Biological Characteristics and Parasitism Capacity of *Telenomus podisi* (Hymenoptera: Platygastridae) on Eggs of *Euschistus heros* (Hemiptera: Pentatomidae)

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Abstract

We evaluated the effects of adult mating and temperature on the biological potential and parasitism of *Telenomus podisi* (Ashmead) (Hymenoptera: Platygastridae) on *Euschistus heros* (Fabricius) (Hemiptera: Pentatomidae). Females were isolated and the characteristics of the F1 generation were compared with those of females previously copulated. The parasitism capacity of *T. podisi* on *E. heros* eggs at 20, 25, 30, 35, and 40 °C was evaluated. The longevity of parental females (days), egg-adult period (days) of the F1 generation, parasitism of parental females (%), and parasitoid emergence (%) were not influenced by the lack or not of the copulation. The offspring of non-copulated females were males, and arrhenotokous parthenogenesis occurred. The temperatures most favorable to the parasitoid were 25 and 30 °C. Even previously copulated females generated mostly males after a few days of oviposition. Therefore, the biological characteristics and reproduction of *T. podisi* were impacted by adult mating prior to parasitism and by different temperatures. Although parasitism of *T. podisi* was not affected by mating parasitoid permanence in the field, it may be affected when unmated females are released.

Keywords: mating, arrhenotoky, biological control, temperature

1. Introduction

Piercing-sucking insects are one of the most important groups of arthropods that attack soybeans in South America. Those pests are noteworthy for feeding directly on the pods, thereby seriously affecting crop yields (Panizzi & Slanky, 1985; Corrêa-Ferreira & Azevedo, 2002). In this complex of insects belonging to the family Pentatomidae, at least 54 species have been reported from soybean-growing areas (Panizzi & Slanky, 1985). Among them, the Neotropical brown stink bug, *Euschistus heros* (Fabricius) (Hemiptera: Pentatomidae), is the most abundant species, mainly in the central region of Brazil at latitudes between 0 and 23° (Panizzi & Corrêa-Ferreira, 1997). Thus, in order to mitigate losses caused by this pest and consequently increase profit, growers control this phytophagous arthropod (Zalucki et al., 2009). Currently, the primary method of pest control adopted by most soybean growers is the use of chemical insecticides (Song & Swinton, 2009; Panizzi, 2013). However, the abuse of insecticides has brought some negative effects (Song & Swinton, 2009), such as the rapid selection of pesticide-resistant pest strains that are resistant to a given active ingredient (Diez-Rodriguez & Omoto, 2001; Sosa-Gómez et al., 2001; Sosa-Gómez & Silva, 2010) or the reduction of natural biological control agents, especially when non-selective insecticides are used (Carmo et al., 2010; van Lenteren & Bueno, 2003).

In this scenario, the use of biological control as a more sustainable form of pest management is becoming more important (van Lenteren et al., 2017). Among the natural enemies used in biological control programs, the egg parasitoid *Telenomus podisi* (Ashmead) (Hymenoptera: Platygastridae) has shown great potential in parasitizing eggs of *E. heros* (Foerster & Queiroz, 1990; Corrêa-Ferreira & Azevedo, 2002; Doetzer & Foerster, 2007; van

Lenteren et al., 2017). However, the success of *T. podisi* releases depends on an understanding of the bioecological characteristics of this parasitoid and on its interaction with the targeted host (Bourchier & Smith, 1996). Therefore, to validate the use of *T. podisi* in controlling *E. heros* in commercial releases, laboratory studies investigating parasitoid biology and its parasitism (Hassan, 1997; Scholler & Hassan, 2001) with biotic and abiotic factors are needed. Among those factors, mating and temperature might affect the biological characteristics of parasitoids, which could influence its efficiency in the field (Berti & Marcano, 1991; Mcdougall & Mills, 1997; Thomson & Hoffmann, 2002).

