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Interspecific interaction between *Telenomus remus* (Hymenoptera: Platygastridae) and *Trichogramma pretiosum* (Hymenoptera: Trichogrammatidae) on *Spodoptera frugiperda* (Lepidoptera: Noctuidae) eggs

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ABSTRACT

This work aimes to evaluate the interspecific interaction between *Trichogramma pretiosum* and *Telenomus remus*, two biological control agents of fall armyworm (*Spodoptera frugiperda*) eggs. Eggs of *Spodoptera frugiperda* previously parasitized by *Telenomus remus* were offered to *Trichogramma pretiosum*, and those parasitized by *Trichogramma pretiosum* were offered to *Telenomus remus*. The previously parasitized eggs were tested at different embryonic development stages for each parasitoid. In addition, to evaluate the competition between species, *Spodoptera frugiperda* eggs were offered to the parasitoids simultaneously. The behavior of the insects was recorded under a stereomicroscope. When *Spodoptera frugiperda* eggs were previously exposed to either parasitoid, there was no emergence of the other parasitoid. When the *Telenomus remus* and *Trichogramma pretiosum* females were placed together with *Spodoptera frugiperda* eggs, *Telenomus remus* had a greater parasitism rate. Except searching time, all *Trichogramma pretiosum* behaviors took a longer time than *Telenomus remus* behaviors. Thus, despite belonging to different families, each of these parasitoids is able to recognize host eggs previously parasitized by the other. So, this suggests that the recognition mechanism involved is not exclusively specific.

Key words: biological control, intraguild competition, egg parasitoid, parasitoid behavior.

INTRODUCTION

Interspecific or intraguild competition can be defined as the interaction between two species for the same food resource and/or for the same host (Rosenheim et al. 1995). It can occur at different trophic levels and has the potential to affect distribution, abundance and evolution of each species involved (Odum 1988, Polis et al. 1989, Arim and Marquet 2004).

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Prior to an introduction or release of natural enemies, such interactions should be well characterized and carefully studied, since various aspects may interfere with the action of biological control agents (Kester and Jackson 1996, Vilela and Pallini 2002, Babendreier et al. 2003, Arim and Jaksic 2005). Researchers have traditionally worked on elucidating only the association between a prey and one (or very few) predator or parasitoid species (Rosenheim et al. 1995). Thus, there is a lack of studies at the community

level. Additionally, if a generalist predator and/or parasitoid develop a preference for another natural enemy, this can cause the insect pest population to increase (Venzon et al. 2001) and impact the whole integrated pest management program.

Several studies have demonstrated the potential of egg parasitoids as biological control agents to control the Fall Armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). These agents include *Trichogramma pretiosum* (Hymenoptera: Trichogrammatidae) and *Telenomus remus* (Hymenoptera: Platygastridae) (Cruz 1995). For the control of *S. frugiperda*, different species of *Trichogramma* and *T. remus* have been used in inundative releases. The latter is able to oviposit on eggs located either on the outer or inner layers of the *S. frugiperda* egg masses, whereas *Trichogramma* species cannot reach the inner layers. In Colombia, Roa (1999) released these parasitoid species and reported a 71% parasitism rate in corn. However, the author did not mention the efficacy of each of these parasitoids. Indeed, the interaction between them may affect such efficacy. In Brazil, releases of *T. remus* alone have not proven successful to date. Some naturally occurring enemies may interact with this egg parasitoid and affect its performance as a biological control agent of *S. frugiperda* eggs. Therefore, the aim of this work is to analyze the interaction between *T. pretiosum* and *T. remus* as well as evaluate their behavior on *S. frugiperda* eggs.

MATERIALS AND METHODS

Insects. Females of *T. pretiosum* were obtained from the Laboratory of Insect Rearing, EMBRAPA (Empresa Brasileira de Pesquisa Agropecuária) Maize and Sorghum, Sete Lagoas, MG, Brazil. They were reared in *Anagasta kuheniella* (Lepidoptera: Pyralidae) eggs. However, prior to the start of the assays, *S. frugiperda* eggs were used as a host for three generations. *T. remus* females were reared solely on *S. frugiperda* eggs. *S. frugiperda* eggs were obtained from the fall armyworm mass rearing in which adults were kept in Polyvinyl Chloride cylinders (25 cm height x 10 cm diameter) with a white paper sheet covering the inner wall. Adults laid their eggs on this sheet and were kept at room temperature (25 ± 3°C)

