

**Discrimination of *Spartocera dentiventris* (Berg, 1884)
(Hemiptera: Coreidae) eggs by *Gryon gallardoi* (Brèthes, 1913)
(Hymenoptera: Scelionidae)**

*Rocha, L. *, Sant'Ana, J. and Redaelli, LR.*

Departamento de Fitossanidade, Faculdade de Agronomia, Universidade Federal do Rio Grande do Sul – UFRGS,
Av. Bento Gonçalves, 7712, CEP 91540-000, Porto Alegre, RS, Brazil

*e-mail: lucianerrocha@yahoo.com.br

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(With 3 figures)

Abstract

This paper aimed to evaluate the stimuli that orient *Gryon gallardoi* females to the eggs of *Spartocera dentiventris* and allow their discrimination. Using a four-arm olfactometer connected to four odor sources - *S. dentiventris* eggs; hexane washed eggs; tobacco leaves; and tobacco leaves with eggs - the arrestment of female parasitoids with previous oviposition experience and without was individually verified. The time of permanence in each odor field was registered for a period of 15 minutes. Host discrimination, regarding age and previous parasitism, was tested using arenas, where females were exposed for 30 minutes, individually, to egg groups with different treatments. To evaluate age discrimination, three groups of eggs, previously washed with hexane, were employed in the following conditions: one day-old eggs; one-day brushed with 12-days-old egg extract; 12-days-old eggs with extract of one day-old eggs; and control (washed eggs, one day-old). The same procedure was done using five and eight days-old eggs jointly with control. Age-dependent egg discrimination was verified exposing four egg groups in the following treatments: parasitized, parasitized and washed with hexane, not parasitized, and not parasitized with extract of parasitized eggs. Olfactometer tests showed that inexperienced females remained more time next to tobacco leaves when compared to experienced ones. Experienced females responded to odors that emanated from eggs. Egg extracts did not promote age discrimination; however, non parasitized eggs, with extract of parasitized eggs were partially avoided. The results obtained indicate that *G. gallardoi* females might modify their responses upon contact with host. This fact suggests learning occurs; however, the acceptance and discrimination of host may be influenced by a complex array of stimuli, difficult to evaluate in isolation.

Keywords: parasitoids, behavior, host selection, Scelionidae.

**Discriminação de ovos de *Spartocera dentiventris* (Berg, 1884) (Hemiptera: Coreidae)
por *Gryon gallardoi* (Brèthes, 1913) (Hymenoptera: Scelionidae)**

Resumo

Este trabalho objetivou avaliar os estímulos que direcionam as fêmeas *Gryon gallardoi* aos ovos de *Spartocera dentiventris* e promovem discriminação deles. Através de um olfatômetro de quatro braços conectado a quatro fontes de odor (ovos de *S. dentiventris* não lavados, ovos lavados com hexano, folhas de fumo e folhas de fumo com ovos) verificou-se, individualmente, o arrestamento dos parasitóides, experientes em oviposição e não experientes, registrando-se o tempo de permanência em cada campo de odor por 15 minutos. Para avaliar a discriminação do hospedeiro, em relação à idade e parasitismo prévio, utilizaram-se arenas, onde as fêmeas foram expostas por 30 minutos, individualmente, a grupos de ovos com diferentes tratamentos. Para a avaliação da idade, utilizaram-se três grupos de ovos, lavados com hexano, nas seguintes condições: ovos de um dia de idade pincelados com extrato de ovos de 12 dias, ovos de 12 dias com extrato de ovos de um dia e controle (ovos lavados de um dia). O mesmo procedimento foi feito utilizando-se ovos de cinco e oito dias de idade, juntamente com o controle. A discriminação de ovos previamente parasitados foi verificada expondo quatro grupos de ovos com os seguintes tratamentos: parasitados, parasitados e lavados com hexano, não parasitados e não parasitados com extrato de ovos parasitados. Testes em olfatômetro demonstraram que as fêmeas inexperientes permaneceram mais tempo junto às folhas de fumo que as experientes. As fêmeas experientes responderam aos odores oriundos dos ovos. Os extratos de ovos não promoveram a discriminação da idade, porém ovos não parasitados, impregnados com extrato de parasitados, foram parcialmente evitados. Os resultados deste trabalho apontam que as fêmeas de *G. gallardoi* podem modificar suas respostas diante do contato prévio com o seu hospedeiro, sugerindo aprendizagem, porém a aceitação e a discriminação do hospedeiro podem ser influenciadas por uma complexa combinação de estímulos, difícil de ser avaliada isoladamente.

Palavras-chave: parasitóides, comportamento, seleção de hospedeiros, Scelionidae.