All biological parameters may be highly influenced by temperature (Noldus, 1989). Therefore, the study of egg parasitoid parasitism under different temperatures is of theoretical and practical interest, as it may provide crucial information for the establishment of biological control programs for *E. heros* in areas having similar temperatures as those tested. Each parasitoid species may present distinct behavior according to its adaptation to these temperatures, making it more or less suitable for a specific climate condition (Bleicher & Parra, 1989). Similarly, mating can also affect parasitoid performance (Sousa & Spence, 2000), since recently emerged adults will focus their energy first on mating and then on parasitism. Therefore, releasing mated or unmated females can differentially impact parasitoid efficacy in the field. Thus, the objective of the present study was to evaluate the effects of adult mating and temperature on the biological potential and parasitism of *T. podisi* on *E. heros* eggs.

2. Method

2.1 Parasitoid and Host Colonies

Telenomus podisi females, as well as the host *E. heros*, used in this study originated from insect colonies kept at Embrapa Soybean, Londrina, State of Paraná, Brazil under controlled environmental conditions inside biochemical oxygen demand (BOD) climate chambers (ELETROLab®, model EL 212, São Paulo, SP, Brazil) set at 80±10% humidity, 25±2 °C, and a 14/10 h photoperiod (L/D). The insects were reared following proposed by Perez and Corrêa-Ferreira (2004) and Panizzi et al. (2000), and are briefly summarized as follows.

Telenomus podisi was originally collected in soybean fields in Londrina, State of Paraná. The population was maintained in the laboratory for approximately 5 years. In the laboratory, *T. podisi* was reared using eggs of *E. heros* glued to pieces of cardboard (2 × 8 cm) and introduced into tubes together with eggs already parasitized by *T. podisi*. Few drops of honey were placed inside these tubes to provide food for the adults as soon as they emerged. The tubes were then closed, and the eggs were allowed to be parasitized for 24 h. Adults emerging from these eggs were used for trials, as well as colony maintenance.

Euschistus heros was also originally collected from soybean plants in Londrina, State of Paraná. This population was maintained in the laboratory for approximately 2 years, during which new field insects were introduced each year to maintain insect quality. The insects were kept in cages (20 × 20 cm sides × 24 cm tall) made of a plastic screen and lined with filter paper. A Petri dish with a cotton wade soaked in distilled water (9 cm diameter) was added to each cage. Cages were cleaned, food was replaced, and egg masses were collected three times per week. After each collection, the egg masses were transferred to acrylic boxes (11 × 11 × 3.5 cm) lined with filter paper moistened with sterile-distilled water (Gerbox®). After eclosion, second-instar nymphs were transferred to new cages identical to those previously described. The laboratory-reared insects were then used for colony maintenance and to produce eggs for the trials.

2.2 Bioassay 1: Influence of Mating on Telenomus podisi Parasitism

The trial was carried out using a completely randomized experimental design with two treatments (unmated and mated females) and five replications, each composed of eight individual females (n = 40 females/treatment) inside glass tubes (12 × 75 mm tall).

To obtain unmated females, *E. heros* eggs were offered to the parasitoids for 24 h in 2 L plastic pots for parasitism, and then the eggs were placed in individual glass tubes (12 × 75 mm tall) until parasitoid emergence. After emergence, a droplet of honey was added to the glass tube to feed the adults. Some of the isolated females were placed with males for 24 h to copulate and some were left alone and remained unmated.

Each female was exposed to approximately 25 *E. heros* eggs, which were glued to white card (0.8 × 5 cm). The eggs were offered to the females for 24 h for parasitism. They were then removed and transferred to plastic bags (4 × 23 cm) where they remained until adult emergence. Both females and cards with parasitized eggs remained under the same conditions [temperature of 25±2 °C, 80±10% RH, and 14/10 h photoperiod (L/D)]. The parameters evaluated included: the longevity of parental females (days), progeny egg-adult period (days), percentage of parasitism, emergence of parasitoids (%), and progeny sex ratio.