Sequential exposure. *S. frugiperda* egg masses containing one or two layers and parasitized by *T. remus* were offered to *T. pretiosum* females, whereas those parasitized by *T. pretiosum* were offered to *T. remus* females, according to the following treatments: 1) One-layer *S. frugiperda* egg mass parasitized by *T. remus* and offered to *T. pretiosum*; 2) One-layer *S. frugiperda* egg mass parasitized by *T. pretiosum* and offered to *T. remus*; 3) Two-layer *S. frugiperda* egg mass parasitized by *T. remus* and offered to *T. pretiosum*; and, 4) Two-layer *S. frugiperda* egg mass parasitized by *T. pretiosum* and offered to *T. remus*.

Glass vials (8 cm height x 2 cm diameter) containing one adult female parasitoid (without oviposition experience and < 24 h old) and a previously parasitized egg mass were used. Honey drops were placed on the inner wall to allow females to feed.

Parasitoids were exposed to eggs for 24 h. Egg masses were removed and transferred into new glass vials for parasitism evaluation. These vials were kept in a climatic chamber at 25 ± 1°C, RH 70 ± 10%, 12L:12D photoperiod until parasitoid emergence, after which insects were separated by species and counted immediately after their death.

In order to verify the influence of eggs containing different embryonic development stages of the first parasitoid's embryonic development on oviposition behavior of the second natural enemy, a similar procedure was used and repeated daily. Twenty previously parasitized *S. frugiperda* egg masses whose age since parasitoid oviposition varied from 1 to 11 days old were offered to the other parasitoid for 24 h. Both parasitized egg masses as well as those egg masses offered to a second parasitoid were kept under controlled conditions (25 ± 1 °C, RH 70 ± 10%, 12L:12D photoperiod).

Interspecific competition: To examine intraguild competition between parasitoid species, *S. frugiperda* egg masses with one or two layers were offered to *T. remus* and *T. pretiosum*, simultaneously. One female of each parasitoid (honey fed, without previous oviposition experience and < 24 h old) and one *S. frugiperda* egg mass (ca. 100 eggs) were placed into glass vials (8 cm height x 2 cm diameter). These vials were covered with plastic wrap to prevent insect escape. Twenty replications were adopted.

Parasitoids remained in contact with the egg masses for 24h, after which the egg masses were removed and placed in other vials for evaluation of parasitism. The egg masses were kept under the same conditions as previously mentioned. After emergence, parasitoids were separated by species and counted.

Behavioral aspects of intraguild competition: Several behaviors of the two egg parasitoids were recorded and evaluated. Parasitoids were observed using one one-layer *S. frugiperda* egg mass (ca. 100 eggs). One female of each parasitoid (honey fed, without oviposition experience and < 24 h old) and one *S. frugiperda* egg mass (ca. 50 eggs and less than 24 h old) were placed together into a 9-cm Petri dish. The egg mass was placed in the center of the Petri dish, and each parasitoid was released at the border of the Petri dish on opposite sides. This assay was replicated twenty times.

Parasitoid activity was recorded using a Sony SSC-DC54A camera coupled to a stereoscopic microscope (Zeiss SV6) and a Sony SVT-S3100 video recorder. Each Petri dish was observed and filmed for 10 min. The time required was recorded for each female to find the egg mass after release in the Petri dish (search time), to meet the egg mass and begin the first oviposition, and the period between the end of the first oviposition and the beginning of the second. The time spent to oviposit on 5 eggs sequentially was also recorded.

Statistical Analysis: Data were analyzed using analysis of variance (ANOVA) using PROC GLM (SAS Institute 2004), and significant differences among means were compared by Tukey's Test ($P > 0.05$).

RESULTS

When *S. frugiperda* egg masses were first exposed to either parasitoid species, no emergence of the other species occurred, regardless of the number of egg layers (Table I). Thus, multiparasitism was not noted. Even when the primary parasitoid was in the first stages of embryonic development, no multiparasitism was observed (Table I).