1. Introduction

Finding a suitable host certainly represents an important challenge to parasitoids, small sized organisms in a structurally complex environment. Therefore, along their evolutionary history, parasitoids have developed searching abilities relying on physical and/or chemicals cues (Nufio and Papaj, 2001).

The chemical stimuli may arise from several sources: the host habitat, the host itself or from the interaction of both. The physical stimuli perceived through sight, hearing, and touch are originated from the host (i.e. size, color, texture, toughness, movements, sounds, etc). Those stimuli, associated or not, may be important in location, selection and host acceptance (Vinson, 1998). The answers to the various stimuli gave rise to a great diversity of behaviors (Harris and Foster, 1995), important either to maintain the natural diversity of communities and/or to regulate insect populations (Quicke, 1997).

Host habitat cues, as plant volatiles seem to elicit female aggregation in the host area. Nevertheless, sexual pheromones and other semiochemicals emanated from hosts are usually utilized because they furnish reliable information about host presence (Noldus and Lenteren, 1985). After host location, the next step is its recognition. Considering that eggs liberate few volatiles, the parasitoids need other signals of short - range or contact. Those are originated from substances deposited in the eggs or around, to glue them to the substrate. These volatiles are perceived through antennal touch or drumming (Steidle and Loon, 2002). The chemical stimuli allow the parasitoid to recognize and evaluate its host condition; avoiding oviposition on those already parasitized or old aged (Vinson, 1998).

Stimuli perception by parasitoids, besides genetic factors, is highly associated to experience and learning (Baaren and Boivin, 1998). Learning allows them to associate the acquired stimuli to those innate, promoting behavioral changes when confronted with a favorable experience. This is essential to the parasitoid foraging strategy assuring a successful development (Godfray, 1994).

Knowledge about the stimuli utilized by parasitoids is essential in diverse steps of biological control. This approach originated a range of works dealing with scelionids egg parasitoids as *Telenomus reynoldsi* Gordh and Coker, 1973 (Cave et al., 1987); *Telenomus podisi* Ashmead, 1893 e *Trissolcus euchisti* Ashmead, 1893 (Okuda and Yeargan, 1988); *Trissolcus basalisi* (Wollaston, 1858) (Bin et al., 1993; Rosi et al., 2001; Colazza et al., 2004); *Telenomus remus* Nixon, 1937 (Faria, 2001); *Trissolcus brochymenae* (Ashmead, 1893) (Conti et al., 2003).

Gryon gallardoii (Brèthes, 1913) (Hym.: Scelionidae) is associated to the tobacco grayish bug, *Spartocera dentiventris* (Berg, 1884) (Hem.: Coreidae), and to other coreids (Becker and Prato, 1982; Souza and Amaral-filho, 1999; Marchiori and Pentead-Dias, 2002). Female drumming behavior allows host egg discrimination and

the recognition of eggs already parasitized avoiding self-superparasitism. Usually, females prefer one to three days old eggs, leading to a greater percentage of adult emergence, with a greater body size (Rocha, 2005).

The mechanisms involved in host selection behavior and the kind of stimuli that is perceived by *G. gallardoii* females are unknown. Therefore, this work aimed to investigate, in laboratory conditions, the role of chemical stimuli in arrestment and host recognition and discrimination by females of *G. gallardoii*.

2. Material and Methods

2.1. General procedures

The insects utilized were obtained from an experimental plot of tobacco (*Nicotiana tabacum* Linnaeus, 1753), reared from *S. dentiventris* adults of the colonizing generation. Females were individually caged when the first egg groups were registered in the tobacco plants, in order to obtain egg groups of known age (Wiedenmann et al., 2003). Other females were let free in the area and so their egg groups could be parasitized. Those parasitized eggs were taken to the laboratory and kept in transparent plastic cages, in controlled conditions (25 ± 1 °C and 12 hours photophase) to initiate *G. gallardoii* rearing. The parasitoid adults were also kept in these conditions and fed with a 10% honey-water solution.

The bioassays were performed with *S. dentiventris* eggs previously washed and with extracts of eggs of different ages. One hundred eggs 1-3 days old were maintained in 200 µL of hexane, during one hour to extract the chorion chemical compounds. This procedure was repeated three times and the eggs were utilized after the complete solvent evaporation, according to Faria (2001). The extracts were obtained from groups of 100 eggs each, of the following ages: 1, 3, 5, 7, 8 and 12 days-old, kept in 100 µL of hexane during one hour, following Conti et al. (2003). The same procedure was done to obtain the parasitized eggs extract, when eggs one to 3 days -old, just marked by females, were utilized. All the extracts were stored at -20 °C.