2.3 Bioassay 2: Telenomus podisi Parasitism Capacity on Eggs of Euschistus heros Under Different Temperatures

The trial was carried out in a completely randomized experimental design with five treatments (20, 25, 30, and 35±2 °C) and five replicates, each one composed of six individualized females (n = 30 females/treatment). Individual mated *T. podisi* (≤ 48-h old) were placed into separate glass tubes (12 ×75 mm tall) covered with PVC film. Droplets of pure honey on the walls of the glass tubes were offered to the females. Then, glass tubes (5 replications of 6 individualized females each) were prepared for each temperature. The tubes were then kept inside environmental chambers at temperatures of 20, 25, 30, and 35±2 °C, 8±10% RH, and 14/10 h photoperiod (L/D). Eggs (≤ 24-h old) from the host colony were frozen in nitrogen liquid and prior to the trial, were unfrozen and offered for parasitism for 24 h. These eggs were glued onto card (40 eggs each), on which the date and information of the treatment and replicate were recorded. These cards (with the eggs) were replaced daily until the death of the parasitoids. The eggs were removed daily from the glasses and maintained inside controlled environmental chambers under the same controlled conditions until the emergence of the parasitoids. The parameters recorded were: 1) the number of eggs parasitized per day; 2) the lifetime number of eggs parasitized per female; 3) parasitoid emergence (%); 4) progeny sex ratio; and 5) longevity of parental females (days).

2.4 Data Analysis

The results obtained in the experiments were submitted to exploratory analysis to evaluate the normality assumptions of the residuals (Shapiro & Wilk, 1965), homogeneity of variance of treatments, and additivity of the model to allow the application of ANOVA (Burr & Foster, 1972). The lifetime number of eggs parasitized per female and the longevity of adult parasitoids when presented with the host (in bioassay 2) were transformed by the emergence (%) of parasitized eggs by arcsine prior to the analysis of variance (ANOVA). Then, the averages were compared by Tukey test, at a 5% error probability, using the statistical analysis program SAS (SAS Institute, 2009).

3. Results

3.1 Bioassay 1: Influence of Mating Status on Telenomus podisi Parasitism

Mating seemed to have a low effect on the evaluated characteristics of *T. podisi* parasitism. Longevity of parental females (days), progeny egg-adult period (days), parasitism (%), and emergence (%) did not differ between mated and unmated *T. podisi* females (Table 1). Only the progeny sex ratio differed between mated and unmated females, with 100% of progeny originating from virgin *T. podisi* females being males and only 46% of the progeny originating from the mated females being males, indicating the occurrence of arrhenotokous parthenogenesis in the absence of copulation (Table 1).

Table 1. Biological parameters of mated and unmated *Telenomus podisi* females that parasitized *Eushistus heros* eggs (bioassay 1) [temperature of 25±2 °C, relative humidity of 80±10%, and a photoperiod of 14/10 h (light/dark)]

Females	Longevity of parental females (days)[1]	Progeny egg-adult period (days)[1]	Parasitism (%)[1]
Unmated	18.02±2.79[ns]	14.30±0.14[ns]	47.84±1.86[ns]
Mated	21.57±2.09	14.70±0.14	48.31±3.17
CV (%)	27.81	2.20	12.09
F	1.04	3.91	0.02
P	0.03379	0.0834	0.9010
Females	Emergence (%)[1]	Progeny sex ratio[1]	
Unmated	81.85±4.42[ns]	0±0.0a	
Mated	82.43±2.35	0.54±0.04b	
CV (%)	9.65	25.61	
F	0.01	152.47	
P	0.9094	<0.001	

Note. [1] Mean±standard error followed by the same letter in the columns did not differ by Tukey test ($p > 0.05$). [ns] ANOVA non-significant.