However, when *T. remus* and *T. pretiosum* females were placed together on *S. frugiperda* egg masses, a predominance of parasitism by *T. remus* was noted (Figure 1). This finding was better evaluated during observations taken in the behavior study. *T. remus* females required approximately 4 min to find the host (Table II). After locating the host, females walked on *S. frugiperda* eggs and drummed the host with their antennae while examining them. Oviposition began only after females had walked on and examined the eggs (Table II). The female introduced the ovipositor into the egg and began a series of movements: compressing her abdomen, flipping the antennae abruptly and performing a gentle irregular head nodding movement. At the end of the oviposition period, the female removed her ovipositor, rubbed the abdomen over the egg and began to search for another egg. Sometimes, an additional behavior was noted before females searched for another egg. Females occasionally rubbed the hind legs against the egg chorion. The beginning of the next oviposition began within approximately 5 seconds (Table II).

On some occasions, *T. remus* females left the egg mass and initiated a body cleaning procedure by passing the front legs over the antennae and head as well as rubbing the hind legs against each other. Such behavior enables the parasitoid to remove *S. frugiperda* scales deposited on the egg mass that adhered to the parasitoid's body.

TABLE I

Mean number (± SEM) of *Telenomus remus* and *Trichogramma pretiosum* emerged from 1- or 2-layer *Spodoptera frugiperda* egg masses previously parasitized. Number of replicates = 20.

First Parasitoid	*Telenomus remus*				*Trichogramma pretiosum*			
Evaluated Parasitoid	*Trichogramma pretiosum*				*Telenomus remus*			
	Egg mass with 1 layer		Egg mass with 2 layers		Egg mass with 1 layer		Egg mass with 2 layers	
Days after first parasitoid's oviposition	*T. remus*	*T. pretiosum*	*T. remus*	*T. pretiosum*	*T. remus*	*T. pretiosum*	*T. remus*	*T. pretiosum*
1 day	88.8 ± 3.1 aA	0.0 ± 0.0 bA	64.7 ± 5.1 aA	0.0 ± 0.0 bA	0.0 ± 0.0 bA	73.1 ± 5.4 aA	0.0 ± 0.0 bA	57.2 ± 3.9 aB
2 days	91.3 ± 3.8 aA	0.0 ± 0.0 bA	87.4 ± 3.4 aA	0.0 ± 0.0 bA	0.0 ± 0.0 bA	70.6 ± 6.2 aA	0.0 ± 0.0 bA	49.2 ± 5.1 aB
3 days	87.3 ± 3.6 aA	0.0 ± 0.0 bA	82.3 ± 3.6 aA	0.0 ± 0.0 bA	0.0 ± 0.0 bA	71.8 ± 6.3 aA	0.0 ± 0.0 bA	50.8 ± 3.3 aB
4 days	89.3 ± 3.3 aA	0.0 ± 0.0 bA	75.9 ± 4.6 aA	0.0 ± 0.0 bA	0.0 ± 0.0 bA	69.8 ± 5.5 aA	0.0 ± 0.0 bA	47.8 ± 4.2 aB
5 days	87.1 ± 3.2 aA	0.0 ± 0.0 bA	90.2 ± 7.1 aA	0.0 ± 0.0 bA	0.0 ± 0.0 bA	61.8 ± 5.5 aA	0.0 ± 0.0 bA	36.8 ± 5.0 aB
6 days	88.1 ± 2.7 aA	0.0 ± 0.0 bA	84.6 ± 2.9 aA	0.0 ± 0.0 bA	0.0 ± 0.0 bA	73.4 ± 4.6 aA	0.0 ± 0.0 bA	42.6 ± 6.3 aB
7 days	94.1 ± 2.9 aA	0.0 ± 0.0 bA	82.4 ± 3.1 aA	0.0 ± 0.0 bA	0.0 ± 0.0 bA	59.7 ± 4.5 aA	0.0 ± 0.0 bA	55.9 ± 4.3 aB
8 days	81.6 ± 2.9 aA	0.0 ± 0.0 bA	79.6 ± 3.9 aA	0.0 ± 0.0 bA	0.0 ± 0.0 bA	65.4 ± 4.4 aA	0.0 ± 0.0 bA	49.4 ± 4.8 aB
9 days	78.4 ± 5.3 aA	0.0 ± 0.0 bA	87.3 ± 3.5 aA	0.0 ± 0.0 bA	0.0 ± 0.0 bA	63.7 ± 5.2 aA	0.0 ± 0.0 bA	42.7 ± 6.2 aB
10 days	88.7 ± 3.3 aA	0.0 ± 0.0 bA	80.2 ± 2.3 aA	0.0 ± 0.0 bA	0.0 ± 0.0 bA	-	0.0 ± 0.0 bA	-
11 days	74.8 ± 4.2 aA	0.0 ± 0.0 bA	87.7 ± 1.2 aA	0.0 ± 0.0 bA	0.0 ± 0.0 bA	-	0.0 ± 0.0 bA	-

