BEHAVIOR OF *Trichogramma atopovirilia* OATMAN & PLATNER AND *T. pretiosum* RILEY (HYMENOPTERA: TRICHOGRAMMATIDAE) ON *Spodoptera frugiperda* (J. E. SMITH) (LEPIDOPTERA: NOCTUIDAE) EGG MASSES

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ABSTRACT

In this study we analyzed the impact of physical barriers of *Spodoptera frugiperda* (J. E. Smith) egg-masses on the behavior of *Trichogramma atopovirilia* Oatman & Platner and *Trichogramma pretiosum* Riley. The duration of drumming, drilling, oviposition, period spent over the egg-mass, and interval between parasitized eggs were timed, and the number of parasitized eggs were recorded. The presence of scales on the egg-masses caused a significant increase in the time spent by both parasitoids on each process and a decrease in the residence time over the egg-mass and in the number of parasitized eggs, with an increase in the number of egg layers. There was a significant decrease in the number of parasitized eggs in relation to egg-masses with one layer and no scales. We observed that the physical barriers in fall armyworm egg-masses changed the behavior of *T. atopovirilia* and *T. pretiosum*, affecting their parasitization capacity.

Key words: egg parasitoid, fall armyworm, parasitization, mechanical defense.

RESUMO

Comportamento de *Trichogramma atopovirilia* Oatman & Platner e *T. pretiosum* Riley (Hymenoptera: Trichogrammatidae) em posturas de *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae)

O trabalho teve por objetivo avaliar o impacto da barreira física presente nas posturas de *Spodoptera frugiperda* (J. E. Smith) sobre o comportamento de *Trichogramma atopovirilia* Oatman & Platner e *Trichogramma pretiosum* Riley. Foram avaliados: duração do período de reconhecimento externo do ovo, penetração do ovipositor, oviposição, tempo de permanência sobre a postura, deslocamento da fêmea entre ovos parasitados e número de ovos parasitados. A presença de escamas sobre as posturas aumentou significativamente o tempo gasto em cada etapa do comportamento para ambos os parasitóides e diminuiu o tempo de permanência da fêmea sobre a postura. O aumento no número de camadas de ovos sobre a postura diminuiu significativamente o número de ovos parasitados em relação a posturas com uma camada de ovos e sem escamas. Foi observado que as barreiras físicas sobre as posturas de *S. frugiperda* alteraram o comportamento de *T. atopovirilia* e *T. pretiosum*, afetando sua capacidade de parasitismo.

Palavras-chave: parasitóide de ovos, lagarta-do-cartucho, parasitismo, defesa mecânica.

INTRODUCTION

The use of egg parasitoids of the genus *Trichogramma* such as *Trichogramma atopovirilia* Oatman & Platner and *Trichogramma pretiosum* Riley (Hym.: Trichogrammatidae) to control corn pests has been investigated by several researchers (Toonders & Sánchez, 1987; Neil & Specht, 1990; Sá & Parra, 1994; Zucchi *et al.*, 1991; Zucchi & Monteiro, 1997). However, the efficiency of these natural enemies to control *Spodoptera frugiperda* (J. E. Smith) has been reduced because of the latter's egg-laying features, which includes overlapped layers of eggs covered by scales (Toonders & Sánchez, 1987). Among the challenges presently facing biological control experts, this is one.

Parasitism behavior is an important indicator of parasitoid performance and successful reproduction (Nurindah *et al.*, 1997). An understanding of the mechanisms and factors involved that interfere with the behavior of a natural enemy can be used to identify the situations in which the release of the parasitoid will impact the pest population. It can also suggest ways of handling the environment so as to increase the efficiency of a given natural outdoors enemy (Thompson & Stinner, 1990).

