

# Multiparasitism of *Piezodorus guildinii* eggs by *Telenomus podisi* and *Trissolcus urichi*

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**Abstract** Multiparasitism involves competition between larvae inside the host. *Telenomus podisi* (Ashmead) and *Trissolcus urichi* (Crawford) (Hymenoptera: Platygasteridae) are solitary egg parasitoids of *Piezodorus guildinii* Westwood (Hemiptera: Pentatomidae), an important soybean pest. Egg masses partially parasitized by one species were offered to females of the other species. Both species attacked randomly unparasitized and parasitized hosts. Emergence from multiparasitized eggs was greater for *T. urichi* than for *T. podisi*, although it was lower than emergence from eggs parasitized by *T. urichi* alone. Emergence of each species was independent of the order in which they parasitized and of time elapsed between ovipositions. Progeny sex ratio obtained from multiparasitized and from parasitized eggs were similar for both parasitoids. Our results suggest that *T. urichi* is a better intrinsic competitor than *T. podisi* for *P. guildinii* eggs. In the field, however, *T. podisi*

was the dominant species, and *T. urichi* could be using other pentatomid eggs as resource.

**Keywords** Hemiptera · Pentatomidae · Hymenoptera · Platygasteridae · Competition · Performance

## Introduction

Multiparasitism occurs when a parasitoid attacks a host that has been already attacked by another species of parasitoid (Godfray 1994). This interaction involves strong competition, mainly in solitary endoparasitoids, because individual hosts are sufficient for the development of one parasitoid only (Quicke 1997). Egg parasitoid females mark the attacked hosts, and have the ability to recognize those marks. Furthermore, some parasitoids mark the surrounding substrate rather than the host itself (Godfray 1994). These marks serve primarily at a specific level, although some studies have reported interspecific recognition, principally among related species (van Baaren et al. 1994; Agboka et al. 2002). Host discrimination is usually achieved by detecting external marking or an internal marker and, in some species, both types of marking can be present (Guillot and Vinson 1972). An external marker may be chemical (pheromones) or physical, for example the parasitoid egg stalk left by *Ooencyrtus nezarae* Ishii (Hymenoptera: Encyrtidae) (Takasu and Hirose 1988; Godfray 1994). An internal marker may

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be a pheromone injected by ovipositing females or may be induced by physiological changes in the host caused by the developing parasitoid (Vinson 1976). Platygastriids apply chemical external markers by scratching the surface of the host egg with the extruded ovipositor after oviposition (Strand 1989). Moreover, a defensive behavior characteristic of parasitoid species that exploit host eggs occurring in discrete clusters (quasi-gregarious parasitoids) (Waage 1982) is to stand on the egg mass they have parasitized (i.e. preemptive behavior) (Field 1998), and physical aggression between females foraging on the same host patch has been observed (Field et al. 1998).

Inside the host, competition occurs between larvae by physical attack or by physiological suppression via toxins, anoxia, or food deprivation (Godfray 1994). It has been observed that the order in which ovipositions occur, and the time interval between them, are important in the outcome of larval competition (Mackauer 1990; Tillman and Powell 1992). First-instar platygastriids are tearform, with large mandibles, which are used for physically eliminating competitors (Volkoff and Colazza 1992). When ovipositions are within 2 h, one of the larvae is eliminated by physical attack. If the interval is more than 2 h, the second female's egg develops normally until the first female's egg hatches. Then the first larva consumes limited resources, giving rise to the physiological suppression of the second larva (Hokyo et al. 1966).

The decision to multiparasitize involves a risk to the parasitoid, because its offspring will be forced into competition that can be lethal. However, this strategy could be advantageous in some circumstances. It may be beneficial when the rate of encounter with unparasitized hosts is low, when female parasitoids have a short life expectancy and a high egg load, and when more than one female is searching for hosts within the same patch (Bakker et al. 1985; Quicke 1997).

Hymenopteran parasitoids can decide the sex of their progeny and for quasi-gregarious species the sex ratio of the progeny is usually female biased, as suggested by the local mate competition theory (Hamilton 1967). Such precise control of brood sex ratio is common in quasi-gregarious platygastriids (Hardy 1992). Besides direct competition between larvae, another consequence of the interaction between parasitoids may be an increase in the proportion of males in the progeny, as occurs in superparasitism (Field et al. 1997). Because males

develop faster than females, the former have a higher probability of outcompeting the other parasitoid developing inside the same host (Field et al. 1997). This mechanism could ensure survival of the female's progeny. When multiparasitizing, a female wasp that can distinguish between unparasitized hosts and already parasitized hosts could also produce male-biased progeny.

