Eur. J. Entomol. **109**: 15–20, 2012
http://www.eje.cz/scripts/viewabstract.php?abstract=1675
ISSN 1210-5759 (print), 1802-8829 (online)

Effect of host egg age on preference, development and arrestment of *Telenomus remus* (Hymenoptera: Scelionidae)

MARIA FERNANDA GOMES VILLALBA PEÑAFLOR, MARIANA MONTAGNER DE MORAES SARMENTO, CHERRE SADE BEZERRA DA SILVA, ANDREA GRAF WERNEBURG and JOSÉ MAURÍCIO SIMÕES BENTO

Depto de Entomologia e Acarologia, Escola Superior de Agricultura "Luiz de Queiroz", ESALQ/USP, Laboratório de Ecologia Química e Comportamento de Insetos, Av Pádua Dias, 11 CP 09, Piracicaba-SP, 13418-900, Brasil; e-mail: jmsbento@esalq.usp.br

Key words. Hymenoptera, Scelionidae, *Telenomus remus*, egg parasitoid, Noctuidae, *Spodoptera frugiperda*, fall armyworm, host selection, egg age discrimination, behaviour, developmental biology

Abstract. Age of host eggs can be a limiting factor for egg parasitoids. It is expected that old eggs are less preferred by egg parasitoids, which can discriminate between eggs of different ages by using chemical cues. The objective of this study was to determine the preference, development and arrestment of *Telenomus remus* Nixon (Hymenoptera: Scelionidae) parasitizing *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) eggs of different ages. This egg parasitoid preferred to parasitize 1- and 2-day-old eggs rather than 3-day-old eggs in choice and no-choice assays. However, although the percentage emergence of parasitoids is significantly lower from 2- and 3-day-old eggs, the sex ratio and developmental time are unaffected. Parasitoids spent longer searching substrates impregnated with extracts of 1- and 2-day old eggs than 3-day-old eggs. Our results reveal that *T. remus* is able to distinguish the most suitable (1-day-old) from the least suitable (3-day-old) host eggs, but unable to recognize the unsuitability of intermediate aged eggs. Egg arrestants may be responsible for the preference of *T. remus* for ovipositing in 1- and 2-day old eggs.

INTRODUCTION

Host selection by parasitoids consists of the following behavioural steps: host habitat location, host location, host recognition and host acceptance (Vinson, 1976; 1984). For this reason, parasitoids mostly exploit chemical and/or physical cues associated with the host, plant, or interaction between plant and host (Borges et al., 1999; Hilker & Meiners, 2002).

Egg parasitoids have to be efficient at locating hosts as the duration of the egg stage is generally short. Moreover, old eggs are less suitable as hosts as they adversely affect several parasitoid biological parameters, such as percentage parasitism, developmental time (Da Rocha et al., 2006), adult emergence (Bruce et al., 2009), body size and sex ratio (Ruberson & Kring, 1993). These effects may be due to changes in the chemical composition as nutrients are gradually consumed by the host embryo and/or changes in the physical characteristics of the chorion, which becomes more rigid as the egg ages (Barret & Schmidt, 1991; Bai et al., 1992).

Preference for hosts of a particular age may enhance the fitness of egg parasitoids (Pyke et al., 1977; Strand & Vinson, 1983; Schmidt & Smith, 1985; Vinson et al., 1998). Thus parasitoids might make use of the physical characters and/or chemicals in and on the surface of eggs, which change with age, as cues indicating the suitability of hosts.

Once egg parasitoids encounter host sites, they are arrested, i.e., they change their behaviour from random walking to an intense directed examination of host-derived chemicals (Kennedy, 1978). This behaviour is well documented for egg parasitoids (Beevers et al., 1981; Gazit et al., 1996), although it is unknown whether the arrestants change with host age and thus affect parasitoid behaviour.

Telenomus remus Nixon (Hymenoptera: Scelionidae) is a specialist parasitoid of the eggs of the genus *Spodoptera* (Schwartz & Gerling, 1974). As *T. remus* is able to parasitize the eggs in the basal layers of *Spodoptera* egg masses, even when they are covered by moth scales, the percentage parasitism by this parasitoid is usually higher than that by *Trichogramma* parasitoids (Cave, 2000). Furthermore, *T. remus* can effectively control fall armyworm in corn fields (Narváez & Zocco, 1996). Thus information on this parasitoid's preference and the suitability of fall armyworm eggs of different ages is of great importance for mass rearing purposes.

The objective of this study was to determine if *T. remus* can discriminate between eggs of *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) of different ages and if egg kairomones play a role in determining their preference for eggs of a particular age.