After these procedures, and under a temperature of 25 ± 1 °C, the following experiments were carried out:

2.2. Experiment 1

Ten females of *G. gallardoii* in each one of the following conditions were utilized: 1) emerged on the host presence, mated, and exposed to a group of 12 eggs, to acquire oviposition experience (experienced) and 2) emerged without host, no-mated and not exposed to eggs (inexperienced). A four-arm olfactometer (Syntec®) was employed in the bioassays, where different odor sources were simultaneously tested: 100 eggs of *S. dentiventris*, 1 to 3 days old, not washed (T1); 100 washed eggs (T2); pieces of tobacco leaves (1.41 g) (T3); and ten groups of 12 eggs each, 1 to 3 - days- old, not washed, on a tobacco leaf (T4). All treatments were held on a filter paper disc moistened with distilled wa-

ter. The airflow inside the arena (5 L/h) was controlled with the aid of a flow meter in each arm, and another one between the arena and the vacuum pump. The air stream entering the system was filtered through charcoal and humidified by bubbling through a distilled water jar. The odor sources were converged to the center of the arena where *G. gallardoi* females were individually liberated. Each female was observed during 15 minutes, being the response to the stimuli considered by the time of permanence in each odor field. The data were registered with the aid of a sound recorder and a chronometer. Ten repetitions for each female condition (experienced and not experienced) were done. At each repetition the odor sources disposal was modified, and the arena cleaned with hexane to eliminate, respectively, the position effect upon females' choice and the likely pheromone traces left by them.

The females' retention times in the odor fields were submitted to the Kruskal-Wallis test with means comparison through the Dunn test ($\alpha = 0.05$). The different females' conditions (experienced versus not experienced) were compared in each treatment through the U test of Mann-Whitney.

2.3. Experiment 2

To evaluate the recognition of egg extracts of different ages, a two-stage experiment was carried out. In the first stage, eggs extracts of one and 12 days-old eggs were utilized, in three groups of 12 eggs each, washed with hexane and placed in a tobacco leaf. They were simultaneously disposed in an arena (9 cm diameter x 10 cm height). For each egg group the following treatments were utilized: group 1 (eggs 1 day-old, brushed with extract of eggs 12 days-old), group 2 (eggs 12 day-old, brushed with extract of eggs 1-day-old) and control (eggs 1-day-old, without extract). In the same manner, in the second stage, extracts of eggs of intermediate ages, five and eight days were tested. Groups and treatments were: group 3 (eggs 5-days-old with extract of eggs 8-days-old), group 4 (eggs 8-days-old with extract of eggs 5-days-old) and control (eggs 1-day-old without extract). In both steps, the egg groups were exposed to a 2-5 days-old parasitoid female, mated and with previous oviposition experience, during 30 minutes. The percentage of accepted eggs (ovipositor penetration followed by marking) was visually registered. In each step, 10 repetitions were done, and in each repetition the disposal of the egg groups inside the arena was randomly selected.

The discrimination of parasitized and not parasitized hosts was done exposing an experienced female, 4 egg groups 1-3 days old, linearly disposed in a Petri dish over a piece of tobacco leaf, in the following conditions: parasitized (P), parasitized washed with hexane (PW), not parasitized (NP) and not parasitized brushed with extract of parasitized eggs (NPE). The percentage of accepted eggs (ovipositor penetration followed by marking) by females was visually registered. Ten repetitions were done, being the ordering of egg groups randomly established.

Data were submitted to the Kruskal-Wallis test with means comparison through the Dunn test ($\alpha = 0.05$).

3. Results and Discussion

Arrestment was verified in all treatments utilized as odor sources in the olfactometer bioassays. Both experienced and not experienced females reacted differently to the treatments ($H = 15.55$; $df = 3$; $P < 0.01$ and $H = 21.15$; $df = 3$; $P < 0.001$, respectively). The experienced females showed a shorter retention time in the field that contained the tobacco leaves (T3) (110.9 ± 28.38 seconds) when compared to the retention time in fields with non-washed eggs (T1) (203.3 ± 26.82 s), washed eggs (T2) (204.7 ± 40.40 seconds) and non-washed eggs over tobacco leaves (T4) (324.2 ± 41.52 seconds) (Figure 1). Otherwise, inexperienced females remained less time in the fields that did not contained tobacco leaves ($T1 = 128.7 \pm 42.40$ s and $T2 = 73.8 \pm 29.72$ seconds, respectively), when compared to T3 (417.0 ± 51.50 seconds) and T4 (247.9 ± 56.82 seconds) (Figure 1).