Means followed by lowercase letters are compared within the same egg mass category (number of layers), whereas means followed by capital letters are compared between egg mass categories (number of layers). The comparisons are only within the same first parasitoid category. Means followed by the same letter in the row are not significantly different ANOVA (P>0.05).

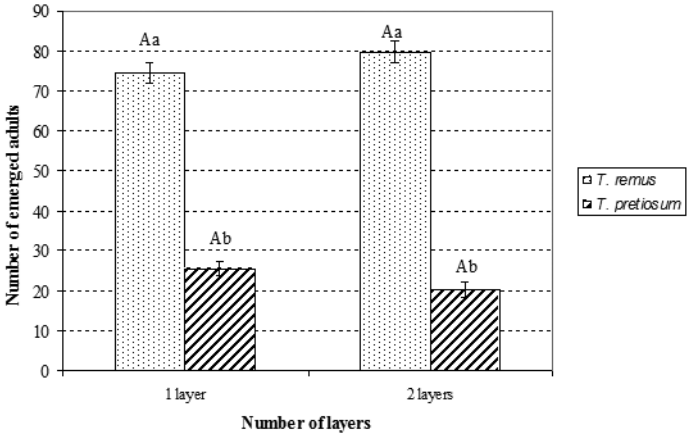

Fig. 1 - Number of adults emerging (± SEM) from 1-layer or 2-layer *Spodoptera frugiperda* egg masses offered to *Telenomus remus* and *Trichogramma pretiosum* simultaneously. Bars under the same lowercase letter are not significantly different (Tukey's Test, *P*>0.05), when comparing different species in the same category (number of layers). Bars under the same capital letter are not significantly different (Tukey's Test, *P*>0.05) when comparing the same species in different categories (different number of layers).

TABLE II
Mean time (± SE) spent performing different oviposition behaviors on *Spodoptera frugiperda* egg masses with one or two egg layers by *Telenomus remus* and *Trichogramma pretiosum*.

Behavior	Egg mass with 1 layer		Egg mass with 2 layers	
	T. remus	*T. pretiosum*	*T. remus*	*T. pretiosum*
Searching time (min)	4.59 ± 0.9 aA	6.32 ± 2.1 aA	4.35 ± 0.7 aA	8.54 ± 4.2 aA
Time until first oviposition (s)	13.8 ± 0.6 aA	32.6 ± 3.7 bA	15.2 ± 0.4 aA	29.5 ± 1.4 bA
Oviposition time (s)	47.6 ± 5.2 aA	73.0 ± 6.2 bA	40.6 ± 3.4 aA	65.1 ± 4.7 bA
Time between first and second ovipositions (s)	5.9 ± 1.3 aA	21.3 ± 2.6 bA	5.2 ± 0.8 aA	14.5 ± 3.2 bB

Means followed by lowercase letters are compared within the same egg mass category (number of layers), whereas means followed by capital letters are compared between egg mass categories (number of layers), but both are compared within the same first parasitoid category. Means followed by the same letter in the row are not significantly different (P>0.05).

In two-layer egg masses, *T. remus* females were able to oviposit into the lower eggs. To oviposit into lower eggs, females compressed their abdomens and placed them between eggs of the upper layer. With their middle and hind legs, they lightly pushed these upper-layered eggs to open a gap into which they could fit their bodies and reach the lower layer. In contrast, *T. pretiosum* females were not able to parasitize the eggs of the lower layers, except those found on the edge of the egg masses, which could be easily reached from the side. This observation also likely explains the reduced amount of parasitism found for *T. pretiosum* when egg masses with two layers were offered to females (Table I).