Trichogramma behavior is usually mediated by chemical (kairomones) (Noldus, 1989) and physical (volume, shape, and texture) stimuli from the host (Schmidt & Smith, 1985). Nevertheless, for a host such as *S. frugiperda*, another factor to be included among characteristics of insect parasitism behavior is the arrangement of the eggs in layers as well as the scales found on the eggs, which can alter parasitism behavior and affect control efficiency possible through the use of *Trichogramma*. The effect of these factors on parasitism behavior can be measured by timing the insect as it finds and parasitizes a host egg. Depending on the host species and related chemical and physical characteristics, and on the physiological condition of a given wasp, the time spent in these behaviors can change (Schmidt & Smith, 1985; Pak *et al.*, 1986; De-Cheng *et al.*, 1988).

The difficulty of *Trichogramma* in parasitizing *S. frugiperda* egg masses has been reported by several researchers (Toonders & Sánchez, 1987; Sifontes *et al.*, 1988; Armas & Ayala, 1993) but most of these studies are restricted to parasitism capacity without considering the effects on parasitoid behavior due to the presence of physical barriers on *S. frugiperda* egg masses. Thus, an analysis under laboratory conditions of behavior, which takes into account these barriers, is required to better understand the parasitoid-host relationship as well as implications for a biological control program targeting *S. frugiperda* and using these egg parasitoids. The goal of this research is to evaluate both the effect of egg distribution in layers and the presence of scales on *S. frugiperda* eggs on oviposition behavior of *T. atopovirilia* and *T. pretiosum*.

MATERIAL AND METHODS

The research was carried out at the Insect Biology Laboratory, Department of Entomology, Plant Pathology, and Agricultural Zoology, ESALQ/USP, Piracicaba, SP, Brazil. *T. pretiosum* originated in *S. frugiperda*-parasitized eggs collected in corn plantations in the region of Piracicaba, SP, Brazil. *T. atopovirilia* was obtained from the Centro de Pesquisa Agropecuária do Trópico Semi-Árido (CPATSA), of the Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA), Petrolina, PE, Brazil. Laboratory rearing was conducted in glass tubes (8.5 x 2.5 cm), with *Anagasta kuehniella* (Zeller) (Lep., Pyralidae) eggs supplied as factitious host following the methodology of Parra *et al.* (1989) and Parra (1997). The temperature, relative, humidity, and photoperiod conditions were, respectively, 25°C ± 2°C, 70% ± 10%, and 14L:10D.

The parasitism behavior of *T. atopovirilia* and *T. pretiosum* was individually evaluated based on different physical characteristics and using newly laid eggs (0-12 hours) of *S. frugiperda*. The treatments follow: 1. one layer of eggs with no scales; 2. two layers of eggs with no scales; 3. one layer of eggs with low scale density; 4. one layer of eggs with high scale density. For each type of eggs laid, 20-30 *T. atopovirilia* or *T. pretiosum* females of up to 24 hours of age, fed on pure bee honey, and without previous oviposition experience, were individualized in glass tubes (12.0 x 7.0 mm). They were filmed for 20 min under a stereoscopic microscope (Leica-Wild M10) coupled to a video camera (VK-C360N, Hotachi®) adapted to a video system. Evaluations, which began after the parasitoid met the host egg, determined the duration of: 1. drumming (period in which the female steps on the egg surface and touches it with her antenna); 2. drilling (characterized by a vertical downward and upward motion of the abdomen during which the female introduces the ovipositor and performs an internal examination of the host egg); 3. oviposition (this parameter was quantified together with the egg-marking time); 4. total time on each egg; 5. female residence parasitizing on the eggs laid; 6. female movement among parasitized eggs (between the end of an oviposition and beginning of the next drumming); and 7. number of parasitized eggs.

The parameters evaluated during oviposition behavior were submitted to analysis of variance, and significance difference was tested according to Fisher's protected least significant difference (PLSD) test ($p \leq 0.05$). The treatments were arranged in a factorial scheme with two factors with interactions: the *Trichogramma* species and type of eggs laid, in a completely randomized block design. A correlation analysis was performed to determine possible relationships between the time during which the female remained parasitizing the eggs and the number of eggs parasitized, and between the number of eggs parasitized and the time elapsed from the end of an egg parasitism to the beginning of the following drumming. This was carried out through SAS software (1998).