Comparisons among experienced and inexperienced females, in each treatment, revealed that the retention time of the inexperienced ones was higher in the field with tobacco leaves (T3) ($U = 4.0$; $P < 0.01$), meanwhile the experienced showed higher retention time in those fields where eggs were present (T1 e T2) ($U = 1.97$; $P < 0.05$ e $U = 2.88$; $P < 0.01$, respectively) (Figure 1). Both experienced and inexperienced females responded in the same manner to T4 ($U = 1.26$, $P > 0.05$) (Figure 1).

The olfactometer bioassays demonstrated that volatiles emitted by tobacco leaves seem to play an important role in the arrestment behavior of *G. gallardoi* females, mainly for the inexperienced ones, whose response was more pronounced in T3 (pieces of tobacco leaves) when compared to the other treatments.

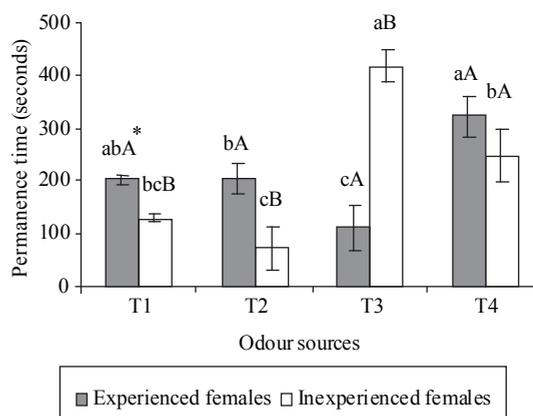


Figure 1. Mean time (s) (\pm SE) of permanence of *Gryon gallardoi* (Hym.: Scelionidae) females in different odor sources (T1 = not washed eggs; T2 = washed eggs; T3 = tobacco leaf and T4 = tobacco leaf with eggs). (Bars followed by the same small letter, among treatments, do not differ by the Dunn test, $\alpha = 0.05$, and the same capital letter, intra-treatment, do not differ by the Mann – Whitney U test, $\alpha = 0.05$).

In a study using olfactometer, similar results were found by Faria (2001), that demonstrated that inexperienced females of the scelionid *Telenomus remus* Nixon, 1937 responded more intensively to corn plants, principal host of *Spodoptera frugiperda* (J.E. Smith, 1797) (Lep.: Noctuidae), than the experienced females.

The higher attraction of the inexperienced females to the stimuli emanated from the plants, verified in the present study and in that of Faria (2001), may be associated to an innate behavior, considering that genetic factors determinate the first stimuli to which they will respond (Vet et al., 1995). When parasitoid females have contact with their hosts, they proceed to associate the new stimuli to the innate ones and may change their behavior. This mechanism is referred to as associative learning (Vinson, 1998) and the individual behavior changes gradually with continued experience (Papaj and Prokopy, 1989). This could explain the fact that experienced females of *G. gallardoi* are more attracted to the stimuli emanated from eggs. According to Vinson (1998), since the moment that the female responds to the emitted stimuli and finds its host in the habitat, it develops what has been described as motivation. This shall ensure its success in searching for other hosts; extremely important to foraging behavior and consequently to the equilibrium of natural populations (Lewis and Takasu, 1990).

The utilization of volatile compound emitted by plants where their hosts occur is extremely important to female parasitoids, chiefly to locate the host habitat. This leads to an aggregation of females in a given area (Vinson, 1998). Nevertheless, those substances could not be reliable, because they do not necessarily indicate the host presence (Steidle and Loon, 2002).

Vinson (1976) points out that in spite of their low reliability, the plant volatiles could mediate the recognition of other stimuli by parasitoid female. Studies conducted by Meiners and Hilker (2000) showed that females of *Oomyzus gallerucae* (Fonscolombe, 1832) (Hym.: Eulophidae), an egg parasitoid of *Xanthogaleruca luteola* (Müller, 1766) (Col.: Chrysomelidae), are attracted to their host's plant damaged by oviposition activity, but only when eggs are present. These authors ascribe such response to the kairomones released by the sticky substance produced by the oviducts to glue the eggs to the substrate, combined with the synomones emitted by the host plant. In a similar manner, Colazza et al. (2004) verified that bean leaves and eggs of *Nezara viridula* (Linnaeus, 1758) (Hemiptera: Pentatomidae) attract parasitoids, but only when eggs are placed on the leaf.

In the present work, it was verified that eggs attracted *G. gallardoi* females, especially the experienced, even in the absence of the tobacco leaf. Nevertheless, according to Canto-Silva (personal communication), the tobacco leaf when placed under the eggs optimizes the parasitism, leading to a higher attraction of *G. gallardoi* females to the host eggs, suggesting the importance of the association of stimuli provided by both plant and host, to parasitoid oviposition.