*Telenomus podisi* (Ashmead) and *Trissolcus urichi* (Crawford) (Hymenoptera: Platygastriidae) are solitary egg parasitoids that limit the numerical increase of *Piezodorus guildinii* Westwood (Hemiptera: Pentatomidae) in the Neotropical region (Corrêa-Ferreira and Moscardi 1995; Castiglioni et al. 2010). This stink bug is a seed-sucking pest mainly on soybean and alfalfa in South America (Castiglioni et al. 2010), and in the lower mid-South of the United States of America (Akin et al. 2011).

*Piezodorus guildinii* lays eggs in masses, so their egg parasitoids are quasi-gregarious. The emergence of several species of parasitoids from the same pentatomid egg mass parasitized in the field has been recorded on several occasions (Corrêa-Ferreira 1996; Castiglioni et al. 2005; Molinari et al. 2008; Cingolani 2012). However, to confirm the occurrence of multiparasitism it is necessary to know the events of oviposition that had happened on each host.

From laboratory experiments we addressed the interspecific interactions between *T. podisi* and *T. urichi*. We investigated:

- 1 whether both species of parasitoid attack *P. guildinii* eggs previously parasitized by the other species;
- 2 the effect of order in the sequence of oviposition on the outcome of the interaction;
- 3 the effect of time elapsed between ovipositions of both parasitoid species on the outcome of the interaction; and
- 4 the sex ratio of each species for offspring developed on parasitized eggs and on multiparasitized eggs.

This research reveals for which species larval competition is superior when *T. podisi* and *T. urichi* multiparasitize *P. guildinii* eggs.

## Materials and methods

Colonies of stink bugs and wasps were established from individuals collected in Argentinean soybean

fields during the 2009–2010 growing crop season. Adults of *P. guildinii* were fed *Phaseolus vulgaris* (L.) (Fabales: Fabaceae). Parasitoids were reared on eggs of this stink bug and honey was provided daily as food source for adults.

The experimental unit consisted of a fresh (less than 24 h old) *P. guildinii* egg mass of 10–15 eggs (natural size range), in a petri dish 4 cm in diameter. A young *T. podisi* female (24 h as an adult), mated, and without previous oviposition experience was released in the experimental unit and was removed after it had parasitized approximately one half of the egg mass (5–7 eggs). An hour later a *T. urichi* female was introduced until it had parasitized a similar number of eggs. All eggs that were marked (i.e. the female parasitoid scraped the egg surface with the tip of her ovipositor) were believed to be parasitized, because marking is a good sign of oviposition by platygastriid egg parasitoids (Higuchi and Suzuki 1996 and references therein). This behavior results in the deposition of chemical substances produced on the Dufour's gland (Rosi et al. 2001).

The whole process of oviposition by both species was observed under a stereomicroscope. We drew a sketch of the egg mass to identify each egg and record the time when each egg was parasitized. Cases in which the first or second wasp did not accept the egg mass (did not start to parasitize) within 5 h were not included in the analysis.

The same procedure was performed using first a *T. urichi* wasp and then a *T. podisi* wasp. Ten replicates were performed exposing first *T. podisi* and then *T. urichi* (Tp→Tu), and 12 replicates exposing first *T. urichi* and then *T. podisi* (Tu→Tp).

The egg masses were incubated at  $24 \pm 1$  °C,  $70 \pm 10$  % RH, and with a photophase of 14 h until emergence of the parasitoids and/or *P. guildinii* nymphs. To determine the result of the interaction, each egg mass was checked at time intervals of 30 min from the moment emergence of the first parasitoid was recorded until emergence of the last. Parasitized eggs from which no parasitoid emerged after 12 days (i.e. average preimaginal development time at the temperature at which the experiments were performed; Corrêa-Ferreira 1993) were dissected a week later.

Selection of resource type (unparasitized eggs or eggs previously parasitized by the other species) for each species parasitizing second was estimated by use of the forage ratio  $w_i$  (Cock 1978):

$$\hat{w}_i = \frac{o_i}{p_i}$$

where  $o_i$  is the proportion of used  $i$  resource, and  $p_i$  is the proportion of available  $i$  resource. In this case, when *T. urichi* parasitizes second, it has two types of resource:  $i = 1$  unparasitized eggs, and  $i = 2$  eggs already parasitized by *T. podisi*.