MATERIAL AND METHODS

Insects

Larvae of *S. frugiperda* were collected from maize crops and fed on an artificial diet (Greene et al., 1976) until pupation. Adults were then transferred to cylindrical rearing cages (10 cm in diameter and 21 cm high) for mating and oviposition. They were fed on a water solution of 10% honey (v/v). Cages were covered by paper in which the moths laid egg masses. Papers containing eggs were collected and replaced daily.

For rearing the egg parasitoid *T. remus* egg masses of *S. frugiperda* were attached to a white paper strip (2.5 cm wide and 5 cm long) and placed inside glass tubes (8.5 cm high and 2.5 cm in diameter) containing gravid wasps. Parasitoid adults were fed

on honey drops placed on the wall of the glass tube. For all bioassays, only 3 and 4 day old honey-fed gravid and naive parasitoids were used. The parasitoid wasps came from cultures maintained at EMBRAPA Milho e Sorgo (Sete Lagoas, MG, Brazil). Occasionally, we introduced individuals collected from corn fields in Piracicaba, SP, Brazil.

Both the host and the egg parasitoid were reared in an acclimatized room at 25 ± 2°C, 60 ± 10% R.H. and a photoperiod of 12L : 12D.

No-choice bioassay

The percentages of 1, 2 and 3 day old eggs of *S. frugiperda* parasitized by *T. remus* females and the development of their larvae in these eggs were evaluated using a no-choice bioassay.

Eggs were carefully separated using a fine brush. Fifty eggs of each age were fixed with nontoxic water soluble glue to a square of paper (1 cm^2) each of which was placed in a glass tube (8.5 cm high and 2.5 cm in diameter). Each glass tube contained one *T. remus* female and one paper square with eggs. In total, there were 30 tubes, 10 replicates of each egg age. All tubes were kept in a climatic chamber at 28 ± 0.5°C, 70 ± 10% R.H. and a photoperiod of 12L : 12D. After 2 h (time enough for *T. remus* to parasitize 50 eggs), *T. remus* females were removed and the glass tubes kept in the climatic chamber until adult emergence. Larvae that hatched from un-parasitized eggs were removed and counted twice a day.

Day of emergence, number of male and female parasitoids that emerged and the number of dark eggs that did not give rise to parasitoid adults or larvae were recorded. These values were used to estimate percentages of parasitism and emergence, the period of time required for development from egg to adult and the sex ratio (number of females / total number of individuals).

Choice bioassay

The percentages of 1, 2 and 3 day old eggs of *S. frugiperda* parasitized by *T. remus* females and the development of their larvae in these eggs were evaluated using a bioassay in which they were able to choose between eggs of different ages.

For this bioassay 3 squares of paper each 1 cm^2 and containing 50 1, 2 or 3 day-old eggs were randomly fixed with nontoxic water soluble glue to a paper strip. Each set of paper squares were placed inside a glass tube (8.5 cm high and 2.5 cm in diameter) containing one parasitoid female. One *T. remus* parasitizes, on average, 20–25 eggs/h (C.D. Bezerra da Silva, data not published). In order to assess the wasp preference in choice assays, we allowed *T. remus* to parasitize the eggs for 4 h. In total, there were 15 glass tubes that were kept in a climatic chamber under similar conditions to those used in the no-choice bioassays.

After 4h the paper squares with 1, 2 and 3 day old eggs for each replicate were separated and placed in glass tubes. Larvae that hatched from the un-parasitized eggs were removed and counted twice a day.

Arrestment bioassay

Arrestment was measured based on the time females of *T. remus* spent (residence time) on a piece of filter paper impregnated with an hexane extract of eggs (Gazit et al., 1996). Assays were conducted in an acclimatized (25 ± 2°C, and 60 ± 10% R.H) room, which was illuminated with red light. Ten minutes before the assay, squares of filter paper (1 cm^2) were impregnated with 20 µl of egg extract, and placed in a Petri dish (14.2 cm diameter) previously cleaned with alcohol (v/v 90%) and acetone (v/v 99%). Then one *T. remus* female was released at the center of the filter paper and the timing started. Each observation lasted up to 5 min and the time spent by the parasitoid female on the filter paper was recorded (Gazit et al., 1996). If the female left the filter paper during the 5-min period and did not return within 20 s the observation ended. However, if a female returned to the filter paper within 20 s, the observation continued. As a control, filter papers impregnated only with hexane were used. Each treatment consisted of 20 replicates and insects were tested only once.

Egg extracts

Moth scales were removed from the eggs before the extractions. In addition egg masses that were well covered with moth scales were not used. However, not all moth scales were always removed.