The fact that experienced females of *G. gallardoi* were also attracted by hexane washed eggs, suggests that they are more skillful in associating other stimuli emitted by eggs as attractants, which would not had been removed with hexane washings. Besides the external compounds adhered to the host egg chorion, the parasitoid female also could use the egg internal content as a cue to host recognition and as an oviposition elicitor. Conti et al. (1996) verified that when the egg internal content of *Lygus hesperus* Knight, 1917 (Hemiptera: Miridae) was applied on filter paper, females of *Anaphes iole* Girault, 1911 (Hym.: Mymaridae) were stimulated to drumming and to insert the ovipositor.

Hu et al. (1999) found, in olfactometer, similar results when eggs of *Leptinotarsa decemlineata* (Say, 1824) (Col.: Chrysomelidae), hexane washed, continued to attract females of *Edovum puttleri* Grissel, 1981 (Hym.: Eulophidae). The authors ascribed this fact to incomplete washing which would not have completely removed the compounds adhered to the chorion. Faria (2001), nevertheless, verified that eggs of *S. frugiperda*, hexane washed, did not elicit responses in females of *T. remus* and *Trichogramma atopovirilia* Oatman and Platner, 1983. According to this author, the absence of arrestment may indicate that chemical compounds of the egg chorion, which would elicit the parasitoid responses, are hexane soluble, and so, would have been removed by washing.

The olfactometer results suggest that *G. gallardoi* females may use a combination of stimuli to locate the eggs of *S. dentiventris* and modify its responses according to the acquired experience. Previous contact with host may induce learning, facilitating the association with other stimuli, and consequently optimizing the search activity.

The experiment dealing with host egg discrimination relative to age, using egg extracts, revealed in the first stage, a higher acceptance percentage in the control group and group 1 (eggs 1-day-old, brushed with extract of eggs 12-days-old) (66.7 ± 2.71 e $71.7 \pm 8.01\%$, respectively), when compared to the group 2 (eggs 12-days-old, brushed with extract of eggs one-day-old) ($35.3 \pm 7.02\%$) ($H = 7.22$; $P < 0.05$) (Figure 2a). In the second stage, eggs of the control group and of group 3 (eggs 5-days-old with extract of eggs 8-days-old) had a greater acceptability (24.7 ± 0.59 and $62.1 \pm 10.79\%$, respectively), relative to the group 4 (eggs 8-days-old with extract of eggs 5-days-old) ($8.7 \pm 0.43\%$) ($H = 7.01$; $P < 0.05$) (Figure 2b). These results indicated that females exhibit a preference for younger eggs, regardless of the applied extract.

This kind of age-dependent preference has been recounted for many Scelionidae species (Morris and Almazan, 1990; Romeis et al., 2000; Sousa and Spence, 2001; Hirose et al., 2003), even for *G. gallardoi* (Rocha, 2005), although little is known about the stimuli utilized by egg parasitoids, which allow them to discriminate egg hosts' age. Studies conducted by Strand and

Vinson (1983) demonstrated that females of *Telenomus heliothidis* Ashmead, 1893 (Hym.: Scelionidae) differentiate the age of *Heliothis virescens* Fabricius, 1781 (Lep.: Noctuidae) eggs using their curvature as a cue – older eggs become less spherical. Some authors, as Bin et al. (1993) and Vinson (1998), had suggested that egg age discrimination might be associated chiefly to egg biochemical alterations. Substances little volatile present in the chorion, detected by direct contact with antennae (drumming), would diminish its concentration along the time, this decrease being perceived by females and associated to host conditions. This hypothesis, however, has not yet been confirmed in other studies.

In the present study, the egg extracts applied did not influence females of *G. gallardoii*, which invariably parasitized the younger eggs. In this way, we could infer that *G. gallardoii* females, in the studied conditions, may have used other stimuli from the egg. According to Izumi et al. (1994), besides some substances in the chorion, females also could detect the internal contents of the host (egg). Although these contents suffer intense changes along the egg aging, studies corroborating the association of internal contents to host age were not found. The methodology employed in the present work did not confirm age discrimination by *G. gallardoii* females through chemical stimuli from the host egg chorion. Hence, other studies, using another kind of solvents including