3.1 Bioassay 2: Telenomus podisi Parasitism Capacity on Eggs of Euschistus heros Under Different Temperatures

The number of parasitized eggs per day varied with temperature, but was higher on the first day of the experiment at 20, 25, and 35 °C and on the second day of parasitism at 30 °C. The average number of eggs parasitized during the first 24 h was 14.3, 14, 11, and 6 at 20, 25, 30, and 35 °C, respectively (Figure 1). The number of daily ovipositions by parasitoids decreased as a function of parasitism time and temperature (Figure 1). Higher numbers of parasitized *E. heros* eggs per day were observed at all temperatures during the first 2 days of parasitism, after which, the numbers significantly decreased (Figure 1). As a result of this pattern of parasitism, *T. podisi* reached more than 80% lifetime parasitism on eggs of *E. heros* on days 24, 15, 10, and 4 at 20, 25, 30, and 35 °C, respectively (Figure 1).
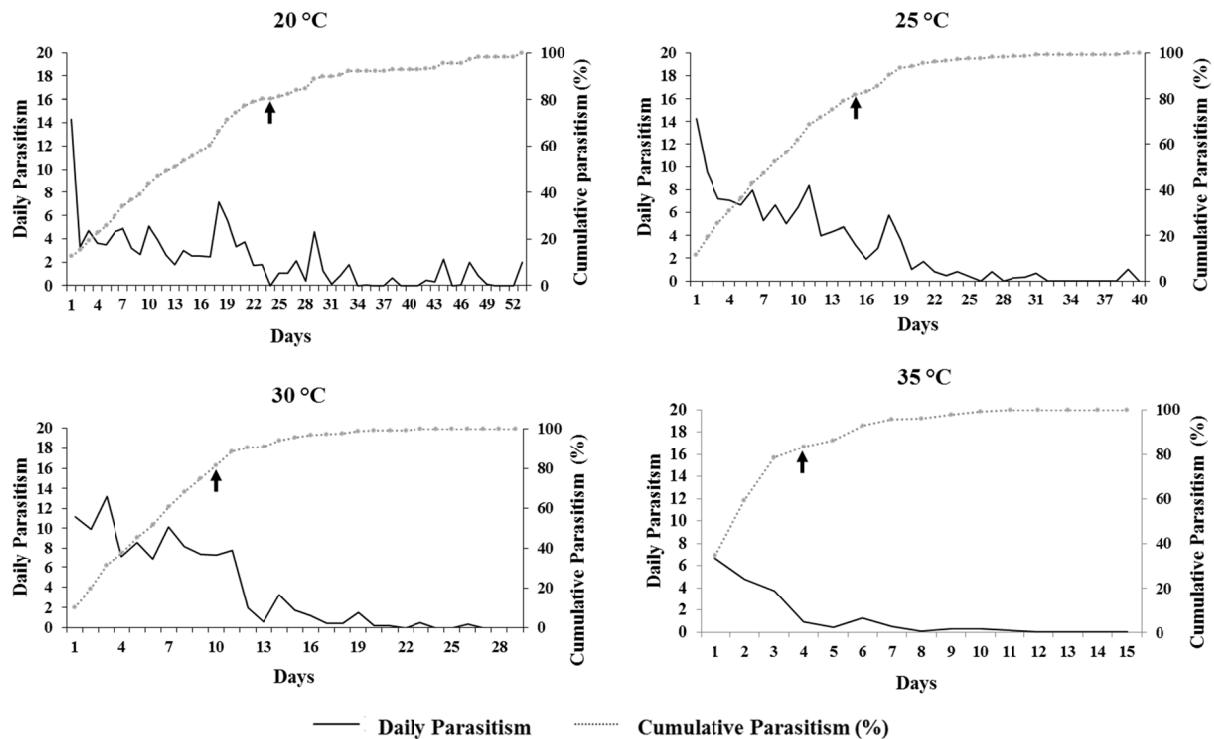

Figure 1. Daily parasitism and accumulation (%) of *Telenomus podisi* in *Euschistus heros* eggs at different temperatures [relative humidity of 80±10%, and a photoperiod of 14/10 h (light/dark)]. The arrows indicate 80% parasitism

As a combination of adult longevity and parasitoid egg load, the lifetime number of parasitized eggs varied among the temperatures (Table 2). The lifetime number of parasitized *E. heros* eggs by females maintained at 20 °C (97.47±5.37), 25 °C (104.10±16.15), and 30 °C (90.47±14.25) differed from the results recorded at 35 °C (18.37±1.68), with fewer eggs parasitized at this higher temperature (Table 2).

