Effect of *Telenomus podisi*, *Trissolcus urichi*, and *Trissolcus basalis* (Hymenoptera: Platygastridae) Age on Attack of *Piezodorus guildinii* (Hemiptera: Pentatomidae) Eggs

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ABSTRACT Parasitoid's performance is subject to parasitism decisions influenced by host quality and parasitoid's age. We evaluated parasitism, emergence, and the progeny sex ratio proportions of *Telenomus podisi* (Ashmead), *Trissolcus urichi* (Crawford), and *Trissolcus basalis* (Wollaston) (Hymenoptera: Platygastridae) females of different age attacking *Piezodorus guildinii* (Westwood) (Hemiptera: Pentatomidae), an important soybean pest. Eggs were offered to females of *T. podisi* 1–10 d old, *T. urichi* 1, 3, 4, or 6 d old, or *T. basalis* 1–6 or 8 d old. Average egg parasitism proportions were 0.71 and 0.79 to *T. podisi* and *T. urichi*, respectively; and preimaginal survivorship was >97% for both species. *Trissolcus basalis* females 1, 2, and 3 d old did not parasitize *P. guildinii* eggs, and high parasitism proportions were recorded from older females, but only 0.5 of females attacked host eggs. A greater proportion of males were produced in the progeny of *T. podisi* and *T. urichi* as maternal age increased, but no differences were found in the progeny of *T. basalis* wasps of different ages. The results from this study indicate that performance of *T. podisi* and *T. urichi* would not be affected by the age of the females. However, aging would induce *T. basalis* females to attack *P. guildinii*, although it is known that their main host is *Nezara viridula* (L.) (Hemiptera: Pentatomidae). Under certain circumstances, such as shortage of preferred host availability, high egg load, and short life expectancy, this wasp may include *P. guildinii* as a host.

RESUMEN El desempeño de los parasitoides depende de las decisiones de parasitismo, influenciadas por la calidad del hospedador y la edad del parasitoide. Evaluamos las proporciones de parasitismo, emergencia de la progenie, y sexos en la progenie de hembras de *Telenomus podisi* (Ashmead), *Trissolcus urichi* (Crawford) y *Trissolcus basalis* (Wollaston) (Hymenoptera: Platygastridae) de diferentes edades, parasitando huevos de *Piezodorus guildinii* (Westwood) (Hemiptera: Pentatomidae), principal plaga de soja. El hospedador fue ofrecido a hembras de *T. podisi* de 1–10 días de edad, *T. urichi* 1, 3, 4 ó 6 días, ó *T. basalis* 1, 2, 3, 4, 5, 6 ó 8 días. Las proporciones promedio de parasitismo fueron 0,71 y 0,79 (*T. podisi* y *T. urichi* respectivamente), y la supervivencia preimaginal superior al 97% para ambas. Hembras de *T. basalis* de 1, 2 y 3 días no parasitaron. La proporción de parasitismo fue alto para las avispas mayores, si bien solo 0,5 de las hembras atacó los huevos ofrecidos. A mayor edad de las avispas, mayor proporción de machos en la progenie de *T. podisi* y *T. urichi*, pero en la progenie de *T. basalis* de distintas edades no hubo diferencias. El desempeño de *T. podisi* y *T. urichi* no sería afectado por la edad de las hembras. Sin embargo, a mayor edad, las hembras de *T. basalis* serían inducidas a atacar a *P. guildinii*, un hospedador de baja calidad. Con escases del hospedador preferido, alta carga de huevos y baja expectativa de vida, esta avispa utilizaría a *P. guildinii* como hospedador.

KEY WORDS parasitoid, age, host quality, parasitism proportion, progeny sex ratio

In host–parasitoid interactions, host quality influences the dynamic processes of parasitoid's growth, development, preadult survivorship, and sex ratio, and parasitoid's progeny could be unable to develop if an unsuitable host is attacked (Godfray 1994). Several host-related factors may influence their quality, such as host age, status with respect to disease or parasitism, host plant fed upon, host species differences, or differences in quality of the same host among parasitoid species. Thus, parasitoid's performance is subject to parasitism decisions, which are influenced by parasitoid's age. During their lives, parasitoids may not find suitable hosts immediately or soon after they emerge,

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being increasingly time-limited as wasps get older (Ventura Garcia et al. 2001). Parasitoid's age can influence acceptance and reproductive success on a given host (Houston 1992, Lucchetta et al. 2007), as a reduced life expectancy of elderly parasitoids leads to a decrease in their selectivity, lowering the quality threshold below which hosts are rejected. As fitness returns to a female parasitoid depend on how it distributes offspring over available hosts and host patches (reviewed in Godfray 1994), and on how immature parasitoids adapt to variation in host resources, the kind of resource provided by the host determines its quality for parasitoid survival and development.