RESULTS

Considering only the females that parasitized the host eggs, the time spent by *Trichogramma* spp. in each of the parasitism behavior steps of proved to vary according to the physical barriers in the *S. frugiperda* egg mass. For both *Trichogramma* species studied, the time in each of these steps increased and the number of parasitized eggs decreased significantly with the presence of scales on the eggs (Tables 1 and 2). On scaly eggs, the females had difficulty walking over the eggs and finding a position, which contributed to the increase in time spent especially for drilling and, accordingly, in total time spent on each parasitized egg (Table 1).

More drastic effects of scale presence on *S. frugiperda* eggs were observed in the behavior of *T. pretiosum*. In eggs with no scales (layers 1 and 2) and eggs with low scale density, 100% of the females parasitized the host. On the other hand, the *T. pretiosum* females had more difficulty in parasitizing high scale-density eggs, and only 60% were able to parasitize, while 100% of *T. atopovirilia* females could.

Significant interactions of the species (*T. atopovirilia* and *T. pretiosum*) and treatment (egg-laying type) factors were observed only for the duration of the drilling period of the ovipositor ($F = 10.6$; $p = 0.0001$), total time on each parasitized egg ($F = 2.7$; $p = 0.04$), and number of parasitized eggs ($F = 4.8$; $p = 0.009$) (Table 1). These results show that *T. atopovirilia* and *T. pretiosum* present differences in relation to each of these three behavioral steps and that for each species, the time in each step of the behavior and the number of parasitized eggs are modified according to the physical barriers of *S. frugiperda* egg laying. Overall, *T. atopovirilia* required a larger period of time to examine and parasitize the host egg than did *T. pretiosum* (Table 1).

The time spent by a female parasitizing the eggs was positively correlated with the number of parasitized eggs, both for *T. atopovirilia* ($t = 5.8$; $p = 0.00008$; $r = 0.56$) and *T. pretiosum* ($t = 15.5$; $p = 0.00001$; $r = 0.85$) (Fig. 1) and these parameters were significantly lower on scaly eggs (Table 2). No significant interaction was observed regarding the time spent by females parasitizing the egg between the species (*T. atopovirilia* and *T. pretiosum*) and treatment (type of eggs laid) ($F = 1.5$; $p = 0.23$). However, a significant difference occurred between the species ($F = 8.39$; $p = 0.0004$) and among treatments ($F = 7.45$; $p = 0.0009$). Overall, *T. atopovirilia* spent a greater period of time parasitizing the eggs than was the case for *T. pretiosum*, although with respect to the number of parasitized eggs a significant difference between species was only observed for eggs with one layer and no scales, and eggs with high scale density. In the latter case, *T. atopovirilia* had a higher parasitism capacity than *T. pretiosum* (Table 2). These results show that the type of eggs has an effect on the time that females spend parasitizing and, therefore, interferes with their parasitism capacity. In addition, the period from the end of parasitizing one egg to beginning the next drumming was longer for scaly eggs.

Scaly eggs were also less parasitized by *Trichogramma* spp. which can be explained by the difficulty the females have in examining and ovipositing on the host egg, and by the time spent by the insect to move on the eggs, as shown in the correlation analysis, with an inverse relationship between the increase of time elapsed between the parasitized eggs and the number of eggs parasitized by *T. atopovirilia* (t = 8.5; p = 0.00001; r = 0.70) and *T. pretiosum* (t = 9.9; p = 0.00001; r = 0.75) (Fig. 2).

TABLE 1
Duration (s) of the parasitism behavior steps of *T. atopovirilia* and *T. pretiosum* in *S. frugiperda* eggs with different physical characteristics. Time of observation: 20 minutes.