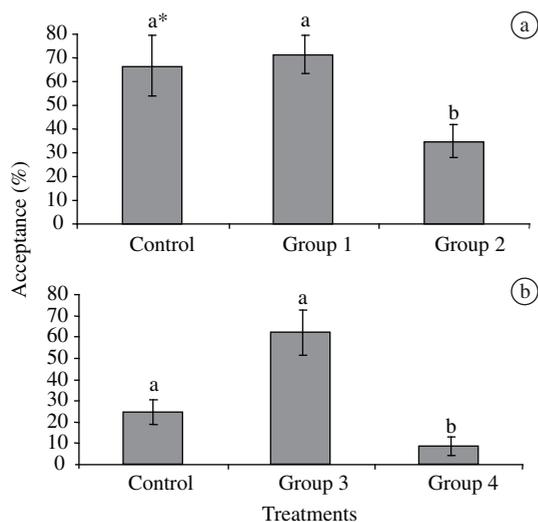


Figure 2. Acceptance percentage (\pm SE) by *Gryon gallardoii* (Hym.: Scelionidae) females, of *Spartocera dentiventris* (Hem.: Coreidae) eggs under different treatments: a) control (1-day-old eggs, hexane washed); group 1 (1-day-old eggs brushed with extract of 12-days-old eggs); group 2 (12-days-old eggs brushed with extract of 1-day-old eggs); and b) control (1-day-old eggs, hexane washed); group 3 (5-days-old eggs brushed with extract of 8-days-old eggs); group 4 (8-days-old eggs brushed with extract of 5-days-old eggs) (Bars followed by the same letter do not differ by the Dunn test, $\alpha = 0.05$).

those that might allow the extraction of the egg internal contents, are necessary. Acetone, according Conti et al. (2003), might be an option, considering its water solubility and consequently its egg penetration capacity. Other cues employed by females in this process, such as host surface and resonance, should not be disregarded as age indicators.

In evaluating the ability to recognize parasitized eggs, the results showed differences among treatments regarding acceptance by *G. gallardoii* females ($H = 21.36$; $df = 3$; $P < 0.01$). Eggs of *S. dentiventris* not parasitized (NP) were more accepted ($85.0 \pm 3.67\%$ (Figure 3). Parasitized eggs (P) and parasitized and washed eggs (PW) and not parasitized, brushed with extract of parasitized eggs (NPE) were less accepted (Figure 3).

Egg markings by egg parasitoids' females are usually external and involve little volatile chemical substances, usually perceived through antennal contact. These markings avoid self-superparasitism and sometimes the conspecific superparasitism (Alphen and Visser, 1990) and generally consist in pheromones secreted by the Dufour's gland (Rosi et al., 2001). Nevertheless, little is known regarding the composition of these substances. In some species, the marking substances are water soluble as found for the scelionids *Telenomus sphingis* (Ashmead, 1887) (Rabb and Bradley, 1970) and *Telenomus euschisti* (Ashmead, 1901) (Okuda and Yeagan, 1988). In both works, parasitized eggs washed in distilled water were accepted by parasitoids.

The rejection of *G. gallardoii* females both to parasitized eggs washed with hexane as to not parasitized eggs brushed with extract of parasitized eggs, suggests that the employed solvent might have eliminated only a fraction of the marking substances.

The host-parasitoid interaction is complex and seems to depend not only on chemical stimuli, but also on an array of factors that interact and influence the egg discrimination ability of the female parasitoid. Thus, behavioral, morphological, physiological, ecological and biochemical studies are essential to understand thoroughly this interaction, important and necessary to biological control programs.

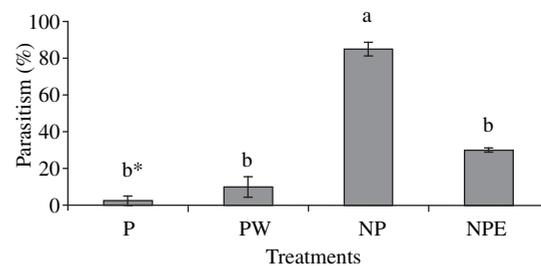


Figure 3. Percentage of parasitism (\pm SE) by *Gryon gallardoii* (Hym.: Scelionidae), of *Spartocera dentiventris* (Hem.: Coreidae) egg groups under different treatments: P = parasitized; PW = parasitized and washed; NP = non parasitized; NPE = non parasitized and brushed with extract of parasitized eggs.