T. pretiosum females walked over the layer, and when an egg was chosen, they moved back and forth while examining it with their antennae. Afterwards, they inserted the ovipositor and remained immobile for some time, possibly examining the host internally. Later, they initiated abdominal movements to oviposit. Once oviposition ended, the ovipositor was removed, and the female started to search for another egg. In contrast to *T. remus*, *T. pretiosum* females never left the egg mass to clean themselves. It was more difficult for them to move on the egg masses with a larger number of *S. frugiperda* scales, and they often avoided using such egg masses as hosts.

When females of the two species met, no sudden movements indicating competition or an attempt to move away from each other were observed. The females rapidly touched each other with the antennae and continued the oviposition processes.

Whenever a *T. remus* female found an egg parasitized by herself, she refrained from ovipositing on it, demonstrating that this species avoids superparasitism. On the other hand, upon meeting an egg already parasitized by *T. pretiosum*, she inserted her ovipositor into it. However, it is believed that *T. remus* either did not oviposit, since in eggs earlier parasitized by *T. pretiosum* there occurred no emergence of *T. remus* or the older embryo won the competition (van Alphen and Bernstein 2008). Also, no abdominal movements were observed during oviposition. Conversely, whenever a *T. pretiosum* female met an egg previously parasitized by herself or *T. remus*, the female inserted the ovipositor into the egg but significantly reduced the time that the ovipositor was inside (35.4 ± 6.04 s, on average). Similarly to *T. remus*, no abdominal movement was performed. Therefore, it is believed that females examined the eggs internally and did not oviposit after realizing that it had already been parasitized.

Except for the search time, all other behaviors by *T. pretiosum* took longer when compared to the same behaviors performed by *T. remus* (Table II).

These differences could explain the higher number of offspring produced by *T. remus*. By being quicker in ovipositing and searching for eggs, *T. remus* likely parasitized a larger number of eggs within a shorter period of time (Figure 1).

DISCUSSION

Multiparasitism was not noted, even when the primary parasitoid was in the first stages of embryonic development. This could be because of the marking processes of parasitized eggs by female parasitoids that prevent other individuals from utilizing the same host (Waage and Hassell 1982), despite belonging to different Hymenoptera families.

T. remus females, after laying eggs, rubbed the chorion of the host's eggs with the ovipositor, as previously noted by Gerling and Schwartz (1974). Such behavior is typical among Platygastridae (Gauld and Bolton 1988). Despite this behavior, Gerling and Schwartz (1974) claimed that superparasitism can occur during the first hour after a parasitoid's oviposition. However, even under high female densities (e.g., 9 females/100 eggs), Carneiro et al. (2009) did not observe more than one individual emergence per egg in laboratory conditions. Similar results were obtained using caged corn plants in field conditions (Carneiro et al. 2009).

T. remus rapidly rubbed its abdomen and ovipositor over the host's egg shortly after oviposition, suggesting deposition of a marking pheromone as described for other species of the genus *Telenomus* (Cave et al. 1987, Vinson 1997, Chabi-Olaye et al. 2001) and *Trissolcus basalis* (Hymenoptera: Platygastridae) which marks hosts using a lipidic substance produced by the Dufour gland (Rosi et al. 2001). It is also possible that hydrocarbons are left on the eggs during rubbing. As traces of hydrocarbons can be detected, they may play important role on modifying parasitoid oviposition behavior (Darrouzet et al. 2010).

Among Trichogrammatidae, internal or external marking can occur, and the occurrence and time of marking vary between species (Vinson 1997). External marking can be detected by the antennae, but for the parasitoid to detect the host's internal marking, a female must introduce her ovipositor into the host (Nufio and Papaj 2001). Beserra and Parra (2003) verified that *T. pretiosum* females rejected an egg that had been previously parasitized after inserting the ovipositor in the host's egg. The authors also reported that they did not notice any sign of external egg marking by the parasitoids.

External marking is a very common feature among parasitoids and is used to avoid superparasitism. On the other hand, internal marking plays a very important role in hyperparasitism reduction (Vinson 1976). Perhaps this is the reason that *T. remus* makes an external marking, because this species avoids superparasitism (Gerling and Schwartz 1974, Welzen and Waage 1987, Cave 2000). In contrast, *T. pretiosum* avoids hyperparasitism performing internal marking, but it does not decrease superparasitism, a behavior common among Trichogrammatidae (Vinson 1997).