The emergence (%) of parasitoids was also affected by temperature when the parasitoid was reared on eggs of *E. heros,* with the highest values observed at 30 °C and the lowest emergence observed at 35 °C (Table 2). The progeny sex ratio was directly related to the increase in temperature (Figure 2). The sex ratio was 0.35, 0.37, 0.85, and 1.0 at 20, 25, 30, and 35 °C, respectively (Table 2).

The longevity of parental adult *T. podisi* females when presented with *E. heros* eggs was inversely correlated with temperature (Table 2). The highest longevity was recorded at 20 °C. At 30 and 35 °C, adult parasitoids had a shorter lifespan, varying from 16.03 to 9.80 days, respectively (Table 2).

Table 2. *Telenomus podisi* parasitism capacity on *Euschistus heros* eggs under different temperatures (bioassay 2) [relative humidity of 80±10%, and a photoperiod of 14/10 h (light/dark)]

Temperatures	Lifetime number of eggs parasitized per female [1,2]	Emergence (%)[1,3]	Progeny sex ratio[1]	Longevity of parental females (days)[1,2]
20 ºC	97.47±5.37a	35.82±2.39b	0.35±0.03c	36.74±3.42a
25 ºC	104.10±16.15a	25.56±2.11c	0.37±0.03c	20.20±2.16b
30 ºC	90.47±14.25a	50.13±0.79a	0.85±0.01b	16.03±1.75bc
35 ºC	18.37±1.68b	0.83±0.12d	1.00±0.00a	9.80±0.75c
CV (%)	15.67	8.35	7.74	11.7
F	22.14	245.28	195.69	28.17
P	<0.0001	<0.0001	<0.0001	<0.0001

Note. [1] Means±standard error followed by the same letter in the columns do not differ by Tukey test (p ≤ 0.05); [2] Original results followed by statistics performed on $\sqrt{X}$ transformed data. [3]Original results followed by statistics performed on arcsine $\sqrt{X/100}$ transformed data; [ns] ANOVA non-significant.
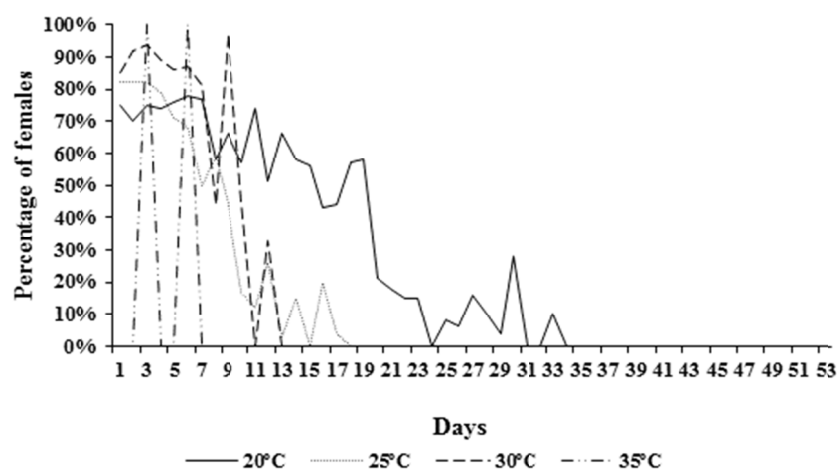

Figure 2. Sexual ratio of *Telenomus podisi* at different temperatures (70±10% RH and photoperiod of 14/10 h light/dark)

4. Discussion

Several biotic and abiotic variables might affect the biological characteristics of egg parasitoids, influencing their efficiency in the field (Mcdougall & Mills, 1997; Thomson & Hoffmann, 2002). A recent strategy to release egg parasitoids in the field has been to use isolated pupae that are spread over the plants, such as those of *Trichogramma* spp., in Brazil. However, a common behavior of *T. podisi* males, which emerge earlier than females owing to their shorter lifecycle, is to wait for females to emerge from the same parasitized egg mass (Hermel et al., 2016), allowing high mating rates directly after emergence. Therefore, the spread of *T. podisi* individual pupae in the field could negatively affect the reproductive behavior of the parasitoid, highlighting the importance of evaluating mating deprivation. This relationship may affect the fitness of the parasitoid when ovipositing females exploit the host eggs (Sousa & Spence, 2000). Therefore, the importance of adult mating must be considered when releasing *T. podisi*, because it can compromise the maintenance of the parasitoid in the field (Pratissoli et al., 2009; Farrokhi et al., 2010), a possibility that was further evaluated in the present study.

