Neotrop Entomol (2018) 47:543–552
https://doi.org/10.1007/s13744-017-0564-5

BIOLOGICAL CONTROL

Host Preferences of *Telenomus podisi* (Hymenoptera: Scelionidae): Parasitism on Eggs of *Dichelops melacanthus*,*Euschistus heros*, and *Podisus nigrispinus* (Hemiptera: Pentatomidae)

AP Queiroz[1], EA Taguti[1], AF Bueno[2], MLM Grande[3], CO Costa[4]

[1]Univ Federal do Paraná, Paraná, Brasil
[2]Empresa Brasileira de Pesquisa Agropecuária – Embrapa Soja, Paraná, Brasil
[3]Univ Estadual de Londrina, Paraná, Brasil
[4]Centro Universitário Filadélfia, Paraná, Brasil

Keywords

Biological control, natural enemy, preference test

Correspondence
AP Queiroz, Univ Federal do Paraná, Caixa Postal 19020, Curitiba, Paraná, Brasil 81531-980; anna.paullaqueiroz@hotmail.com

Edited by Christian S Torres – UFRPE

Received 16 May 2017 and accepted 24 October 2017

Abstract

Successful biological control requires detailed knowledge about host preferences of the released parasitoid, because the presence of alternative hosts may affect the control of the target pest. The objective of this work was therefore to evaluate host preferences of *Telenomus podisi* Ashmead among the eggs of three stink bug species: *Dichelops melacanthus* Dallas, *Euschistus heros* Fabricius, and *Podisus nigrispinus* Dallas (Heteroptera: Pentatomidae). Three independent experiments were carried out to study host preferences among the following: (1) *E. heros*, *D. melacanthus dallas*, and *P. nigrispinus* (bioassay 1); (2) *E. heros* and *D. melacanthus* (bioassay 2); and (3) *D. melacanthus* and *P. nigrispinus* (bioassay 3). A single bioassay (bioassay 4) was carried out to evaluate the egg size of *E. heros*, *D. melacanthus*, and *P. nigrispinus*. Two more bioassays were carried out: bioassay 5 to study the biological characteristics of *T. podisi* reared on *E. heros*, *D. melacanthus*, and *P. nigrispinus* eggs, and bioassay 6 to study the morphological characters of *T. podisi* reared on those different host eggs. Overall, *T. podisi* consistently preferred eggs of *D. melacanthus* to those of the other studied hosts, due to probably their better nutritional value; hypothesis that is supported by the fast *T. podisi* development and bigger parasitoids when reared on *D. melacanthus* and *P. nigrispinus* eggs. This allows suggesting that neither pre-imaginal conditioning nor associative learning nor α-conditioning are relevant to *T. podisi* parasitism. Thus, *E. heros* eggs could be successfully used for mass rearing of this parasitoid for successive generations since it would not affect its parasitism on other species of the Pentatomidae family in the field.

Introduction

Seed suckers are one of the most important groups of insects that attack soybeans in South America. Noteworthy for feeding directly on the pods, they seriously affect crop yields, substantially lowering the physiological and sanitary quality of the seeds (Panizzi & Slansky 1985; Corrêa-Ferreira & Azevedo 2002). In this group, the Neotropical brown stink bug, *Euschistus heros* (Fabricius) (Hemiptera: Pentatomidae), is the most important and abundant species (Panizzi & Corrêa-Ferreira 1997). More recently, the green-belly stink bug, *Dichelops melacanthus* (Dallas) (Hemiptera: Pentatomidae), has increased in importance in soybean fields at the end of the crop season (summer season), seriously impacting plants during the second crop season (winter season), sown immediately after soybean harvest (Bueno *et al* 2015). The second crop season is frequently sown with maize. *Dichelops melacanthus* feeds on the seedlings of maize, killing or severely disrupting the development of the young plants (Chocorosqui & Panizzi 2004; Bueno *et al* 2015).

Most commonly, stink bug pests are managed by the application of insecticides (van Lenteren & Bueno 2003), which are often overused (Bueno *et al* 2011). Although chemical control is an important tool in agriculture, its abuse may have undesirable consequences such as rapid selection of resistant pest strains or the elimination of parasitoids and predators. Such consequenceswould cause biological imbalance in the agroecosystem and consequently the increase of other pest species that were formerly under control (secondary pests) (Fernandes *et al* 2010; Sosa-Gómez *et al* 2001; Sosa-Gómez and Silva 2010). Therefore, the use of biological control as a more sustainable pest management is important (van Lenteren *et al* 2017).

Among the different natural enemies that might be used in biological control programs, *Telenomus podisi* Ashmead (Hymenoptera: Scelionidae) stands out. It has been successfully reared in the laboratory on *E. heros* eggs (Peres & Corrêa-Ferreira 2004). The species is a quasi-gregarious egg parasitoid (which is a solitary species that develop in hosts that are aggregated) of several stink bugs including both herbivorous and predatory species (Koppel *et al* 2009). It has shown great performance in parasitizing eggs of *E. heros* after inundative releases across approximately 30,000 soybean hectares in South America (Pacheco & Corrêa-Ferreira 2000, van Lenteren *et al* 2017). However, little is known about how host species can influence maternal oviposition decisions of *T. podisi* in augmentative biological control (ABC).