The proposed index is an estimate of selection of one or other resource types, using the relationship between the proportion of eggs from one or another of the listed resource types on which *T. urichi* oviposits, divided by the proportion of the total number of eggs offered which that resource represents (Krebs 1999).

This is:

$O_{\text{unparasitized egg for } T. urichi}$  = number of eggs parasitized by *T. urichi* that were not previously parasitized by *T. podisi*/total number of eggs parasitized by *T. urichi*;

$P_{\text{unparasitized egg for } T. urichi}$  = number of eggs offered that were not previously parasitized by *T. podisi*/total number of eggs offered;

$O_{\text{eggs previously parasitized for } T. urichi}$  = number of eggs parasitized by *T. urichi* that were previously parasitized by *T. podisi*/total number of eggs parasitized by *T. urichi*; and

$P_{\text{eggs previously parasitized for } T. urichi}$  = number of eggs offered that were previously parasitized by *T. podisi*/total number of eggs offered.

So,

$$w_{\text{unparasitized}} = \frac{O_{\text{unparasitized egg}}}{P_{\text{unparasitized egg}}} \quad \text{and} \quad w_{\text{parasitized}} = \frac{O_{\text{parasitized egg}}}{P_{\text{parasitized egg}}}$$

In the same way, the indexes ( $w_{\text{unparasitized}}$  and  $w_{\text{parasitized}}$ ) were estimated for *T. podisi* when she parasitized second.  $\hat{w}_i$  takes values between 0 and  $\infty$ . Values  $<1$ ,  $=1$ , or  $>1$  indicate negative selection (the  $i$  resource is avoided), indifference (they select the resource at random), and positive selection (the  $i$  resource is preferred), respectively. To test the null hypothesis that parasitoids are indifferent towards the types of resource ( $\hat{w}_i = 1$ ), we analyzed the difference between the mean value of  $\hat{w}_i$  and unity by use of the two-tailed  $t$  test for differences between a population mean and a hypothesized population mean (Zar 1996).

For *T. podisi*, the proportion of adults emerging from multiparasitized eggs was compared with that from eggs parasitized by the species only (i.e. 0.99)

(Cingolani 2012), as a contingency table using a normal approximation of the  $\chi^2$  test (Zar 1996). The same comparison was made for *T. urichi*. The effect of the order in the sequence of oviposition on the outcome of the interaction was examined by comparing the proportion of each species emerging from multiparasitized eggs, by use of ANOVA, after applying the angular transformation of the data.

The time elapsed between ovipositions was divided into four intervals of equal magnitude (45 min) to evaluate its effect on the outcome of the interaction. The expected number of *T. podisi* individuals emerging from multiparasitized eggs in each interval was estimated as: total number of *T. podisi* adults emerging from eggs parasitized by this species only. The same procedure was followed for *T. urichi*. In both cases, the number of individuals observed to emerge in each time interval and the number expected were compared by use of the  $\chi^2$  test.

Finally, the proportion of females in offspring emerging from multiparasitized eggs was compared with the average proportion of females for the species when it parasitizes eggs not previously parasitized by the other species (0.900 for *T. podisi* and 0.919 for *T. urichi*) (Cingolani 2012), as a contingency table using a normal approximation of the  $\chi^2$  test (Zar 1996).

## Results

Selection by *T. urichi* of unparasitized eggs ( $w_{\text{unparasitized}} = 0.91$ ) or eggs previously parasitized by *T. podisi* ( $w_{\text{parasitized}} = 1.08$ ) were not significantly different from unity ( $t = -1.77$ ,  $df = 9$ ,  $p = 0.114$  and  $t = 1.97$ ,  $df = 9$ ,  $p = 0.080$ ), indicating that the distribution of *T. urichi* attacks was at random. Similar results were obtained for *T. podisi*: selection indices ( $w_{\text{unparasitized}} = 0.81$  and  $w_{\text{parasitized}} = 1.13$ ) were not significantly different from unity ( $t = -2.10$ ,  $df = 11$ ,  $p = 0.060$  and  $t = 2.17$ ,  $df = 9$ ,  $p = 0.053$ ).