Spodoptera frugiperda eggs were carefully separated to avoid rupture, weighed and placed in clean glass vials. Sufficient solvent (hexane) was added to give a concentration of 60 mg/ml. After 3 h, the solvent in the vial containing the eggs was transferred to another new vial, which was kept at –20°C until required. Before testing, egg extracts were evaporated in N_2 gas to reduce volume of solvent to 200 µl resulting in a concentration of 150 mg/ml.

Treatments

As moth females age, they lose scales and produce less oviduct secretion. Both represent important egg kairomones (Beevers et al., 1981; Norlund et al., 1987). So, preliminary tests were performed to verify if moth age affected the attractiveness of extracts of 1, 2 and 3-day old eggs. To do this extracts of 1-day-old eggs that were laid by 4, 6, 7, 8 and 9-day-old moths were tested.

Since the eggs deposited by females of 4-to-8-days-old did not differ significantly in their attractiveness for *T. temus* (see results of Fig. 5), the extracts were of eggs laid by 4-to-8-day-old females. The results of these treatments were compared with the solvent (hexane) control using the method described above.

Statistical analysis

All data was tested for parametric assumptions (normal distribution and equal variance) using a Kolmogorov-Smirnov test. Based on that test the data on percentage parasitism and sex ratio from no-choice assays were analyzed using a Kruskal-Wallis test and means compared by Dunn's method ($P \leq 0.05$). While data on emergence, percentage parasitism in choice assays and residence time (arrestment assays) were analyzed using One-Way ANOVA and means compared using a Duncan test ($P \leq 0.05$).

RESULTS

In the no-choice bioassay *T. remus* equally parasitized 1- and 2-day-old eggs. However, the percentage parasitism of 3-day-old eggs was significantly lower (Fig. 1; Kruskal-Wallis; H = 17.11; $P < 0.01$; Dunn $P < 0.05$). Similarly, in the choice bioassay, the parasitism of 3 day-old eggs was significantly lower than that of 1- and 2-day-old eggs (Fig. 2, ANOVA F = 3.581 $P = 0.037$; Duncan $P < 0.05$).

Mean percentage parasitoid emergence significantly decreased with egg age. The highest emergence was recorded from 1-day-old eggs and the lowest from 3-day-old eggs. Percentage parasitoid emergence from 2-day-old eggs was intermediate and differed from that of 1- and 3-day-old eggs (Fig. 3; *ANOVA* F = 49.935; $P < 0.001$; Duncan $P < 0.05$). In contrast, the sex ratio was unaffected by the age of the eggs (Fig. 4; Kruskal-Wallis

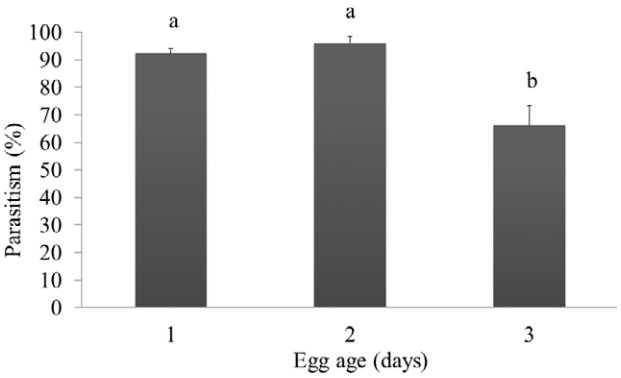

Fig. 1. Percentage parasitism (mean ± SE) of 1-, 2- and 3-day-old eggs of *Spodoptera frugiperda* by *Telenomus remus* in a no-choice bioassay. Bars with different letters indicate significant differences between treatments (n = 10; Dunn $P < 0.05$).

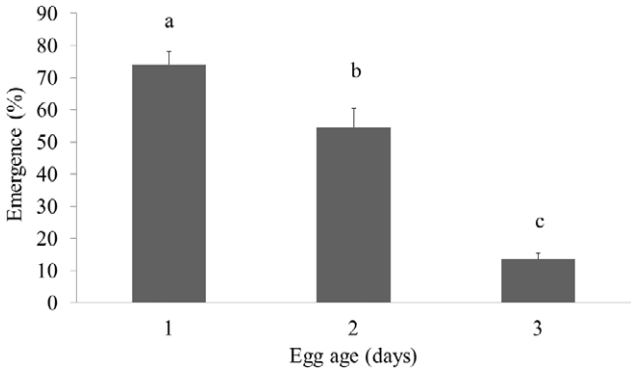

Fig. 3. Percentage emergence (mean ± SE) of *Telenomus remus* from 1-, 2- and 3-day-old eggs of *Spodoptera frugiperda* parasitized in a no-choice bioassay. Bars with different letters indicate significant differences between treatments (n = 10; Duncan $P < 0.05$).