Treatment	**Behavioral step**	
	Drumming[1]	
	T. atopovirilia	***T. pretiosum***
One layer with no scales	23.9 ± 1.3 A[3] (n = 20)	15.9 ± 0.7 A (n = 20)
Two layers with no scales	29.1 ± 1.2 AB[3] (n = 20)	20.1 ± 1.2 B (n = 20)
One layer with low scale density	30.4 ± 2.0 B (n = 20)	21.7 ± 1.3 B (n = 19)
One layer with high scale density	31.2 + 2.4 B (n = 18)	23.9 ± 1.5 B (n = 18)
Overall average	28.6 ± 0.9 a	20.4 ± 0.7 b
	Drilling	
	T. atopovirilia	***T. pretiosum***
One layer with no scales	44.7 ± 3.5bA[3] (n = 20)	23.2 ± 0.6 aA (n = 20)
Two layers with no scales	38.2 ± 1.9 bA (n = 20)	32.3 ± 2.5 aB (n = 20)
One layer with low scale density	53.2 ± 7.0 bB (n = 20)	39.7 ± 2.1 aC (n = 19)
One layer with high scale density	73.0 ± 5.5 bC (n = 18)	41.1 ± 2.1 aC (n = 18)
Overall average	52.3 ± 2.8 a	34.1 ± 1.3 b
	Oviposition	
	T. atopovirilia	***T. pretiosum***
One layer with no scales	43.9 ± 4.2 A[3] (n = 20)	38.3 ± 2.5 A (n = 20)
Two layers with no scales	41.5 ± 3.6 A (n = 20)	54.8 ± 6.4 AB (n = 20)
One layer with low scale density	62.6 ± 14.0 A (n = 20)	54.7 ± 7.8 AB (n = 19)
One layer with high scale density	53.0 ± 7.6 A (n = 18)	62.1 ± 4.9 B (n = 18)
Overall average	50.2 ± 4.3 b	52.5 ± 3.1 a
	Mean total time on each parasitized egg[2]	
	T. atopovirilia	***T. pretiosum***
One layer with no scales	125.8 ± 8.2 bA[3] (n = 20)	87.2 ± 2.8 aA (n = 20)
Two layers with no scales	123.6 ± 6.0 aA (n = 20)	118.6 ± 9.7 aB (n = 20)
One layer with low scale density	160.2 ± 19.5 aAB (n = 20)	128.3 ± 9.3 aBC (n = 19)
One layer with high scale density	171.7 ± 12.3 aB (n = 18)	139.8 ± 7.2 aC (n = 18)
Overall average	145.3 ± 12.1 b	118.5 ± 7.3 a

[1,2] Data transformed into log x and x^{-1}, respectively.

[3] Means followed by the same lower-case letter in rows and capital letter in columns do not differ by the PLSD test ($p < 0.05$).

TABLE 2
Time spent by females of *T. atopovirilia* and *T. pretiosum* on *S. frugiperda* eggs, time elapsed among parasitized eggs, and knumber of eggs parasitized together with their different physical characteristics. Time of observation: 20 min.