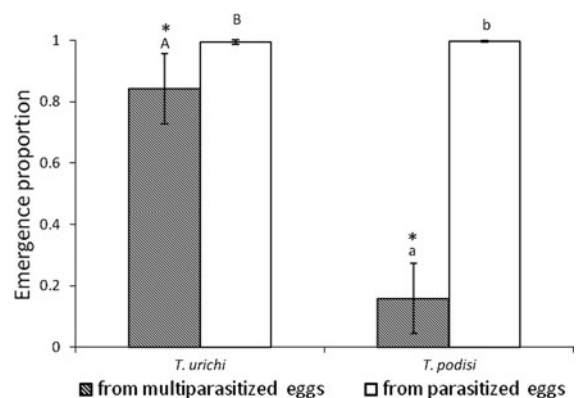
The total emergence of wasps of both species from multiparasitized eggs was 77.08 % (for Tp→Tu) and 66.66 % (for Tu→Tp). The proportion of *T. urichi* emerging from multiparasitized eggs was significantly lower than that emerging from eggs parasitized by that species only ( $z = -2.62$ ,  $p = 0.004$ ) (Fig. 1). Similar results were obtained for *T. podisi*, i.e. emergence from multiparasitized eggs was significantly lower

than from eggs parasitized by that species only ( $z = -14.316$ ,  $p < 0.05$ ) (Fig. 1).

The proportion of *T. urichi* emerging from multiparasitized eggs was always high and similar whether *T. urichi* parasitized first or second ( $F = 0.48$ ;  $df = 1$ , 18;  $p = 0.496$ ). In contrast, the proportion of *T. podisi* emerging from multiparasitized eggs was always low and similar whether *T. podisi* parasitized first or second ( $F = 0.71$ ;  $df = 1$ , 18;  $p = 0.412$ ). In the Tu→Tp treatment there was no emergence of either species of parasitoid from a small proportion of the multiparasitized eggs (0.0625). Dissection revealed that some of those eggs were empty. The content of the others was unknown, and may indicate unsuccessful parasitism (Table 1).

The number of individuals of *T. podisi* or *T. urichi* emerging was independent of the time between ovipositions ( $\chi^2 = 1.20$ ,  $df = 1$ ,  $p = 0.272$  and  $\chi^2 = 0.58$ ,  $df = 2$ ,  $p = 0.750$ , respectively) in Tp→Tu (Fig. 2a). Similar results were obtained for the Tu→Tp sequence of oviposition ( $\chi^2 = 0.57$ ,  $df = 2$ ,  $p = 0.751$  and  $\chi^2 = 0.72$ ,  $df = 1$ ,  $p = 0.395$  for *T. urichi* and *T. podisi*, respectively) (Fig. 2b).

The average proportion of females in the progeny of *T. urichi* developed from multiparasitized eggs was 0.91, similar to the proportion of females when individuals parasitize unparasitized eggs ( $z = -0.95$ ,  $p = 0.172$ ). For Tu→Tp, only three individuals of *T. podisi* emerged from multiparasitized eggs and the proportion of females of the progeny was 0.66.

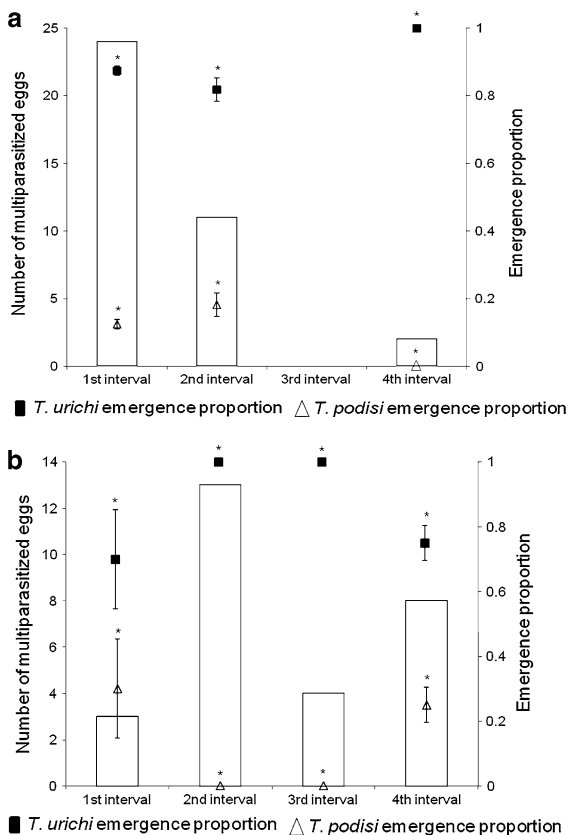


**Fig. 1** Proportions of *T. urichi* and *T. podisi* adults emerging from multiparasitized and parasitized eggs. Bars indicate 95 % confidence intervals. Significant differences between multiparasitized and parasitized eggs for the same species are indicated by different letters. The asterisks indicate significant differences between species in multiparasitized eggs