In addition, the host quality and parasitoid's age should influence the progeny sex ratio (Charnov et al. 1981). Most hymenopteran parasitoids reproduce by arrhenotokous parthenogenesis, where an unfertilized egg develops into a haploid male and a fertilized egg into a diploid female (Heimpel and de Boer 2008). Mated females can control the sex ratio of their progeny by choosing to release sperm or not at the time of oviposition. Males are often allocated to low-quality hosts, given that generally females suffer more when they develop in low-quality hosts (King 1987). Moreover, the quantity and quality of sperm during its storage in the female's spermatheca affects the sex ratio of the progeny of arrenotokous wasps (Damiens et al. 2003). Sperm stock can decrease over time as a result sperm depletion, sperm death, active sperm digestion by the female, and sperm disintegration while stored in the spermathecae (Cunningham et al. 1971). Sperm deterioration leads to a decrease in the fertilization capacity in older females, with the consequent increase in the proportion of haploid progeny, that is, males.

Egg parasitoids are important natural enemies that limit the numerical increase of stink bugs, and some of them can attack several host species. *Telenomus podisi* (Ashmead), *Trissolcus urichi* (Crawford), and *Trissolcus basalis* (Wollaston) (Hymenoptera: Platygastridae) are the most common stink bugs egg parasitoids in the Neotropical region (Corrêa-Ferreira and Moscardi 1995) and numerous records suggest *Piezodorus guildinii* Westwood (Hemiptera: Pentatomidae) as a suitable host for *T. podisi* and *T. urichi* (Pacheco and Corrêa-Ferreira 1998, Sujii et al. 2002), and *Nezara viridula* (L.) (Hemiptera: Pentatomidae) for *T. basalis* (Liljesthrüm and Coviella 1999, Ehler 2002).

From early 1970s to 1995, *N. viridula* (L) was the predominant soybean pest in Argentina; however, in the last two decades, *P. guildinii* relative abundance has been increasing significantly and has currently become the most important species in several provinces (Gamundi and Sosa 2008). It is also one of the most relevant stink bugs in Brazil (Corrêa-Ferreira 2008) and Uruguay (Castiglioni et al. 2008) and the predominant pest of soybeans of several states of the United States (Akin et al. 2011, Temple et al. 2013). From the whole complex of stink bug species attacking soybeans, *P. guildinii* provokes the deepest seed damage (Depieri and Panizzi 2011) and causes greater leaf retention (Corrêa-Ferreira and de Azevedo 2002). Moreover, *P. guildinii* is highly mobile, more difficult to control with insecticides (Temple 2011), and adults are not attacked by parasitoids (Liljesthrüm and Ávalos 2009), as happens with the other stink bugs species.

Although so many aspects of the performance of parasitoids attacking *N. viridula* in the laboratory have been studied (Powell and Shepard 1982, Liljesthrüm and Cameán 1992, Corrêa-Ferreira 1993, Colazza and Bin 1995), little is known about parasitoids attacking *P. guildinii* as the host. Moreover, although a high rate of emergence was reported for *T. basalis* from this host's eggs (Sujii et al. 2002), most field studies report very low rates of parasitism of *P. guildinii* eggs by this parasitioid species (Thomazini 2001, Godoy et al. 2005, Ribeiro and Castiglioni 2008, Cingolani 2012).

The objective of this study was to evaluate the effect of parasitoid female age on parasitism rate, parasitoid's preadult survivorship, and progeny's sex ratio of *T. podisi*, *T. urichi*, and *T. basalis* attacking *P. guildinii* eggs. Knowing how female age influences egg parasitism of *P. guidinii* for different parasitoid species may help in biological control programs using these parasitoid species.