ABC is one of the biological control strategies, which is aiming at the release of a large number of natural enemies in order to have a fast pest control, has great potential for pest management, and is applied today to more than 30 million ha worldwide (van Lenteren *et al* 2017). In those field situations, it is likely that foraging *T. podisi* individuals would encounter the eggs of one host species before the eggs of another due to temporal or spatial differences in the hosts' ovipositional activities. Although *T. podisi* is known to parasitize eggs of many different stink bug species (Corrêa-Ferreira & Moscardi 1995), in general, egg parasitoids assess host suitability using a number of factors including egg size and shape, chorion characteristics, interior chemical cues, and chemical factors of the egg surface (Klomp & Teerink 1962; Pak & Jong 1987; Godfray 1994; Pluke & Leibee 2006; Zhou *et al* 2014). This assessment provides them with the necessary information to determine ovipositional activity and egg allocation in target species and to even accept non-target species (Mansfield & Mills 2004).

It is still uncertain how the presence of different stink bug species might affect parasitism levels of *T. podisi*. Therefore, it is of theoretical and practical interest to understand the host preferences of the parasitoid. The species diversity of stink bugs may interfere with the performance of a parasitoid in suppressing a target pest, due to a higher availability of eggs (Siqueira *et al* 2012). Therefore, this study aimed to determine the host preference of *T. podisi* by offering the eggs of three different stink bug species (Heteroptera: Pentatomidae). These included two possible target species (the herbivorous stink bugs *D. melacanthus* and *E. heros*) and a non-target species [the predatory stink bug *Podisus nigrispinus* (Dallas)]. The hypothesis that bigger host eggs could be more suitable to *T. podisi* development and that those hosts could be preferred by parasitoid adults was tested and the results further discussed in order to provide essential information that will help to understand parasitoid performance in field releases.

Material and Methods

Parasitoid and host colonies

Eggs of *E. heros*, *D. melacanthus*, and *P. nigrispinus* as well as *T. podisi* females used in the experiments 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, a temperature of 25 ± 2°C, and a 14/10 h photoperiod (L/D). *Euschistus heros*, *D. melacanthus*, and *T. podisi* were reared according to Peres & Corrêa-Ferreira (2004) and Panizzi *et al* (2000). *Podisus nigrispinus* was reared according to Denez *et al* (2014) as briefly summarized in the following paragraph.

Euschistus heros and *D. melacanthus* were originally collected from soybean plants in Londrina, State of Paraná. This population was kept in the laboratory for approximately 2 years during which new field insects were introduced in each year to maintain quality. *Podisus nigrispinus* was also originally collected from soybean plants in Embrapa Soybean Londrina, State of Paranáin 2016. The insects were kept in cages (20 cm × 20 cm sides × 24 cm tall) made of plastic screen and lined with filter paper. A Petri dish with a cotton wad soaked in distilled water (9 cm of diameter) was added to each cage. Cages were cleaned, food was replaced, and egg masses were collected three times a week. After each collection, the egg masses were transferred to acrylic boxes (11 cm × 11 cm × 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 the experiments as well as for colony maintenance.

Telenomus podisi was also originally collected in soybean fields in Londrina, State of Paraná. The population was kept in the laboratory for approximately 5 years. In the laboratory, *T. podisi* was reared using eggs of *E. heros*. Host eggs were glued to pieces of cardboard (2 cm × 8 cm) and introduced into glass tubes (8 cm long and 2 cm Ø) together with eggs already parasitized by *T. podisi* close to adult's emergence. Small 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 allowed to be parasitized for 24 h. Adults that emerged from these eggs were used for trials as well as colony maintenance.

Bioassays

Three independent experiments were carried out to study host preference of *T. podisi*. Parasitoid adults were allowed to choose among eggs of the following: (1) *E. heros*, *D. melacanthus*, and *P. nigrispinus* (bioassay 1); (2) *E. heros* and *D. melacanthus* (bioassay 2); and (3) *D. melacanthus* and *P. nigrispinus* (bioassay 3). A single bioassay (bioassay 4) was carried out to evaluate the egg size of *E. heros*, *D. melacanthus*, and *P. nigrispinus*. Also, two more bioassays were carried out. One experiment (bioassay 5) to study the biological characteristics of *T. podisi* reared on *E. heros*, *D. melacanthus*, and *P. nigrispinus* eggs and a second experiment (bioassay 6) to study the morphological characters of *T. podisi* reared on those different host eggs. All trials were carried out in controlled environmental conditions inside BODs as previously described for the parasitoid and host colonies.

Host preference of T. podisi *among eggs of* E. heros, D. melacanthus, *and* P. nigrispinus *(bioassay 1)*

A three-choice experiment was carried out in a completely randomized design with three treatments (eggs of *E. heros*, *D. melacanthus*, and *P. nigrispinus*) and 15 replicates, using one arena per replicate. The arenas in this test, adapted from Thuler *et al* (2007), were made of polyethylene bottles (4 cm high and 2 cm in diameter) and six plastic microtubes (8 cm x 2 cm) arranged equidistantly in the lower part of the bottle, and 1 microtube (8 cm x 2 cm) placed at the top of the arena (Fig 1a). Two tubes were used, each containing pieces of white cardboard (2.5 cm × 5 cm) with approximately 40 eggs of each stink bug species. The pieces of cardboard were introduced into the microtubes, with the eggs of each host placed into two opposite tubes of the arena (Fig 1a). Six mated females of *T. podisi* (≤ 48 h old, with no previous parasitism experience) were released at the top of each arena (Fig 1a) for 24 h. A proportion of one parasitoid female was used for each 40 host eggs. The evaluated parameter was the number of eggs parasitized for each host.