Treatment	Behavioral step	
	Time spent by the female on the eggs[1]	
	T. atopovirilia	***T. pretiosum***
One layer with no scales	1168.5 ± 11.8 A[3] (n = 20)	1151.8 ± 11.1 A (n = 20)
Two layers with no scales	1187.3 ± 6.7 A (n = 20)	1142.1 ± 8.5 A (n = 20)
One layer with low scale density	1136.8 ± 15.0 A (n = 20)	1050.4 ± 15.0 B (n = 19)
One layer with high scale density	1028.3 ± 48.6 B (n = 18)	746.1 ± 76.3 C (n = 30)
Overall average	1130.2 ± 47.9 a	1022.6 ± 31.6 b
	Gap among parasitized eggs[2]	
	T. atopovirilia	***T. pretiosum***
One layer with no scales	9.7 ± 1.5 A[3] (n = 20)	13.3 ± 2.3 A (n = 20)
Two layers with no scales	8.4 ± 0.9 A (n = 20)	15.6 ± 2.0 A (n = 20)
One layer with low scale density	32.5 ± 4.7 B (n = 20)	46.8 ± 5.5 B (n = 19)
One layer with high scale density	94.2 ± 23.4 C (n = 18)	128.1 ± 31.3 C (n = 18)
Overall average	36.2 6.6 a	51.0 ± 9.0 b
	Number of parasitized eggs	
	T. atopovirilia	***T. pretiosum***
One layer with no scales	7.9 ± 0.5 bA[3] (n = 20)	9.5 ± 0.4 aA (n = 20)
Two layers with no scales	8.2 ± 0.4 aA (n = 20)	7.0 ± 0.5 aB (n = 20)
One layer with low scale density	5.6 ± 0.4 aB (n = 20)	4.8 ± 0.4 aC (n = 19)
One layer with high scale density	4.1 ± 0.5 aC (n = 18)	2.2 ± 0.4 bD (n = 30)
Overall average	6.4 ± 0.3 a	5.9 ± 0.3 a

[1,2] Data transformed into log x and x^{-1}, respectively.

[3] Means followed by the same lower-case letter in rows and capital letters in columns do not differ by the PLSD test ($p < 0.05$).

DISCUSSION

Trichogramma females use physical (shape, texture, size, etc.) (Schmidt & Smith, 1985) and chemical stimuli (kairomones) (Noldus, 1989) as signs to recognize and parasitize a host egg. The scales found on Lepidoptera eggs are identified as a chemical stimulus that attracts parasitoids of this genus. However, in *S. frugiperda* eggs, these scales accounted for the time increase in each step of the parasitism behavior and for the decreased number of eggs parasitized by *T. atopovirilia* and *T. pretiosum*.

Regardless of the changes observed in the parasitism behavior as a consequence of scales on the eggs, *T. atopovirilia* and *T. pretiosum* showed differences in relation to their behavioral pattern. Overall, *T. atopovirilia* required more time to recognize and parasitize the host egg than did *T. pretiosum*. On the other hand, the values observed or the time spent in each step of the behavior of *T. atopovirilia* and *T. pretiosum* were lower than those observed by Suzuki *et al.* (1984), Pak *et al.* (1990), and Nurindah *et al.* (1999) for *Trichogramma chilonis* Ishii on eggs of *Papilio xuthus* L. (Lep., Papilionidae); *T. maidis*, *T. brassicae* Voegelé, and *T. evanescens* Westwood on eggs of *Mamestra brassicae* L., *Pieris brassicae* L., and *Pieris rapae* L. (Lep., Pieridae); and for *T. australicum* Girault on eggs of *Helicoverpa armigera* (Hübner) (Lep., Noctuidae). In this case, in addition to the different behavioral patterns, other dissimilarities observed can be attributed to the host egg type. In the species studied by Suzuki *et al.* (1894), Pak *et al.* (1990), and Nurindah *et al.* (1999), the parasitoids were offered isolated eggs with no scales, whereas in this study, *S. frugiperda* eggs were supplied in groups, with less distance between one another, a lesser superficial area and, apparently, lesser host volume, which according to Schmidt & Smith (1985), accounts for the decreased evaluation time of an egg parasitized by *Trichogramma* spp.

According to Schmidt & Smith (1985), *Trichogramma* females estimate the total egg volume based on the superficial area exposed in order to define the progeny to be deposited, and a relationship exists between exposed surface area, time of evaluation, and number of offspring laid per host egg. Thus, in egg-mass laying insects such as *S. frugiperda*, that which is laid appears to have less volume and area surface due to contact with neighboring eggs, which contributes to a decrease in the time of evaluation and oviposition and, consequently, in the number of individuals laid per host egg.

