative biological control programs. It helps to evaluate the adaptability of parasitoid species to different climate conditions, as well as the potential parasitoid efficiency to control both studied stink bug species (*E. heros* and *D. melacanthus*). In general, the results clearly identify temperature as an abiotic factor that significantly affects the development of *T. teretis*. Previous studies have reported a strong influence of thermal conditions on the biological traits of poikilothermic organisms, such as insects (Colinet et al., 2015; Furlong and Zalucki, 2017). However, to our knowledge this is the first report of the impact of temperature on *T. teretis* while parasitizing and developing on *E. heros* and *D. melacanthus* eggs.

The observed decrease of the egg-to-adult period (days) was inversely related to an increase in temperature, and is most likely a consequence of the increase in metabolic activity of the parasitoid at higher temperatures (Hernández and Díaz, 1996).

The egg-to-adult period was also shorter for *T. teretis* reared on *D. melacanthus* eggs. Such differences might occur due to different egg characteristics of each host species, for example surfaces, size and volume, and chorion structure. Differences in all of these traits can affect not only female parasitoid handling time and exploitation, but also host suitability to parasitoid development, thus influencing the egg-to-adult period (days) (Cônsoi et al., 1999).

Larval survival of *T. teretis* was significantly impacted when immature parasitoids were exposed to different temperatures during development. A lower emergence (%) of *T. teretis* was observed at 15°C from *E. heros* eggs (24.6%) as well as from *D. melacanthus* eggs (39.7%) compared with the highest temperatures studied. A decrease in emergence may be observed because 15°C is close to the lower lethal

temperature of *T. teretis* in which 100% mortality occurs (Bueno et al., 2008). Similar results were previously reported for other species of the Scelionidae family. Yeargan (1980) observed low emergence of *Telenomus podisi* Ashmead 1893 (Hymenoptera: Scelionidae) on eggs of *Podisus maculiventris* (Say, 1832) (Hemiptera: Pentatomidae) at 15.5°C. Torres et al. (1997) and Nakama and Foerster (2001) reported a viability of less than 50% when *T. podisi* was exposed to 15°C. However, to our knowledge this is the first report regarding *T. teretis*.

In warmer regions, parasitoids can benefit from faster development, so that parasitoid pupae released in augmentative biological control are not exposed for long periods to predators or insecticides that could harm their field efficiency. In this context, it is important to highlight that despite reduced emergence at the highest tested temperature (30°C), parasitoid emergence was still higher than 70%. *Trissolcus teretis* emergence of 75.6% and 70.8% was observed from eggs of *E. heros* and *D. melacanthus*, respectively. In general, the more suitable the temperature, the higher the recorded parasitoid survival rates (higher emergence) will be (Yeargan, 1980; Sujji et al., 2002).

Sex ratio is an important trait to be considered in biological control, since only females parasitize, and therefore control the target host in the field. Thus, the production of a higher number of females is desirable (Bueno et al., 2009). In general, sex ratio can be impacted by temperature in two different ways: 1) by the different ability of males and females to survive and develop to an adult stage at different temperatures or 2) by the ability of adults to recognize different temperatures and selectively produce male or female progeny (Vinson, 1997). Only the first way seems to apply to our results since different sex ratios were recorded only when larvae developed under different temperatures. When adult parasitoids were exposed to different temperatures for

parasitism and larval development occurred at 25°C, no changes in sex ratio was observed in the progeny. In general, regardless of the temperature impact observed on larval and adult stages of *T. teretis*, neither progeny emergence (%) nor progeny sex ratio were altered.

The higher sex ratio recorded when larvae developed at 15°C on both host species might be due to larger size or larger fat body of female larvae (Renault et al., 2002), which would make females more tolerant to cold temperatures than males. This hypothesis is supported by the results of Yeargan (1980), who reported that at 15.5°C only *T. podisi* females emerge. Likewise, Doetzer and Foerster (2007) reported a higher occurrence of both *Trissolcus basalis* (Wollaston, 1858) (Hymenoptera: Scelionidae) and *T. podisi* females under natural conditions during the coldest months in the off-season of soybean in southern Paraná, Brazil.