Telenomus podisi *preference between* E. heros and D. melacanthus *eggs (bioassay 2) and between* D. melacanthus *and* P. nigrispinus *eggs (bioassay 3)*

Two-choice experiments were carried out in a completely randomized design with two treatments (*E. heros* and *D. melacanthus* eggs for bioassay 2 and *D. melacanthus* and *P. nigrispinus* eggs for bioassay 3) and 15 replicates using one arena per replicate (Fig 1b). As in bioassay 1, arenas were adapted from Thuler *et al* (2007). Bioassay 2 involved two tubes containing pieces of white cardboard with approximately 40 eggs of *E. heros* and two tubes containing approximately 40 *D. melacanthus* eggs. In bioassay 3, two tubes containing approximately 40 eggs of *D. melacanthus* and 2 tubes with approximately 40 eggs of *P. nigrispinus* were used. The eggs were exposed to parasitism for 24 h after releasing four mated parasitoid females (≤ 48 h old, with no previous parasitism experience) into each arena through the upper hole of the lid. Similarly to bioassay 1, the proportion of one parasitoid female for each 40 host eggs was kept.

Host egg size (bioassay 4)

This trial was conducted in a completely randomized design with three treatments (eggs of *E. heros*, *D. melacanthus*, and *P. nigrispinus*) and 10 replicates (a single egg per replicate). The evaluated parameters were egg width and length. To measure these parameters, the eggs were first photographed using a stereomicroscope (Leica Application Suite-Version 1.6.0) and later measured using the software Image J-Version 1.47.

Telenomus podisi *biology on different host eggs (bioassay 5)*

The experiment was conducted in a completely randomized design with three treatments (*E. heros*, *D. melacanthus*, and *P. nigrispinus* eggs) and 15 replicates (each replicate consisting of one individualized female). Mated *T. podisi* individuals (newly emerged: ≤ 48 h old) were placed into separate glass tubes (12 mm Ø × 75 mm tall), which were then covered with PVC film. Droplets (around 100 μl each) of pure honey were placed on the walls of the glass tubes to feed the females. Forty-five glass tubes (15 replicates of each host) were prepared for each treatment. Approximately 50 eggs of each host accordingly to each treatment (≤ 24 h old) were glued onto cards made of white Bristol board paper (2.5 cm × 5 cm). Each paper was previously labeled with the respective treatments. Then, these cards were exposed to parasitism for 24 h. Then, the eggs were removed from the glass tubes and maintained inside the same environmental chamber under controlled conditions until the emergence of parasitoids. Evaluated parameters were as follows: egg-to-adult