Materials and Methods

Colonies of stink bugs and wasps were established from field collected individuals, from the Experimental Station "Julio Hirschhorn" of the Faculty of Agricultural Sciences and Forestry of the National University of La Plata (34° 59′ 24.32″ S, 58° 0′ 18.51″ W; 27 m s. n. m.). Adults of *P. guildinii* were fed *Phaseolus vulgaris* (L.) pods, and maintained at 24 ± 1°C, 70 ± 10% relative humidity, and a photoperiod of 14:10 (L:D) h. Stink bug deposited eggs were collected daily. Parasitoids were kept on glass tubes with host eggs, under the same laboratory conditions, and honey was provided daily as a food source. After copulation was observed, female wasps were maintained separately on glass tubes with honey as a food source and no hosts (wasps were unexperienced), until they reached the age required for the experiments.

To evaluate the effect of parasitoid's age, 50 *P. guildinii* eggs (<24 h old) were offered to females of *T. podisi* 1–10 d old (10 replicates for each age), females of *T. urichi* 1, 3, 4, or 6 d old (between seven and eight replicates for each age), or females of *T. basalis* 1–6 or 8 d old (between six and seven replicates for each age). Host eggs were exposed to parasitoids for 24 h.

The number of parasitized eggs was calculated as the number of emerged parasitoids plus the number of pupa or adult parasitoids completely developed but dead inside the host (observed by means of dissections).

We calculated the proportion of parasitism (the number of parasitized eggs by the total number of offered eggs), the proportion of emergence (the number of emerged wasps by the total number of parasitized eggs), and the proportion of female progeny (the number of developed females by the total number of developed adult wasps). These proportions calculated for each combination were compared using one-way analysis of variance (ANOVA). Data that did not show normality or homoscedasticity, were transformed to

the arcsine of the square root of the proportion. Means were compared by Tukey's honestly significant difference (HSD) test. When ANOVA assumptions were not met, we performed the Kruskal–Wallis test. Comparisons of the average ranks for each pair of combinations were made computing normal *z*-values for each comparison, as well as post hoc probabilities (corrected for the number of comparisons) for a two-sided test of significance (Zar 1996).

Results

All *T. podisi* and *T. urichi* females attacked *P. guildinii* eggs, and average egg parasitism proportions were 0.71 and 0.79, respectively. Preimaginal survivorship was >97% for both species. Parasitoid's age did not affect parasitism (*T. podisi:* $H_{(9, N = 70)} = 8.072$, $P = 0.527$; *T. urichi:* $F = 1.531$, df = 3, 26, $P = 0.230$) nor emergence proportion (*T. podisi:* $H_{(9, N = 67)} = 12.853$, $P = 0.169$; *T. urichi:* $F = 0.509$, df = 3, 26, $P = 0.680$; Fig. 1a and b). However, the proportion of female progeny was different in females of different ages (*T. podisi:* $F = 3.30$, df = 9, 122, $P = 0.001$; *T. urichi:* $F = 3.182$, df = 3, 71, $P = 0.029$). Female progeny was higher for *T. podisi* 4 d old (0.91) than for wasps 10 d old (0.79), and higher for *T. urichi* 1, 3, and 4 d old (0.94 in average) than for wasps 6 d old (0.84; Fig. 2a and b).

Based on emergence and dissection data (Fig. 1c), *T. basalis* females 1–3 d old did not parasitize any *P. guildinii* eggs. The only emergence we observed from eggs were host nymphs. In addition, although a high proportion of host eggs were parasitized by females older than 3 d (Fig. 1c), only half (0.5) of the *T. basalis* females we used in experiments attacked *P. guildinii* eggs. Parasitism from wasps 4–6 d old was higher than that from wasps 8 d old ($F = 12.116$; df = 7, 82; $P < 0.001$; Fig. 1c). The same trend was observed for emergence proportion ($F = 4.795$; df = 4, 41; $P = 0.003$; Fig. 1c). Offspring of *T. basalis* females 8 d old was not considered for sex ratio analysis because individuals from only two replicates reached the adult stage, and all of them were females. Among all other ages, progeny's female proportion was similar (0.91 on average; $F = 0.388$, df = 2, 8, $P = 0.691$; Fig. 2c).