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References

- VAN ALPHEN, J.J.M. and VISSER, ME., 1990. Superparasitism as an adaptative strategy for insect parasitoids. *Ann. Rev. Entomol.*, vol. 35, p. 59-79.
- VAN BAAREN, J. and BOIVIN, G., 1998. Learning affects host discrimination behavior in a parasitoid wasp. *Behav. Ecol. Soc.*, vol. 42, p. 9-16.
- BECKER, M., PRATO, MD., 1982. Natality and natural mortality of *Spartocera lativentris* Stal 1870 (Heteroptera: Coreidae) in the egg stage. *An. Soc. Entomol. Bra.*, vol. 11, p. 1344-1348.
- BIN, F., VINSON SB., STRAND, MR., COLAZZA, S. and JONES, WA., 1993. Source of an egg kairomone for *Trissolcus basalis*, a parasitoid of *Nezara viridula*. *Physiol. Entomol.*, vol. 18, p. 7-15.
- CAVE, RD., GAYLOR, MJ. and BRADLEY, JT., 1987. Host handling and recognition by *Telenomus reynoldsi* (Hymenoptera: Scelionidae) an egg parasitoid of *Geocoris* spp. (Heteroptera: Lygaeidae). *Ann. Entomol. Am.*, vol. 80, no. 2, p. 217-223.
- COLAZZA, S., FUCARINO, A., PERI, E., SALERNO, G., CONTI, E. and BIN, F., 2004. Insect oviposition induces volatile emission in herbaceous plants that attracts egg parasitoids. *J. Exp. Biol.*, vol. 207, p. 47-53.
- CONTI, E., JONES, WA., BIN, F. and VINSON, SB., 1996. Physical and chemical factors involved in host recognition behaviour of *Anaphes iole* Girault, na egg parasitoid of *Lygus hesperus* Knight (Hymenoptera: Mymaridae; Heteroptera: Miridae). *Biol. Control.*, vol. 7, p. 10-16.
- CONTI, E., SALERNO, G., BIN, F., WILLIAMS, HJ. and VINSON, SB., 2003. Chemical cues from *Murgantia histrionica* eliciting host location and recognition in the egg parasitoid *Trissolcus brochymenae*. *J. Chem. Ecol.*, vol. 29, no. 1, p. 115-129.
- FARIA, CA., 2001. *Resposta de Telenomus remus Nixon (Hymenoptera: Scelionidae) e Trichogramma atopovirilla Oatman & Platner (Hymenoptera: Trichogrammatidae) a voláteis de plantas e ovos de Spodoptera frugiperda (J. E. Smith) (Lepidoptera: Noctuidae)*. Dissertação de Mestrado. UFV, Viçosa, 50 p.
- GODFRAY, HCJ., 1994. *Parasitoids Behavioral and Evolutionary Ecology*. Princeton University Press, Princeton, 473 p.
- HARRIS, MO. and FOSTER, SP., 1995. Behaviour and integration. In CARDÉ, RT. and BELL, WJ. (Eds.), *Chemical Ecology of Insects 2*. Chapman & Hall, New York, p. 3-46.
- HIROSE, Y., EHLER, LE. and HIROSE, Y., 2003. Influence of host age on patch use by a quasi-gregarious egg parasitoid. *Environ. Entomol.*, vol. 32, no. 4, p. 789-796.
- HU, JS., GELMAN, DB. and BELL, RA., 1999. Effect of selected physical and chemical treatments of Colorado potato beetle eggs on host acceptance and development of the parasitic wasp, *Edovum puttleri*. *Entomol. Exp. App.*, vol. 90, p. 237-245.
- IZUMI, S., YANO, K., YAMAMOTO Y. and TAKAHASHI, SY., 1994. Yolk proteins from insect eggs: structure, biosintesis and programmed degradation during embryogenesis. *J. Insect Physiol.*, vol. 40, no. 9, p. 735-746.
- LEWIS, WJ. and TAKASU, K., 1990. Use of learned odours by a parasitic wasp in accordance with host and food needs. *Nature*, vol. 348, p. 635-636.
- MARCHIORI, CH. and PENTEADO-DIAS, AM., 2002. Nova ocorrência de *Gryon gallardoi* (Hymenoptera, Scelionidae) parasitóide de Hemiptera em Itumbiara, Goiás, Brasil. *BioCiências*, vol. 10, no. 1, p. 177-179.
- MEINERS, T. and HILKER, M., 2000. Induction of plant synomones by oviposition of a phytophagous insect. *J. Chem. Ecol.*, vol. 26, no. 1, p. 221-232.
- MORRIL, WL. and ALMAZON, LP., 1990. Effect of host plant species and age of rice bug (Hemiptera: Alydidae) eggs parasitism by *Gryon nixonii* (Hymenoptera: Scelionidae). *J. Entomol. Sci.*, 25, no. 3, p. 450-452.
- NOLDUS, LPJ. and VAN LENTEREN, JC., 1985. Kairomones for the egg parasite *Trichogramma evanescens* (Hymenoptera: Trichogrammatidae) Westwood. I- Effect of volatile substances released by two of its hosts, *Pieris brassicae* L. (Lepidoptera: Pieridae) and *Mamestra brassicae* L. (Lepidoptera: Noctuidae). *J. Chem. Ecol.*, vol. 11, no. 6, p. 781-791.
- NUFIO, CR. and PAPA, DR., 2001. Host marking behaviour in phytophagous insects and parasitoids. *Entomol. Exp. Apl.*, vol. 99, p. 273-293.
- OKUDA, MS. and YEARGAN, KV., 1988. Intra and interspecific host discrimination in *Telenomus podisi* and *Trissolcus euschisti* (Hymenoptera: Scelionidae). *Ann. Entomol. Am.*, vol. 81, p. 1017-1020.
- PAPA, DR., and PROKOPY, RJ., 1989. Ecological and evolutionary aspects of learning in phytophagous insects. *Ann. Rev. Entomol.*, vol. 34, p. 315-350.
- QUICKE, DLJ., 1997. *Parasitic Wasps*. Chapman & Hall, London, 470 p.
- RABB, RL. and BRADLEY, JR., 1970. Marking host eggs by *Telenomus sphingis*. *Ann. Entomol. Soc. Am.*, vol. 63, no. 4, p. 1053-1056.
- ROCHA, L., 2005. *Resposta de Gryon gallardoi (Brèthes) (Hymenoptera: Scelionidae) à qualidade dos ovos de Spartocera dentiventris (Berg) (Hemiptera: Coreidae) e evidências dos mecanismos de seleção envolvidos*. (Tese de Doutorado) – UFRGS, Porto Alegre, 158 p.
- ROMEIS, J., SHANOWER, TG. and MADHURI, K., 2000. Biology and field performance of *Gryon cravigrallae* (Hymenoptera: Scelionidae), an egg parasitoid of *Clavigralla* spp. (Hemiptera: Coreidae) in Índia. *Bull. Entomol. Res.*, vol. 90, p. 253-263.
- ROSI, MC., ISIDORO, N., COLAZZA, S. and BIN, F., 2001. Source of the host marking pheromone in the egg parasitoid *Trissolcus basalis* (Hymenoptera: Scelionidae). *J. Insect Physiol.*, vol. 47, p. 989-995.
- SANTOS, SR., REDAELLI, LR. and DIFENBACH, LMG., 2001. Ocorrência de parasitismo em ovos de *Spartocera dentiventris* (Berg) (Hemiptera: Coreidae) em cultura de fumo. *Neo. Entomol.*, vol. 30, no. 4, p. 731-733.