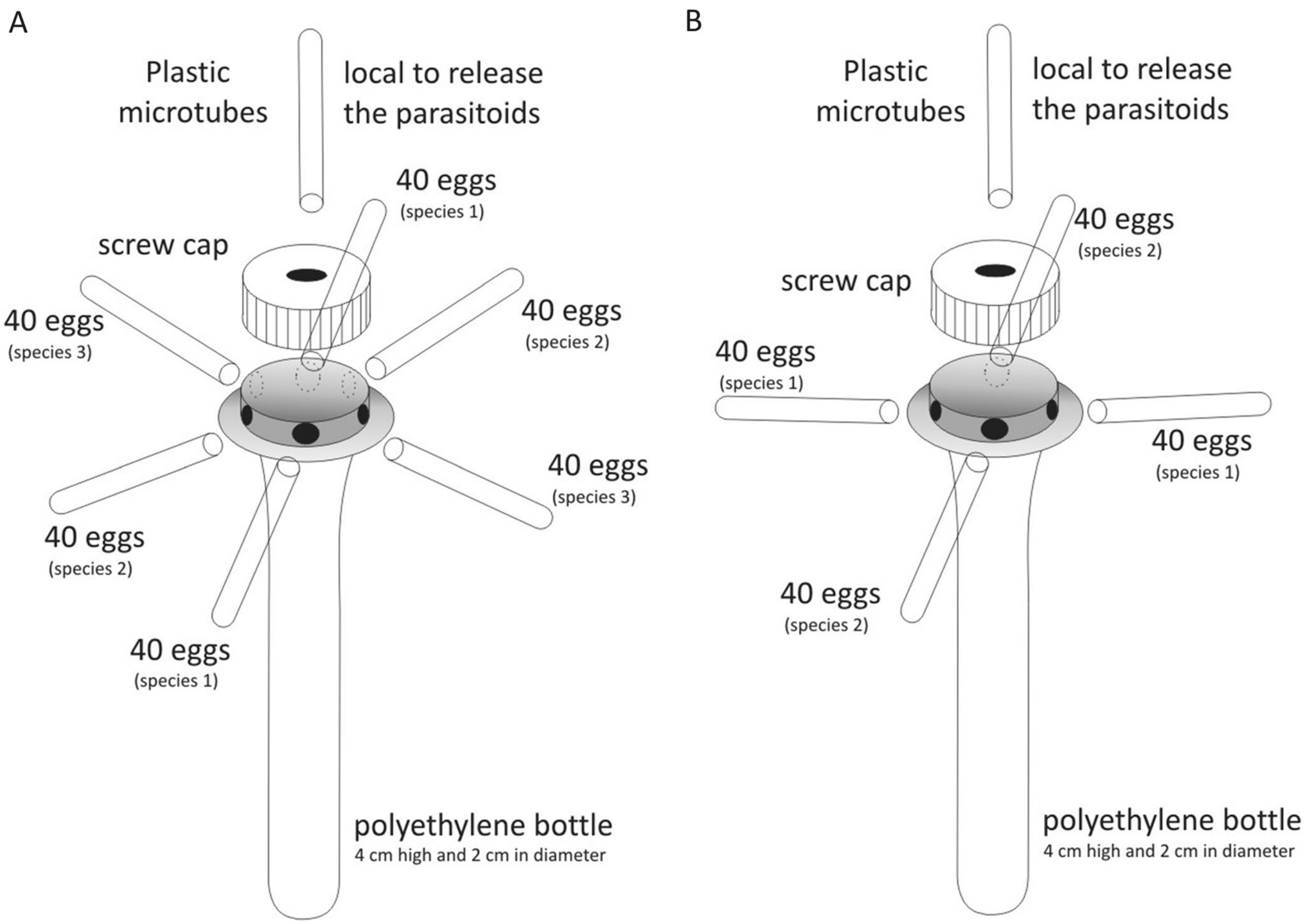

Fig 1 Arenas adapted from Thuler *et al* (2007) used in the parasitoid host preference test. **a** Arena used to test parasitoid host preference among three-host species. **b** Arena used to test parasitoid host preference among two-host species.

duration (days), viability of parasitism (%) (percentage of parasitized eggs from which parasitoids emerged), and progeny sex ratio.

Morphological characters of T. podisi *reared on different host eggs (bioassay 6)*

The experiment was carried out in a 3 × 2 factorial completely randomized design; 3 parasitoid hosts (*E. heros*, *D. melacanthus*, and *P. nigrispinus* eggs) × 2 parasitoid genders (female and male). Fifteen replicate adults of both genders were measured individually. Thus, 15 males and 15 females were measured for each parasitoid host, totaling 90 adults in bioassay 1. Length and width of the right anterior wing, length of the right hind tibia, and body length (head to tip of the abdomen) were measured in each replicate (adult insect). To measure the morphological characters, each specimen was photographed using a stereoscopic microscope (Leica Application Suite, Version 1.6.0). Images were used for morphometric analysis with the software Image J (Version 1.47) (Queiroz *et al* 2017).

Data analysis

For the analysis of bioassays 1, 2, and 3, data were compared using Chi-square statistics (Sas Institute 2009). Differently, the results obtained in the bioassays 4, 5, and 6 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). Then, the averages were compared by the Tukey test, at a 5% error probability, using the statistical analysis program SAS (Sas Institute 2009).

Results

Host preference of T. podisi *among eggs of* E. heros, D. melacanthus, *and* P. nigrispinus *(bioassay 1)*

In the three-choice experiment (bioassay 1), *T. podisi* consistently parasitized more *D. melacanthus* (30.8 eggs) than *P. nigrispinus* (23.7 eggs) (Table 1, X^2 = 120.0, p < 0.0001, *df* = 29) and *E. heros* (11.8 eggs) eggs (Table 1, X^2 = 119.8, $p < 0.0001$, *df* = 29). The second host with more parasitism was *P. nigrispinus* (23.7 eggs), which was higher than *E. heros* (11.8 eggs) eggs (Table 1, X^2 = 164.6, $p < 0.0001$, *df* = 29). The percentages of parasitized eggs (proportional parasitism) were 45.5, 36.6, and 17.9% for *D. melacanthus*, *P. nigrispinus*, and *E. heros*, respectively (Table 1).

Telenomus podisi preference between E. heros and D. melacanthus eggs (bioassay 2) and between D. melacanthus and P. nigrispinus eggs (bioassay 3)

In the two-choice experiments (bioassays 2 and 3), *T. podisi* clearly preferred *D. melacanthus* eggs to those of *E. heros* (Table 1, bioassay 2, X^2 = 115.3, $p < 0.0001$, *df* = 29) and *P. nigrispinus* (Table 1, bioassay 3, X^2 = 155.9, $p < 0.0001$, *df* = 29). In bioassay 2, the percentages of parasitized *E. heros* and *D. melacanthus* eggs were 34.7 and 65.3%, respectively, while in bioassay 3, the percentages of parasitized eggs of *D. melacanthus* and *P. nigrispinus* were 59.6 and 40.4%, respectively (Table 1).