Discussion

Several authors have investigated the performance of platygastrids on different hosts under laboratory conditions (Pacheco and Corrêa-Ferreira 1998, Kivan and Kilic 2002, Sujii et al. 2002), although very few have evaluated *P. guildinii* as a host. Our results confirmed that *P. guildinii* is a more suitable host for *T. podisi* and *T. urichi* than for *T. basalis.* For *T. podisi*, Pacheco and Corrêa-Ferreira (1998) reported a rate of parasitism of 70% of *P. guildinii* eggs, similar to that found by us. Otherwise, for *T. urichi*, Sujii et al. (2002) obtained a very low parasitism (12%) in Brazil, contrasting our results. This discrepancy could be attributed to different biological characteristics of the strains of *T. urichi* used in both studies. Divergence in different strain's performance was reported for several platygastrids (Powell and Shepard 1982, Corrêa-Ferreira and Zamataro 1989, Colazza and Rosi 2001).

We did not find significant differences in parasitism or progeny's emergence proportions for *T. podisi* or *T. urichi* females of different ages. This indicates that during the evaluated period (up to 10 d after adult emergence) wasp's reproductive capacity is unaffected.

As suggested by the local mate competition theory (Hamilton 1967), shifts in typically female-biased progeny sex ratios of parasitoids can occur in response to changes in parasitoid age and host quality, among other reasons. We observed a trend toward the production of a greater proportion of males in the progeny of *T. podisi* and *T. urichi* as maternal age increased. The increase in the proportion of male progeny of older wasps is documented for several platygastrid species (Yeargan 1982, Corrêa-Ferreira and Zamataro 1989, Corrêa-Ferreira 1993).

No pupae or adults of *T. basalis* developed from *P. guildinii* eggs exposed to young wasps (1–3 d old); however, in a few cases (6 of 1,050 exposed eggs) we observed by means of dissection a viscous and yellowish substance, an unusual content, suggesting unsuccessful parasitism. According to Ganesalingam (1966) females of *T. basalis* can kill embryos of *N. viridula* in the act of introducing the ovipositor into the host egg but without ovipositing, resulting in dead hosts with a disrupted content similar to that found in this work.

In turn, several authors reported field parasitism of *T. basalis* from *P. guildinii* eggs. Corrêa-Ferreira and Moscardi (1995) mentioned an average parasitism of 44% for this parasitoid–host combination. They argued that parasitism of *P. guildinii* eggs caused by *T. basalis* in northern Paraná State, Brazil, increased progressively as a result of frequent releases of this parasitoid in the frame of an augmentative biological control program for stink bugs (Corrêa-Ferreira 1993). In contrast, in Uruguay, Ribeiro and Castiglioni (2008) obtained a single individual of *T. basalis* from 1,388 parasitized egg masses of *P. guildinii* collected in the field. This is consistent with soybean and alfalfa fields' data from a 5 yr study in Argentina (Cingolani 2012), where *T. basalis* caused at most an average parasitism of 0.04%. In the last two cases, there were no augmentative releases of parasitoids.

Even though inexperienced young *T. basalis* females did not parasitize *P. guildinii* eggs, the absence of a more suitable host as the female wasp aged may have influenced its decision to parasitize. It is known that wasp's selectivity decreases with a decrease in its life expectancy. In this concern, the life history theory proposes a trade-off among several attributes (Rosenheim 1999), and predicts that animals should be sensitive to both the amount of resources available and life expectancy in making reproductive decisions. Although some older *T. basalis* females parasitized *P. guildinii* eggs, the proportion of parasitism declined significantly with the age of mother wasp. This could have happened because the parasitoids could have reabsorbed their eggs (Bell and Bohm 1975). How-