Not only does temperature influence *T. teretis* larval development but also adult stages. The decrease in longevity of parental females in relation to the increase in temperature could be mostly a consequence of increased metabolism at higher temperatures and, consequently, energy expenditure (Gerling, 1972). Similar results were previously reported for other parasitoid species (Kivan and Kilic, 2006; Doetzer and Foerster, 2007; Bueno et al., 2010), indicating greater female longevity at lower temperatures. This might be because *T. teretis* adults are incapable of lipogenesis, as observed for most parasitoid species (Visser and Ellers, 2008). As observed for other ectothermic insects, *T. teretis*'s metabolic-rate and lipid consumption (Huey and Berrigan, 2001) are temperature-dependent.

The temperature impact on *T. teretis* indicates that the frequency of parasitoid release in the field must be adjusted, depending on the average temperature of the region. Higher release frequency will probably be required as the average temperature of the region increases. However it is also important to consider that despite the longer adult longevity recorded at lower temperatures, the highest total number of parasitized eggs per *T. teretis* female was recorded at high temperatures of 30°C (29.2 eggs) when exposed to *E. heros* eggs and between 20°C (54.1 eggs) and 30°C (41.0 eggs) when exposed to *D. melacanthus* eggs.

It is also important to analyze the distribution of *T. teretis* parasitism over the parasitoid lifespan because the active time of parasitoid females might vary related to temperature (Reznik and Vaghina, 2006), hosts (Reznik et al., 2001) or parasitoid species (Pratissoli and Parra, 2000), and must be taken into account for parasitoid use in the field. For example, whether parasitoid activity is higher during the first days of life or is evenly distributed throughout adulthood is an important factor to be considered when establishing the best parasitoid release strategy (Bueno et al., 2010). This knowledge helps to calculate release times in order to optimize synchronization between adult parasitoid and susceptible host in the field. Thus, when analyzing lifetime parasitism of *T. teretis* females, it becomes apparent that the number of parasitized eggs per day (both hosts) varied among the different temperatures. However, in all cases *T. teretis* oviposition peaked during the first 48 h of parasitism. Similar results were reported by Silva et al. (2018) and Yeargan (1982) for *T. podisi*. Similar observations have been made not only in Scelionidae, but also in other parasitoid families such as Trichogrammatidae. Oviposition peaks of egg parasitoids from the genus *Trichogramma* on the first day after adult emergence have been reported for several different species of the genus (Pak and Oatman, 1982; Bai et al., 1992; Volkoff and Daumal, 1994). The reason for this is that most of these egg parasitoids have the capacity to store a full complement of mature eggs in the ovaries or oviducts, and complete oogenesis either before or shortly after adult emergence (pro-ovigenic parasitoids) (Mills and Kuhlmann, 2000) and, therefore, adults emerge ready to lay eggs. Despite highest parasitism during the first 48 h

after mating, *T. teretis* only reached 80% of lifetime parasitism after 9 or 10 days, regardless of the tested temperature.

The sooner the parasitoid reaches 80% of its lifetime parasitism, the more beneficial it will be, because parasitoids would be less exposed to factors causing mortality under field conditions. In practice, those factors could be insecticide spraying necessary for crop management or an abrupt change in weather conditions that can kill the egg parasitoid (Carmo et al., 2010; Denis et al., 2011). On the other hand, one of the factors that can reduce field efficiency of egg parasitoids is the lack of synchronization between the occurrence of the most susceptible stage of the target host and the period of greater adult parasitism activity (Cingolani et al., 2014). Thus, longer *T. teretis* lifetime parasitism increases the chances of synchronized occurrence in the field and therefore can be considered a positive biological trait of the parasitoid species for augmentative biological control purposes.

It is important to point out that, even though temperature is considered one of the most important factors for the success of a biological control agent, it is not the only one responsible for changes in development and survival of egg parasitoids. Other biotic and abiotic factors, such as photoperiod, relative humidity, interspecific and intraspecific competition, may interfere with biological control (Bueno et al., 2012) and should be always taken into consideration for field decisions.

## Conclusions

*Trissolcus teretis* is influenced by temperature when reared on eggs of both *E. heros* and *D. melacanthus*. An extreme temperature of 15°C is unfavorable for *T. teretis* parasitism (although it still occurs), because parasitoid biological traits are impaired, especially larval survival and adult parasitism. Thus, in crop fields where temperatures of 15°C or lower commonly occur, additional studies are necessary to investigate the possible need for increased parasitoid numbers during releases, or shorter intervals between multiple releases.

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## Conflicts of interest

The authors declare no conflicts of interest.

## Compliance with ethical standards

This study was carried out following ethical standards.

## Author contribution statement

JPFC carried out trials. JPFC and AFB coordinated the studies and wrote the final version of the article.

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