Host egg size (bioassay 4)

Egg size also differed between hosts (Table 2) with the largest eggs observed for *D. melacanthus* (Table 2). Egg width was higher for *D. melacanthus* (0.82 mm) and *E. heros* (0.83 mm) compared with *P. nigrispinus* (0.76 mm) ($p < 0.0001$; $F = 19.81$). Similarly, egg length was highest for *D. melacanthus* (0.98 mm), followed by *E. heros* (0.91 mm) and *P. nigrispinus* (0.86 mm) ($p < 0.0001$; $F = 57.39$; Table 2).

Telenomus podisi biology on different host eggs (bioassay 5)

Egg-to-adult duration (days) was around 1 day shorter for *T. podisi* that emerged from both *P. nigrispinus* and *D. melacanthus* eggs compared with parasitoid that emerged from *E. heros* eggs ($p = 0.0008$; $F = 8.56$; Table 2). Similarly, viability of parasitism (% of parasitoids that emerged from parasitized eggs) also differed among hosts ($p = 0.0323$; $F = 3.74$) with the highest viability observed for parasitoids that emerged from *D. melacanthus* (99.22%) and *P. nigrispinus* (98.02%) eggs (Table 2). Differently, progenie sex ratio did not differ among parasitoids that emerged from the studied hosts ($p = 0.1059$; $F = 2.38$; Table 2).

Morphological characters of T. podisi reared on different host eggs (bioassay 6)

Factorial analysis did not detect a significant interaction between parasitoid host and gender regarding the morphological character body length ($p_{host*gender} = 0.4141$; $F_{host*gender} = 0.89$), wing length ($p_{host*gender} = 0.3283$; $F_{host*gender} = 1.13$), wing width ($p_{host*gender} = 0.9335$; $F_{host*gender} = 0.07$), and right hind tibia length ($p_{host*gender} = 0.3961$; $F_{host*gender} = 0.94$) (Table 3). However, body length differed between hosts ($p_{host} = 0.0340$; $F_{host} = 3.52$) with the higher length (1 mm) observed for *T. podisi* that emerged from *P. nigrispinus* (Table 3). Similarly, differences were also observed between female and male body length being female body length (1.02 mm) higher than male ones (0.92 mm) ($p_{gender} = < 0.0001$; $F_{gender} = 51.20$) (Table 3).

Wing length also differed between hosts ($p_{host} = < 0.0001$; $F_{host} = 17.07$). *Telenomus podisi* emerged from *P. nigrispinus* and *D. melacanthus* eggs had the highest wing length (0.93 mm) when compared to the parasitoid that emerged from *E. heros* eggs (0.87 mm) (Table 3). Differently, wing length was similar between parasitoid genders ($p_{gender} = 0.0677$; $F_{gender} = 3.43$) (Table 3).

Regarding to *T. podisi* wing width, there were differences among hosts ($p_{host} = 0.0192$; $F_{host} = 4.15$) with the highest values observed for parasitoids that emerged from *P. nigrispinus* (0.31 mm) and *D. melacanthus* (0.30 mm) eggs (Table 3). Unexpectedly, female wing width (0.29 mm) was lower than male ones (0.31 mm) ($p_{gender} = 0.0.0011$; $F_{gender} = 11.37$; Table 3).

Similar to the previous reported parameters, right hind tibia length also differed among hosts ($p_{host} = 0.0053$; $F_{host} = 5.58$) with the highest values observed for parasitoids

Table 1 Number of eggs of the three tested hosts [*Dichelops melacanthus* (D), *Euschistus heros* (E), and *Podisus nigrispinus* (P)] parasitized by *Telenomus podisi*, with the percentage of parasitism on each host for each bioassay given in parentheses. Bioassays were performed under controlled environmental conditions (25 ± 2°C, 80 ± 10% RH, and photoperiod of 14/10 h L/D).

Host	Number of parasitized eggs[a] ± SE (distribution of parasitism%)		
	Bioassay 1 (D × E × P)	Bioassay 2 (D × E)	Bioassay 3 (D × P)
D. melacanthus	30.8 ± 3.8 a (45.5)	16.5 ± 1.6 a (65.3)	27.9 ± 2.8 a (59.6)
E. heros	11.8 ± 2.0 c (17.9)	8.6 ± 1.4 b (34.7)	–
P. nigrispinus	23.7 ± 3.6 b (36.6)	–	19.5 ± 3.1 b (40.4)
X^2; *p*; *df* (D × E)	199.8; < 0.0001; 29	115.3; <0.0001; 29	–
X^2; *p*; *df* (D × P)	120.0; < 0.0001; 29	–	155.9; < 0.0001; 29
X^2; *p*; *df* (E × P)	164.6; < 0.0001; 29	–	–

[a] Means ± standard error followed by the same letter in the column are not significantly different from each other (Chi-square test, $p > 0.05$); "–" parameter not existent.

Table 2 Egg size of the stink bug hosts tested in the parasitoid host preference bioassays (*Dichelops melacanthus*, *Euschistus heros*, and *Podisus nigrispinus*) (bioassay 4) and biological characteristics of *Telenomus podisi* reared on different host eggs (bioassay 5) under controlled environmental conditions (25 ± 2°C, 80 ± 10% RH, and photoperiod of 14/10 h L/D).