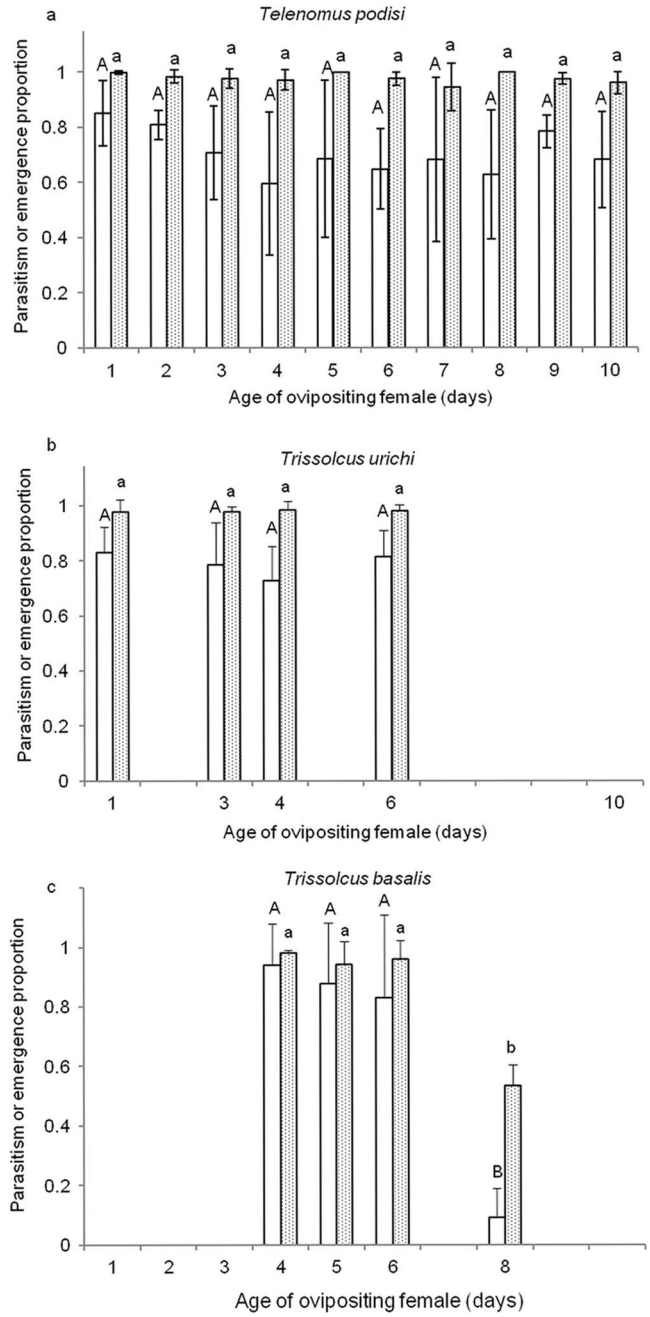

Fig. 1. Parasitism proportion (the number of parasitized eggs by number of offered eggs; white bars) and emergence proportion (the number of emerged wasps by the number of parasitized eggs; dotted bars) from *P. guildinii* eggs parasitized by female parasitoids of different species and ages. Scale bars indicate the 95% CI. Different letters indicate significant differences between treatments, according to Tukey's HSD test ($P < 0.05$). a) *T. podisi*; b) *T. urichi*; c) *T. basalis*.

ever, given the relatively low energy content of an egg, oosorption is generally regarded as a poorly efficient and costly strategy to improve survival in times of nutrient stress, and is thus considered to be a "last–resource" strategy (Jervis et al. 2001). Besides, wasps in the experiments were fed ad-libitum as they aged, so nutritional stress was unlikely.

Another possible explanation for the lower proportion of parasitism observed as *T. basalis* females aged would be the lack of oviposition stimulation mediated by the presence of a suitable host. Parasitoid's oviposition decisions are dynamic, changing in response to the received information on host quality and availability (Papaj 2000). In this sense, previous experience