In Hymenoptera, several species reproduce by parthenogenesis. On one hand, thelytokous parthenogenesis occurs when offspring are composed only of females, as observed in *Leptocybe invasa* Fisher & La Salle (Hymenoptera: Eulophidae) (Zheng et al., 2014). On the other hand, arrhenotokous parthenogenesis occurs when the offspring are composed only of males, such as in some species of the genus *Trichogramma* (Hohmann et al., 2001) and *Cirrospilus* (Foelkel et al., 2008). For biological control programs, it is important to have more females, since they are responsible for parasitism (Navarro, 1998; Bueno et al., 2008).

Based on the results observed in the present study, *T. podisi* present arrhenotokous parthenogenesis, since the absence of mating directly influenced the offspring sex ratio, leading to the production of haploid males only. Reproduction via parthenogenesis of the arrhenotoky type has been described as the most common reproductive strategy for insects in the order Hymenoptera (Pratissoli et al., 2014). However, other biological parameters were not affected. The longevity of parental females, the progeny egg-adult period, parasitism capacity (%), and emergence of parasitoids from the parasitized eggs were similar between mated and unmated females. Queiroz et al. (2016) reported similar results for *T. remus*, where in progeny from mated females displayed a sex ratio of 0.6, while it was 0 for the unmated females.

Regarding the parasitism capacity of *T. podisi*, the results illustrate that temperature interferes in all evaluated biological aspects, as previously reported for other Platygastridae species (Yeargan, 1980; Nakama & Foerster, 2001). It is worth emphasizing that, although temperature is considered extremely important, other abiotic factors, such as relative humidity, may interfere with these biological characteristics (Parra, 1997; Pratissoli & Parra, 2001). Another point to be considered is the specific ability of *T. podisi* to introduce the ovipositor into the corium of the host eggs once these eggs lose their turgidity following a gradual increase in temperature (Bueno et al., 2009). The possible effects of temperature on this ability can affect the quantity and uniformity of *T. podisi* parasitism, which was not recorded in our study, and should be investigated in future.

Our results, show that the lifetime number of eggs parasitized per *T. podisi* female was lower at the highest studied temperature (35 °C). This value is directly related to the longevity of parental adult *T. podisi* females when presented with *E. heros* eggs. It was inversely correlated with temperature. The reduced longevity of parental adults owing to increased temperature has been previously reported for different parasitoid species (Maceda et al., 2003; Hansen & Jensen, 2002; Bourchier & Smith, 1996; Scholler & Hassan, 2001; Pratissoli & Parra, 2000; Pereira et al., 2004), and determines how long *T. podisi* is active in the field (how long *T. podisi* females are parasitizing host eggs). This might vary owing to differences in temperature (Reznik & Vaghina, 2006) or parasitoid species (Pratissoli & Parra, 2000; Pizzol et al., 2010). Thus, it might directly influence the success of biological control programs using egg parasitoids (Smith, 1996; Wajnberg & Hassan, 1994).

It is important to consider whether parasitism is more active during the first days of life or is evenly distributed throughout adulthood, when choosing the best parasitoid release strategy (Bueno et al., 2010). Then, those parasitoid characteristics should be considered when choosing the most suitable parasitoid species to be used in the field. The sooner the parasitoid reaches 80% of its lifetime parasitism, the better, because, while the parasitoids are exposed in the field, they might be susceptible to biotic and abiotic factors that can hinder their action. In practice, these factors might include fungicide or herbicide spraying that are necessary for crop management, or an abrupt change in temperature that can more easily kill the egg parasitoids (Carmo et al., 2010; Denis et al., 2011) but will rarely kill the pests. Egg parasitoids are usually small wasps, and are more susceptible to chemicals used in agriculture, such as herbicides and fungicides, than their hosts (Carmo et al., 2010). Furthermore, parasitoids differ from herbivorous insects by their usual inability to synthesize lipids as adults, which makes them more vulnerable to increases in temperature than most pests (Denis et al., 2011).