Host	Egg size (mm)[a] Bioassay 4		Biological characteristics[a] Bioassay 5		
	Width	Length	Egg-adult period (days)	Viability of parasitism (%)	Progenies × ratio
E. heros	0.83 ± 0.01 a	0.91 ± 0.01 b	18.6 ± 0.2 a	92.06 ± 3.24 b	0.94 ± 0.02[ns]
D. melacanthus	0.82 ± 0.01 a	0.98 ± 0.01 a	17.5 ± 0.3 b	99.22 ± 0.54 a	0.86 ± 0.04
P. nigrispinus	0.76 ± 0.01 b	0.86 ± 0.01 c	17.6 ± 0.1 b	98.02 ± 0.89 ab	0.91 ± 0.01
CV (%)	3.08	2.56	4.49	7.95	11.31
P	< 0.0001	< 0.0001	0.0008	0.0323	0.1059
F	19.81	57.39	8.56	3.74	2.38
df_{total}	29	28	43	43	42

[a] Means ± standard error (SE) followed by the same letter within a column, did not differ statistically (Tukey test at 5% probability). [ns] ANOVA non-significant.

that emerged from *D. melacanthus* (0.30 mm) and *P. nigrispinus* eggs (0.29 mm) (Table 3). However, no differences were observed between genders (p_{gender} = 0.1681; F_{gender} = 1.93; Table 3).

Discussion

Overall, *T. podisi* consistently preferred to parasitize eggs of *D. melacanthus* rather than eggs of *E. heros* and *P. nigrispinus*, which might be due to a better nutritional value. Optimal foraging theory predicts that organisms should find, assess, and exploit resources containing the most energy to maximize their lifetime fitness. Numerous studies have confirmed this theory by demonstrating that, when food is abundant, consumers tend to avoid items yielding low net energy return and specialize on more energetically rewarding items (Stephens & Krebs 1986). Even though better nutritional value is frequently related to host size, this might not be applied to our results since *T. podisi* preferred to parasitize *P. nigrispinus* over *E. heros* eggs despite of its smaller size.

Accordingly to our findings, parasitoid's decisions of *T. podisi* adults seem to be low influenced by the host species they came from. This result differs from Tognon *et al* (2014) report. Accordingly to those authors, *T. podisi* is more likely to parasitize the host in which it developed and the original host can exert influence on the choice by those parasitoids. Parasitoid host preference can also be due to chemical substances released by the host (Borges & Aldrich 1994), which was not studied in this research but might help to explain *T. podisi* preference for different host eggs. Even substances secreted by the host for adhesion of their eggs to a substrate can be important for parasitoid oviposition decisions (Bin *et al* 1993), adding even more complexity to this relationship. However, it is important to consider that *T. podisi* is a generalist parasitoid that parasites eggs of a variety of species of agricultural stink bugs (Corrêa-Ferreira & Moscardi 1995) and as a generalist, this parasitoid species tends to use chemical cues from a variety of hosts, while specialist or foretic parasitoids use chemical cues exclusive to their target species (Vet & Dicke 1992; Fatouros *et al* 2008). Thus, the difference observed in our results and those reported by Tognon *et al* (2014) might be due to the different host comparison made on both studies. While we tested parasitoid preference from *T. podisi* reared on *E. heros* among hosts that might be of superior quality such as *D. melacanthus* and *P. nigrispinus*, Tognon *et al* (2014) compared *T. podisi* preference between *E. heros* and *Tibraca limbativentris* Stal (Hemiptera: Pentatomidae) which might be a host of worse nutritional quality when compared to *E. heros*. This hypothesis could help to explain the difference observed on both papers and should be further studied in future research.

Nevertheless, it is important to consider that *T. podisi* has a flexible host range. According to Jones *et al* (2015), some parasitoid species can adapt to new host species, depending on environmental conditions. Thus, *T. podisi* has evolved mechanisms to utilize different host resources with relatively minor fitness consequences (Zhou *et al* 2014), which might provide this species with bigger flexibility in host use decisions. This is different from other parasitoid species. Host size has been reported to influence parasitoid's maternal decisions of different parasitoid species (Pluke & Leibee 2006). For example, Nurindah *et al* (1999) found that *Trichogramma australicum* (Jargees) (Hymenoptera: Trichogrammatidae) reared on smaller host eggs attempted to drill smaller host model eggs in the second generation. They suggested that this behavior is due to cues that *Trichogramma* neonate females may receive at emergence by walking over and antennating the eggs they had just emerged from what do not happen with *T. podisi*.

It is also important to point out that host quality can vary not only with egg size but also with factors such as host species and age (Vinson & Iwantsch 1980). Although

Table 3 Morphological characters (mm) of *Telenomus podisi* reared on different host eggs (bioassay 6) under controlled environmental conditions (25 ± 2°C, 80 ± 10% RH, and photoperiod of 14/10 h L/D).