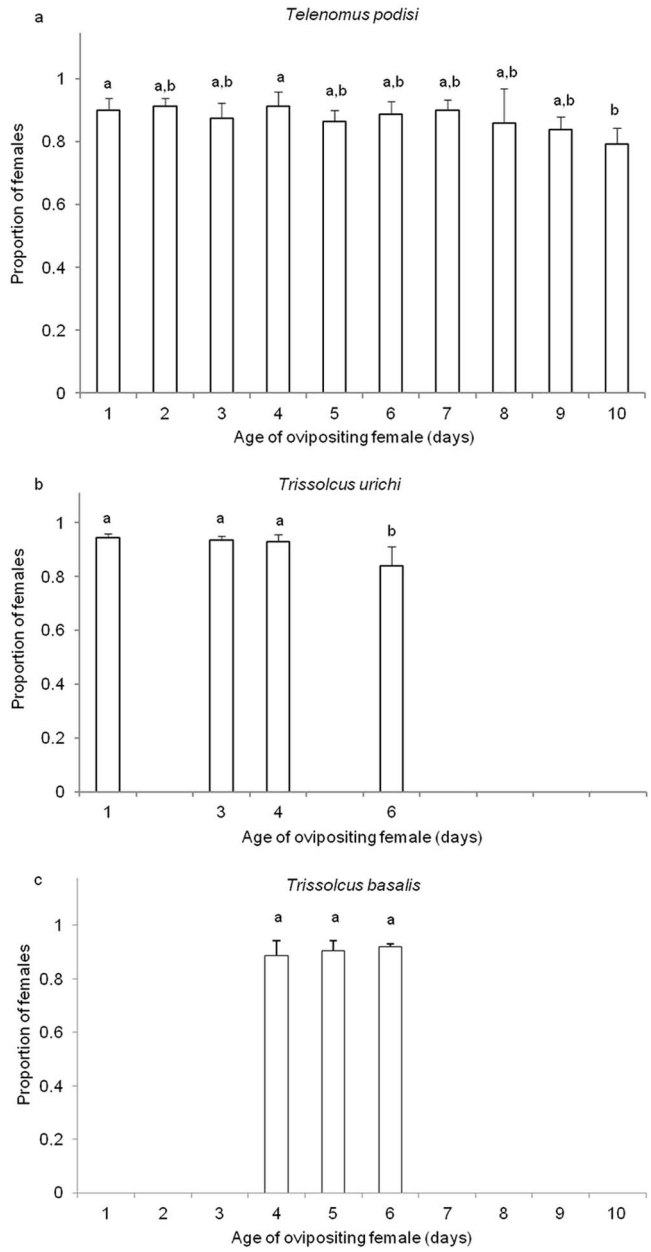

Fig. 2. Progeny's females proportion from *P. guildinii* eggs parasitized by female parasitoids of different species and ages. Scale bars indicate the 95% CI. Different letters indicate significant differences among treatments, according to Tukey's HSD test ($P < 0.05$). a) *T. podisi*; b) *T. urichi*; c) *T. basalis*.

on a given host may improve parasitism performance on that host, so it would be interesting to look into this phenomenon for future studies.

Regarding the proportion of females, no significant differences were found in the progeny of *T. basalis* wasps of different ages, although differences were found in the progeny of the other two studied parasitoid species. These results suggest that during the studied period (8 d from the emergence of *T. basalis* wasps) the quantity and quality of sperm were not affected negatively. Considering that this species has a life span of up to 25 d when it oviposits ad libitum, and up to 50 d if it never oviposits (Corrêa-Ferreira 1993), the evaluated period in this study (≈25% of its life span) would not be long enough to reflect the effect of maternal age on sex ratio of their offspring. Life span of *T. podisi* and *T. urichi* are considerably shorter (15 d on average), and the studied period represented as much as 67% of that time.

The importance of parasitoid fitness in biological control has been considered in the context of mass release augmentation; however, the influence of aging egg parasitoids on parasitism capacity is not well-documented (Ventura Garcia et al. 2001; Tarla 2011). Another important aspect is that parasitoid fitness may be enhanced by the availability of alternative hosts, especially when the preferred host is scarce, as alternative hosts can help improve the synchrony between parasitoids and their hosts as well as the distribution of parasitoids (van den Bosch and Telford 1964).

The results from this study indicate that the potential of *T. podisi* and *T. urichi* as control agents of *P. guildinii* would not be affected by the age of the females released (1–10 d old). Moreover, the parasitoid age would not be a limitation when host is scarce because the parasitoid would have more time to find it. In addition, our results suggest that aging would induce *T. basalis* females to attack low-quality host eggs of *P. guildinii.* Although it is known that the main host for *T. basalis* is *N. viridula,* under certain circumstances, such as shortage of preferred host availability, high egg load, and short life expectancy, this wasp may include *P. guildinii* as an alternative host.

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