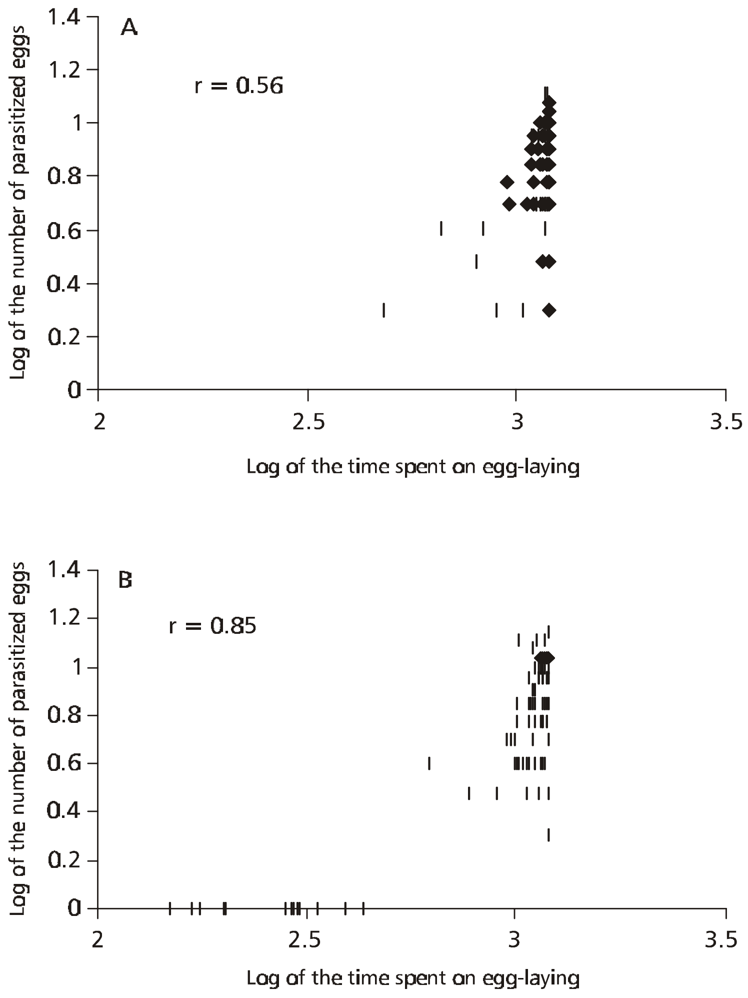
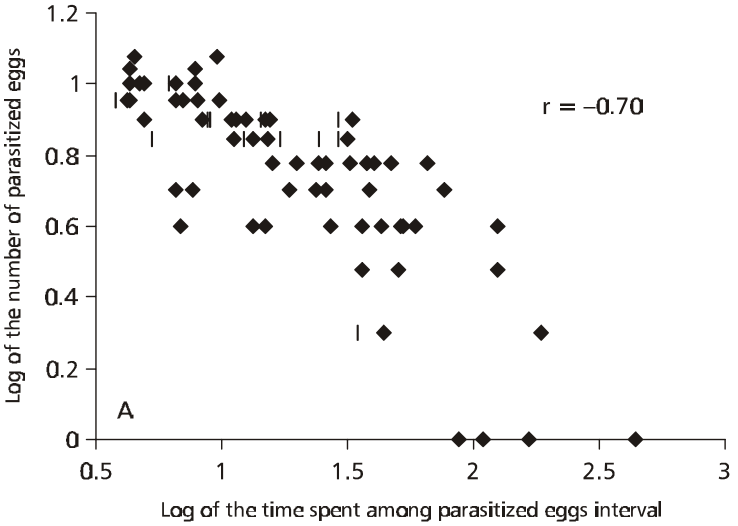


Fig. 1 — Correlation between time spent by the parasitoid female on *S. frugiperda* eggs and number of parasitized eggs. Time of observation: 20 min. (A) *T. atopovirilia*; (B) *T. pretiosum*.