Parameter		Morphological characters (mm)[a]			
		Body length	Wing length	Wing width	Right hind tibia length
Parasitoid host	*E. heros*	0.96 ± 0.01 ab	0.87 ± 0.01 b	0.29 ± 0.01 b	0.28 ± 0.00 b
	D. melacanthus	0.95 ± 0.02 b	0.93 ± 0.01 a	0.30 ± 0.01 ab	0.30 ± 0.01 a
	P. nigrispinus	1.00 ± 0.02 a	0.93 ± 0.01 a	0.31 ± 0.01 a	0.29 ± 0.01 a
Gender	Female	1.02 ± 0.01A	0.90 ± 0.01^{ns}	0.29 ± 0.00 B	0.29 ± 0.00^{ns}
	Male	0.92 ± 0.01 B	0.92 ± 0.01	0.31 ± 0.01 A	0.28 ± 0.00
Statistics	CV(%)	6.79	5.25	10.69	8.45
	p_{host}	0.0340	< 0.0001	0.0192	0.0053
	p_{gender}	< 0.0001	0.0677	0.0011	0.1681
	$p_{host*gender}$	0.4141	0.3283	0.9335	0.3961
	F_{host}	3.52	17.07	4.15	5.58
	F_{gender}	51.20	3.43	11.37	1.93
	$F_{host*gender}$	0.89	1.13	0.07	0.94

[a] Means ± standard error followed by the same letter in the column of each parameter (lower-case letters for parasitoid host and upper-case letters for parasitoid gender) are not significantly different from each other (Tukey test, $p > 0.05$); ^{ns} ANOVA non-significant.

P. nigrispinus eggs are smaller than *E. heros* eggs in both width and length, *T. podisi* preferred to parasitize eggs of *P. nigrispinus* to eggs of *E. heros*. Future research should study this host preference in more detail.

Host preference is more complex related to the nutritional quality of the host chosen for parasitism, as well as to the characteristics of the host on which the parasitoid was reared (Molina *et al* 2005). The smaller *P. nigrispinus* egg did not limit *T. podisi* oviposition which indicates a better nutritional quality in spite of its smaller size. This better nutritional quality of *P. nigrispinus* as well as *D. melacanthus* eggs was confirmed in the biology of the parasitoid reared on the studied hosts since the parasitoid developed faster on *P. nigrispinus* and *D. melacanthus* when compared to *E. heros* eggs. This extended duration of the egg-adult period (days) observed for *T. podisi* on *E. heros* eggs can be due to a longer larva-adult period described as a compensatory action for larva of insects to recover when feeding on a lower-quality host and still be able to pupate, achieve enough weight to turn into adults (Behmer 2009).

Similarly to those observed in the parasitoid host preference, the higher viability of *T. podisi* parasitism on parasitoids reared on both *P. nigrispinus* and *D. melacanthus* eggs might also be a consequence of differences found in these hosts. Differences in host eggs had been previously pointed out as an important feature to parasitoid survival and development by Bai *et al* (1992) and Cônsoli *et al* (1999). Thus, it might also be a matter of host nutritional quality. This hypothesis might be studied in future researches where the amounts of proteins, carbohydrates, and other nutrients should be measured in different host species. In studying the nutrition of egg parasitoids, it is important to consider their metabolic dependence on the host to provide the essential nutrients to assure parasitoid development. This aspect of nutrition is of critical importance in understanding the nature of parasitism and the parasite-host interaction (Thompson 1986). Despite the importance of this knowledge to the success of biological control using egg parasitoids, little is known on the subject and very few studies have been published so far.

Even though we do not investigate host egg composition, measuring protein, carbohydrate, and essential nutrient compounds, the better nutritional quality hypothesis of *D. melacanthus* and *P. nigrispinus* eggs over *E. heros* eggs is supported by the bigger parasitoids; those hosts supported in the biology trial in all the morphological characters that were evaluated in our research (body length, wing length, wing width, and right hind tibia length). Despite of any critics that this theory might have, it is essential to consider the importance of physiological and metabolic adaptation in understanding the nature of parasitism (Thompson 1986). Studies indicate that insect parasites are in many ways adapted physiologically and biochemically for survival and development in a living host making the larval stages of parasitoids to display high nutritional efficiency (Fisher 1981; Wiegart & Peterson 1983; Slansky 1986). As a consequence, notwithstanding the differences between hosts, in general, *T. podisi* had a good biological performance on eggs of all studied hosts, including the two possible target species (the herbivorous stink bugs *D. melacanthus* and *E. heros*) and also the non-target species (the predatory stink bug *P. nigrispinus*). Similar findings were previously reported by Laumann *et al* (2010) who concluded that *T. podisi* may successfully use *D. melacanthus* eggs as host. However, those authors did not observe host preference among *E. heros* and

D. melacanthus eggs and reported a higher immature survivorship on *E. heros* eggs.The higher efficiency detected for *T. podisi* on our study to explore *D. melacanthus* eggs might probably be attributed to the fact that those parasitoid colony founders were collected in a soybean field in Parana State, Brazil, in which *D. melacanthus* had actually been a major pest for many years. Thus, the co-evolution between this pest species and that strain of *T. podisi* might had allowed an adaptation of the parasitoid to the eggs of this specific host higher than the *T. podisi* tested by Laumann *et al* (2010) which was collected in Distrito Federal, Brazil where *D. melacanthus* is more rarely a problem. This difference performance for strains of the same parasitoid species had been previously reported for other species of parasitoids (Bueno *et al* 2009), but as far as we know, it is the first report for *T. podisi*.