Although the number of parasitized eggs per day varied among the different temperatures, *T. podisi* oviposition peaked during the first 48 h of parasitism. Similar results were reported by Yeargan (1982) for *T. podisi* and *Trissolcus euschisti* (Ashmead) (Hymenoptera: Platygastridae) reared at 21 °C. This biological characteristic is not only observed in Trichogrammatidae, but also in Platygastridae. Peak oviposition of egg parasitoids from the genus *Trichogramma* has been reported during the first day after adult emergence for several different species of this genus (Pak & Oatman, 1982; Bai et al., 1992; Volkoff & Daumal, 1994). This is usually because 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 & Kuhlmann, 2000) and, thus, adults emerge ready to lay eggs. In contrast, other studies have indicated that some parasitoid species emerge with an egg load that accounts for only a fraction of their potential parasitism, which exceeds their capacity to store mature eggs in their ovaries or oviducts (synovigenic parasitoids) (Houseweart et al., 1983; Smith & Hubbes, 1986; Kuhlmann & Mills, 1999).

Moreover, peak oviposition can vary as a consequence of pro-ovigenic or synovigenic relationships between oogenesis and oviposition, and also because of changes in parasitoid behavior (Denis et al., 2011). Adults of most Platygastridae species are incapable of lipogenesis; however, as an ectotherm insect, temperature is inversely related to their metabolic-rate and lipid consumption (Huey & Berrigan, 2001). Thus, in those species, the allocation of lipids accumulated during the larval stage determines adult lifespan and fecundity (Visser & Ellers, 2008) and, therefore, its lifetime reproductive success (Hyey & Berrigan, 2001). Because foraging decisions are affected by the state of external and internal variables, such as the lipid reserves and the number of

mature eggs (Godfray, 1994) in females, lipids carried over from the larval stage can be allocated to either egg production or to adult lipid reserves, leading to a trade-off between reproduction and lifespan (Pexton & Mayhew, 2002). This confirms the importance of this knowledge with regards the developmental rate for widespread *T. podisi* augmentative release (Butler & Lopez, 1980). In this context, the higher number of parasitized eggs/day observed during the first 48 h in the present study is a positive characteristic of *T. podisi*.

The biological characteristics and reproduction of *T. podisi* were affected by adult mating prior to parasitism and different temperatures. Although parasitism of *T. podisi*, and therefore its control efficiency, was not affected by mating, parasitoid permanence in the field may be affected when unmated females are released. However, in augmentative biological control (ABC), parasitism capacity is more important than parasitoid maintenance in the field. Biocontrol agents are seasonally released in large numbers to rapidly reduce pests (van Lenteren et al., 2017); therefore, releasing mated females might not be important considering that the parasitism of available eggs in the field would not be affected (Carneiro et al., 2009). In addition, *T. podisi* exhibited high survival, as well as a high number of parasitized *E. heros* eggs, even at 30 °C. These results indicate that *T. podisi* might be well adapted to the studied temperature range (20 to 30 °C) and, thus, be potentially suitable for use in biological control programs of *E. heros* in different geographical areas within this range. However, it is important to emphasize that the results presented herein are from laboratory studies, and, therefore, additional field studies are needed to fully develop a biological control program using this egg parasitoid and to confirm the hypotheses presented here.

5. Conclusions

The biological characteristics and reproduction of *T. podisi* were influenced by adult mating prior to parasitism and by different temperatures. Although parasitism of *T. podisi* was not affected by mating parasitoid permanence in the field, it may be affected when unmated females are released.

Acknowledgements

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