**Table 1** Outcome of multiparasitized host eggs (mean proportion  $\pm$  SE)

	<i>T. podisi</i> emergence	<i>T. urichi</i> emergence	Empty eggs	Unknown content
Tp→Tu	0.145 ( $\pm 0.066$ )	0.800 ( $\pm 0.066$ )	0.030 ( $\pm 0.021$ )	0.025 ( $\pm 0.025$ )
Tu→Tp	0.110 ( $\pm 0.053$ )	0.890 ( $\pm 0.053$ )	0	0

Tp→Tu, *T. podisi* parasitizing first; Tu→Tp, *T. urichi* parasitizing first



**Fig. 2** Number of multiparasitized eggs (bars) and proportion of *T. urichi* and *T. podisi* adults emerging ( $\pm$ SE) from multiparasitized eggs (markers) as a function of time between ovipositions. **a** *T. podisi* was the first to parasitize (Tp→Tu); **b** *T. urichi* was the first to parasitize (Tu→Tp). The asterisks indicate significant differences between species within each time interval

## Discussion

*Telenomus podisi* and *T. urichi* did not avoid multiparasitism, attacking either unparasitized eggs or eggs

previously parasitized by the other species. This could have happened because the wasps could not distinguish the marks left by wasps of the other species. Even if the marks were recognized, it is still possible that females did not avoid multiparasitism because the optimum host was scarce (only approximately five unparasitized eggs were offered to each female) and the female had a high life expectancy, was fed ad libitum, and had a high eggs load. Inability to distinguish the marks could occur because of lack of previous oviposition experience (Kearse et al. 2001) or because of the ability to distinguish intraspecific but not interspecific marks, as has been demonstrated for other platygastriids (Okuda and Yeargan 1988a). Nonetheless some aspects of host marking in *Trissolcus* sp. and *Telenomus* sp., for example chemical identity of mark pheromones and frequency of use, are still unclear. However, in our study scraping of the host egg surface with the tip of the wasp's ovipositor was observed and this behavior is believed to be evidence of oviposition by several platygastriids (Colazza et al. 1991; Bin et al. 1993).

The outcome of multiparasitism was different for the two species involved in terms of relative adult emergence. This interaction was less favorable for *T. podisi*, because, irrespective of whether it was first or second to parasitize the egg mass, the number of its adults emerging was significantly lower than for *T. urichi*. Furthermore, the proportion of *T. podisi* emerging from multiparasitized eggs was lower than the proportion emerging from eggs parasitized by this species only.

Different behavior of competing parasitoids has been described. One is ovidicide, accomplished when the second wasp uses its ovipositor to destroy the egg of the female that oviposited first (Netting and Hunter 2000; Collier et al. 2007). During this study, some females of *T. urichi* conducted a "test" with the ovipositor on eggs previously parasitized by *T. podisi* and then they did not mark. Ovidicide might have occurred for these eggs, because wasp emergence was not recorded and when the eggs were dissected the content was uncertain. Ganesalingam (1966) described a process by which a parasitoid kills the eggs of another parasitoid when introducing the ovipositor into the host, even without ovipositing. Collier et al. (2002) indicated that two species of *Encarsia* sp. Foerster (Hymenoptera: Aphelinidae) parasitizing *Bemisia tabaci* Gennadius and

*Trialeurodes vaporariorum* Westwood (Hemiptera: Aleyrodidae) committed ovidice by ovipositor movement. This behavior has been observed in species of several families of hymenopteran larval parasitoids (Pteromalidae, Aphelinidae, Bethylinidae, Ichneumonidae, Braconidae) (Godfray 1994). Nonetheless, ovidice seems much less feasible for egg parasitoids, because the difficulties associated with the act of locating a parasitoid egg floating inside the host egg, and then bracing it sufficiently to hold and destroy it, make it highly improbable (Field et al. 1997).