- SOUSA, JM. and SPENCE, JR., 2001. Host age and parasitismo by *Thiphodytes gerriphagus* (Hymenoptera: Scelionidae), an egg parasitoid of water striders (Heteroptera: Gerridae). *Ann. Entomol. Soc. Am.*, vol. 94, no. 5, p. 681-685.
- SOUZA, CEP. and AMARAL-FILHO, BF., 1999. Ocorrência natural de parasitóides de *Leptoglossus zonatus* (Dallas) (Heteroptera: Coreidae). *An. Soc. Entomol. Bra.*, vol. 2, n. 4, p. 757-759.
- STEIDLE, JLM. and VAN LOON, JJA., 2002. Chemoecology of parasitoid and predator oviposition behaviour. In HILKER, M. and MEINERS, T. (Eds.), *Chemoecology of insect egg deposition*. Blackwell Publishing, Oxford. p. 291-317.
- STRAND, MR. and VINSON, SB., 1983. Factors affecting host recognition and acceptance in the egg parasitoid *Telenomus heliothidis* (Hymenoptera: Scelionidae). *Environ. Entomol.*, vol. 12, no. 4, p. 1114-1119.
- VET, LEM., LEWIS, WJ. and CARDÉ, RT., 1995. Parasitoid foraging and learning. In CARDÉ, RT. and BELL, WJ. (Eds.). *Chemical Ecology of Insects 2*. Chapman & Hall, New York, p. 65-101.
- VINSON, SB., 1976. Host selection by insect parasitoids. *Ann. Rev. of Entomol.*, vol. 21, p. 109-133.
- , 1998. The general host selection behaviour of parasitoid hymenoptera and a comparison of initial strategies utilized by larvaphagous and oophagous species. *Biol. Control.*, vol. 11, p. 9-96.
- WIEDEMANN, LM., CANTO-SILVA, CR., ROMANOWSKI, HP. and REDAELLI, LR., 2003. Oviposition behaviour of *Gryon galardoii* (Hym.: Scelionidae) in eggs of *Spartocera dentiventris* (Hem.: Coreidae). *Braz. J.Biol.*, vol. 63, no. 1, p. 133-139.