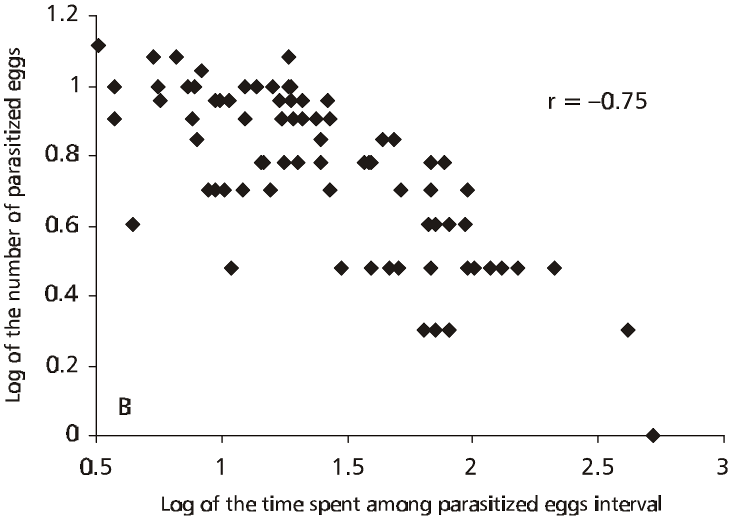


Fig. 2 — Correlation between time elapsed among parasitized eggs and the number of *S. frugiperda* eggs parasitized. Time of observation: 20 min. (A) *T. atopovirilia*; (B) *T. pretiosum*.

In addition to the volume, features such as chorion thickness and hardness are factors that can affect the behavior of a *Trichogramma* female (Schmidt, 1994). Nevertheless, these features do not seem to interfere with parasitism by *T. atopovirilia* and *T. pretiosum* in *S. frugiperda* eggs, since scale absence resulted in their acceptance by 100% of the females tested, confirming that these structures work as barriers to parasitism by *Trichogramma* spp.

The females had more difficulty in parasitizing high scale-density eggs, and the number of parasitized eggs was greatly reduced by both *T. atopovirilia* and *T. pretiosum*. In many cases the difficulty imposed by the scale barrier immediately prevented the female from drumming and parasitizing the first egg found, often leading the female to move away from the eggs and failing to parasitize or, when parasitizing, doing so only in the few eggs available at the edge of the mass. This decreased the time in which the female parasitized. So, under field conditions, an unsuccessful parasitism experience on high scale-density eggs, in which the insect is not able to parasitize immediately, leads the female to move in her search for new eggs, thereby decreasing her parasitism capacity. Similar observations were made by Garnier-Geoffroy *et al.* (1996) for *T. brassicae* that left an area with *Ostrinia nubilalis* (Hübner) (Lep., Pyralidae) eggs, which they had been unable to contact or parasitize immediately. In addition, Berti & Marcano (1991) verified that a longer time of absence of host eggs increased egg reabsorption by *T. pretiosum* and decreased parasitism in *S. cerealella* eggs. These discussions show the need of the females to find and parasitize host eggs within a given period of time in order to efficiently control a particular pest.

Parasitoids like *Trichogramma* show a behavioral pattern involving from locating a susceptible host to its recognition and acceptance (Vinson, 1998). The efficiency with which each step is performed indicates the degree of parasitism success (Hezewijk *et al.*, 2000). In this study, egg distribution in layers and scale presence changed oviposition behavior and the parasitism efficiency of *T. atopovirilia* and *T. pretiosum*. Although these results cannot be used to measure parasitoid efficiency in the field, they indicate behavior to be expected in a release program for *S. frugiperda* control. Under field conditions, factors like interactions with other biotic components (intra- and interspecific interactions) (Bleicher & Parra, 1989) and climatic conditions (Bourchier & Smith, 1996) can interfere in the performance of the parasitoids *T. atopovirilia* and *T. pretiosum*.

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