Vinson (1997) reported that Trichogrammatidae carefully examine the host eggs by touching them with their antennae to determine the quality and quantity of available resources for the number of eggs to be laid. As *T. remus* is able to identify external markers by touching the antennae on the host, this procedure is faster than probing each host with the ovipositor to detect internal markers. This also helps *T. remus* avoiding superparasitism (Gerling and Schwartz 1974, Welzen and Waage 1987, Cave 2000). However, even in situations when superparasitism occurs, larval competition within the host causes the development and emergence of just one adult, without affecting the biological characteristics of the adults (Gerling 1972). As *T. remus* females lay only one egg per host, it seems that a detailed examination is not an important requirement prior

to oviposition. Therefore, not only the oviposition but also the searching time is performed more rapidly. Although *T. remus* is reported to be an egg parasitoid of several noctuids and pyralids (Cave 2000), this species seems more adapted to egg mass-laying noctuid insects such as *Spodoptera*.

The *Spodoptera* scales appeared to be more troublesome for *T. pretiosum* females. It was more difficult for them to move on the egg masses, and they often avoided using such egg masses as hosts. This has also been described by Beserra and Parra (2004), who noted that besides the number of layers, high scale densities also led to reduced parasitism.

T. remus females tolerate the presence of *T. pretiosum* on the same egg mass, as they tolerate the presence of other females of the same species (Welzen and Waage 1987, Carneiro et al. 2009).

When studying the competition between *T. remus* and *Chelonus insularis* (Hymenoptera: Braconidae) on the eggs of *Spodoptera exigua* (Lepidoptera: Noctuidae), Earl and Graham (1984) only obtained adults of *T. remus*, even from eggs previously parasitized by *C. insularis*. *C. insularis* females avoided eggs parasitized by *T. remus*. However, according to the authors, *T. remus* acted as a hyperparasitoid, eliminating *C. insularis*. Also, they suggested that *T. remus* larvae competed for resources with *C. insularis* larvae, although studies on the embryology of these species to confirm this suspicion have not yet been conducted. Thus, it is possible that *T. remus* is not able to recognize eggs parasitized by *C. insularis*. However, a marker deposited by *T. pretiosum* may permit formerly parasitized eggs to be recognized, thus preventing multiparasitism.

Environmental conditions may also affect competition between Trichogrammatidae and Platygastridae (Kfir and van Hamburg 1988). Thus, studies should be carried out to characterize marking substances, to evaluate larval competition and to verify the effects of abiotic factors on competition between *T. remus* and *T. pretiosum*.

According to Vet et al. (1983), typically closely related species show interspecific discrimination. However, although *T. remus* and *T. pretiosum* belong to different families and are taxonomically distant, they were able to recognize eggs parasitized by each other. Further studies to elucidate the mechanisms involved should be carried out.

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RESUMO

Este trabalho objetiva avaliar a interação interesespecífica entre *Trichogramma pretiosum* e *Telenomus remus*, dois agentes de controle biológico de ovos de *Spodoptera frugiperda*. Posturas de *Spodoptera frugiperda* previamente parasitadas por *Telenomus remus* foram ofertadas a *Trichogramma pretiosum* e aquelas parasitadas por *Trichogramma pretiosum* foram ofertadas a *Telenomus remus*. As posturas previamente parasitadas foram testadas em diferentes estágios de desenvolvimento embrionário para cada parasitoide. Ainda para verificar a competição entre as espécies, posturas de *Spodoptera frugiperda* foram ofertadas aos parasitoides simultaneamente. O comportamento dos insetos foi observado sob microscópio estereoscópico. Quando as posturas de *Spodoptera frugiperda* foram previamente expostas a qualquer um dos dois parasitoides, não houve emergência do outro parasitoide. Quando as fêmeas de *Telenomus remus* e de *Trichogramma pretiosum* foram colocadas juntas com as posturas de *Spodoptera frugiperda*, *Telenomus remus* apresentou maior taxa de parasitismo. Com exceção do tempo de busca, todos os comportamentos de *Trichogramma pretiosum* foram mais demorados do que os de *Telenomus remus*. Portanto,

apesar de pertencerem a famílias diferentes, cada um desses parasitoides pode reconhecer ovos de hospedeiro previamente parasitados pela outra espécie. Este fato sugere que o mecanismo de reconhecimento envolvido não é exclusivamente específico.

Palavras-chave: controle biológico, competição intraguilda, parasitoide de ovos, comportamento do parasitoide.

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