Overall, *T. podisi* has high potential to be used in programs of biological control of stink bugs on the soybean crop, despite of this possible negative side effect on the beneficial insect *P. nigrispinus*. According to Torres *et al* (1997), there is a strong potential impact of *T. podisi* on the eggs of *P. nigrispinus*, inducing significant levels of egg mortality, and thus impairing the predation of this beneficial (predatory) stink bug on leafhoppers, caterpillars, and other pests. However, the effect of the first and second trophic level in the foraging behavior of the parasitoids could modify the host/parasitoid interaction (Laumann *et al* 2010). Therefore, different plant age and pest density might impact parasitism of *T. podisi* including its parasitism on *P. nigrispinus*. It has been shown that volatile substances of different plant species, induced by different stink bugs, can act as synomones attracting parasitoids *T. podisi* females (Moraes *et al* 2005, 2008). Since *P. nigrispinus* do not feed on plants, they might be less attractive to *T. podisi* parasitism in the field compared to pest species. Moreover, *T. podisi* may respond to substrate-borne vibratory signals used in the stink bug sexual communication (Laumann *et al* 2007).

In this possible *T. podisi* negative effect on *P. nigrispinus* scenario, it is important to remind that any pest control practice must be not overused. All insect control tools must be used only when necessary in the concept of integrated pest management (IPM) respecting existing economic thresholds and avoiding unnecessary environmental disturbance. However, even considering this possible *T. podisi* negative side effect, it will certainly still be lower than pesticide use (Bueno *et al* 2011).

It is important to point out that the successive mass rearing of *T. podisi* in *E. heros* eggs did not affect its parasitism on other species of the Pentatomidae family and that *D. melacanthus* can also be a possible host to be used in parasitoid rearing facilities. Goulart *et al* (2011) studying the host preference of an egg parasitoid of the same genus, *Telenomus remus* Nixon (Hymenotpera: Scelionidae), also reported that host acceptance behavior and the preferences of parasitoid females could not be attributed to pre-imaginal conditioning during larval development as previously described by Cobert (1995) and Kaiser *et al* (1989). Similarly, parasitoid preference could not also be attributed to associative learning or α-conditioning in the present study. In this case, females associate new stimuli (acquired) to the innate ones and are able to adapt to the environment they have lived in as adults or juveniles (Kaiser *et al* 1989; Vinson 1998; Nurindah *et al* 1999). More recently, Queiroz *et al* (2016) reported similar results for *T. remus* reared for successive generations on a factitious host [*Corcyra cephalonica* (Stainton) (Lepidoptera: Pyralidae) eggs] in the laboratory without affecting host preference for eggs of *Spodoptera frugiperda* (Smith) (Lepidoptera: Noctuidae). This lack of pre-imaginal conditioning observed for *T. remus* as well as *T. podisi* might be a common trait for all species of the Scelionidae family, which needs further confirmation in future research. An important finding of our study is the clear indication that *T. podisi* can be maintained in the laboratory for several generations in eggs of a single host species (*E. heros*) without reducing the parasitism efficiency on other target pests in the field.

In addition, despite the low preference of *T. podisi* females for *E. heros* eggs reported in this study, there are some results that provide evidence for the efficacy of this parasitoid in controlling *E. heros* in the field (Pacheco & Corrêa-Ferreira 2000). These authors demonstrated the plasticity of the parasitoid in controlling different host species. Even though, Henry *et al* (2010) reported that parasitoid species that exhibit host-specificity are considered better and more effective for ABC, the use of a more flexible parasitoid in their host use can also be successful, mainly to manage a pest species that is predominant as *E. heros*. This species is today the most common stink bug in Brazil and other soybean producing areas in South America (Bueno *et al* 2015).

In this context, host diversity and the general behavior of *T. podisi* must be considered, since this parasitoid may prefer to parasitize other hosts, such as *D. melacanthus* or even the non-target predator *P. nigrispinus*. In conclusion, *T. podisi* has a host preference for *D. melacanthus* and also for *P. nigrispinus* compared with *E. heros*. However, the common host used for laboratory rearing (*E. heros*) did not impact parasitoid maternal decision. Thus, this result suggests that parasitoid species could be reared for successive generations on *E. heros* eggs without impacting its capacity to parasitize other stink bug species in the field. This conclusion is also supported by results recorded on viability of parasitism and progenie sex ratio. The viability of *T. podisi* parasitism, even though lower on *E. heros* when compared to *D. melacanthus* eggs, was both higher than 90%. Similarly, the sex ratio which is another important biological feature in biological control programs since greater proportion of females is desirable because they are responsible for parasitism (Navarro 1998) was not impacted by the host *T. podisi* was reared. In this context, the absence of difference between hosts also supports that the use of *E. heros* or *D. melacanthus* as host in massive rearing does not affect the development of *T. podisi* females. Thus, the smaller size of the *E. heros* eggs in relation to the preferred hosts did not influence this biological parameter.

Acknowledgments The authors thank Embrapa Soja, the Coordination for the Improvement of Higher Education Personnel (CAPES) and the National Council for Scientific and Technological Development (CNPq), grants 303779/2015-2 and 402797/2016-7, for their financial support and fellowships. Authors also thank Adair Vicente Carneiro, laboratory technician, for the help provided with the trials and Fig 1, and Dr. Orcial C. Bortolotto for the manuscript correction and help provided with the Chi-square analysis.

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