Another mechanism involved in competition between parasitoids implies direct physical attack between larvae of the first stage, which use their jaws to attack and destroy their competitors. Second-instar platygastriid larvae, although larger, are less mobile and have no jaws, which makes them more susceptible (Volkoff and Colazza 1992) to attack by first-instar larvae. The larva of the species that parasitizes second would have a better chance of surviving if the time between ovipositions is enough for the first larva to molt to the second instar. In our work, the order of oviposition of each species in multiparasitized eggs did not affect the outcome of the interaction—we did not observe significant differences between the proportion of each species emerging after the different treatments (*T. podisi* first and then *T. urichi*, and vice versa). Neither did the time between the two ovipositions on the same host egg have an effect on the emergence of wasps species. When the emergence of one or other of the species is not affected either by the order in which the two wasps laid their eggs or by the period between the two ovipositions, elimination of supernumerary larvae would be mediated not by physical attack between them but by physiological suppression (Cusumano et al. 2011). Although it is not possible to preclude physical attack by larvae, the results of this study suggest physiological suppression could be the mechanism involved. Physical attack indicates interference competition whereas physiological suppression leads to competition for exploitation, with different implications in parasitoid–host dynamics (Hassell 2000). Cusumano et al. (2012) found that *Ooencyrtus telenomicida* (Vassiliev) (Hymenoptera: Encyrtidae) always outcompetes *Trissolcus basalidis* (Wollaston) (Hymenoptera: Platygastriidae) by using physiological mechanisms to mediate intrinsic competition on eggs of *Nezara viridula* (L.) (Hemiptera: Pentatomidae).

Zwölfer (1971) classified parasitoids as “intrinsically superior” if they have better skills in larval competition and as “extrinsically superior” if they have better skills in location of their hosts. “Intrinsically superior” parasitoids would have a shorter development time, enabling them to have the host available during a longer period of time (Hokyo et al. 1966). The results suggest that *T. urichi* is a better competitor than *T. podisi* on *P. guildinii* eggs. However, *T. podisi* was always the dominant species on this host in the field whereas *T. urichi* was recorded only when host abundance was high (Castiglioni et al. 2010; Cingolani 2012). Females of *T. urichi*, whose larvae are good competitors, would be less efficient in locating the egg masses of *P. guildinii*. DeBach (1964) stated that it is possible to obtain an indication of the searching ability of a parasitoid from the ease with which it finds egg masses at low host densities. This ability to search for the egg masses is mediated by several environmental cues, many of which are of chemical origin from plants (synomones) or the hosts (kairomones, Colazza et al. 1999, 2004, 2009). Moreover, Amarasekare (2000) proposed coexistence can occur if the inferior larval competitor is superior at finding unparasitized hosts.

Interspecific competition between parasitoids can affect species coexistence and community structure (Godfray 1994). Coexistence is favored when niche overlap is minimal. Okuda and Yeagan (1988b) observed field parasitism in the sympatric species *T. podisi* and *Trissolcus euschisti* and found that the first species parasitized significantly more *Podisus maculiventris* egg masses in alfalfa crops (*Medicago sativa* L. Fabales: Fabaceae) and the second only parasitized egg masses in *Celtis occidentalis* L. (Rosales: Ulmaceae) trees that were present in surrounding areas. The authors suggest that the coexistence of both species in the studied environments would be favored by niche segregation.

*Trissolcus urichi* had a good performance on *Dichelops melacanthus* (Dallas) (Laumann et al. 2010), *Euschistus heros* (Fabricius) (Laumann et al. 2008), and *Acrosternum aseadum* Rolston (Sujii et al. 2002). As far as we are aware, these stink bug species (Hemiptera: Pentatomidae) are not present in our region. In our region, *T. urichi* is more frequently recovered from *Edessa mediatubunda* (F.) and *Dichelops furcatus* (F.) (Hemiptera: Pentatomidae) egg masses (Molinari et al. 2008) in soybean fields, and vegetation patches surrounding them, than from *P. guildinii* egg masses.

The coexistence of *T. urichi* and *T. podisi* in soybean fields could be favored by simultaneous occurrence of alternative hosts. Moreover, skills in larval competition and searching efficiency of *T. urichi* and *T. podisi* seem to be compensated, contributing to their coexistence.

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## Author Biographies

**M. Fernanda Cingolani** This research is part of the Ph.D. project of Dr M. Fernanda Cingolani, which is devoted to study of the biology and ecology of egg parasitoids of the redbanded stink bug, *Piezodorus guildinii*.

**Nancy M. Greco** is studying the ecology of natural enemies as biological control agents.

**Gerardo G. Liljeström** is studying the eggs and adult parasitoids of pentatomids. The interspecific interactions between parasitoids are relevant to understanding the dynamics of biological control agent populations. This study was performed by the Ecology of Pests group at CEPAVE, La Plata, Argentina.