H = 0.324; $P = 0.850$) and the parasitoid developmental time was 10 days in all treatments.

In the arrestment tests (measured in terms of parasitoid residence time), females usually remained longer on filter papers treated with egg extracts: walking in circles, or stopping and vibrating their antennae. Sometimes, the parasitoid left the filter paper but returned within a few seconds. The extracts of eggs laid by 4-to 8-day-old moths elicited the same arrestment response from *T. remus* females. Parasitoid residence time was longer on filter papers impregnated with egg extracts derived from these eggs compared to the extract of eggs laid by 9-day-old moths and the hexane control (Fig. 5; Kruskal-Wallis H = 48.87; P < 0.001; Dunn P < 0.05). Therefore, the extracts of eggs of different ages were obtained using eggs collected from 4-to-8-day-old *S. frugiperda*.

In the egg age test, *T. remus* spent longer on filter papers impregnated with egg extracts than the hexane control (Fig. 6; *ANOVA* F = 10.337; $P < 0.001$) and significantly more time on those impregnated with the extract of 1-day-old eggs than of 3-day-old eggs (Duncan $P < 0.05$).

DISCUSSION AND CONCLUSIONS

Host quality for egg parasitoids basically consists of two parameters: species and host age (Liu et al., 1998). The latter can be restrictive because host embryo development depletes the nutrients stored in the egg. Therefore, old eggs are usually low-quality hosts. Moreover, a parasitoid larva is not capable of digesting the cuticle of its host and therefore cannot consume nutrients from embryos in an advanced stage of development (Strand et al., 1986).

Thus, the selection of young eggs is advantageous because of their better nutritional quality for the development of parasitoid offspring. Egg parasitoids usually prefer young or intermediate aged eggs for parasitism (Reznik & Umarova, 1990; Monje et al., 1999; Moreno et al., 2009), including members of the Scelionidae (Romeis et al., 2000; Da Rocha et al., 2006).

Most studies indicate that old eggs are poor quality hosts for egg parasitoids (Souza & Spence, 2001; Tunçbilek & Ayvaz, 2003). However, there are reports that old eggs do not have any deleterious effect on preference or offspring performance (Pak et al., 1986; Jacob et al., 2006).

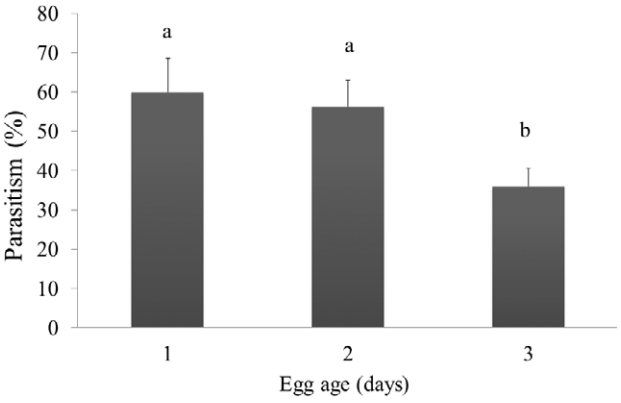

Fig. 2. Percentage parasitism (mean ± SE) of 1-, 2- and 3-day-old eggs of *Spodoptera frugiperda* by *Telenomus remus* in a choice bioassay. Bars with different letters indicate significant differences between treatments (n = 15; Duncan $P < 0.05$).

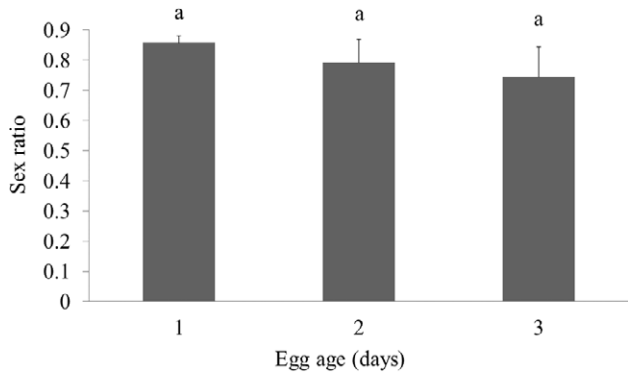

Fig. 4. Sex ratio (mean ± SE) of *Telenomus remus* that emerged from 1-, 2- and 3-day-old eggs of *Spodoptera frugiperda* parasitized in a no-choice bioassay. Bars with the same letters indicate non-significant differences between treatments (n = 10; Kruskal-Wallis $P > 0.05$).

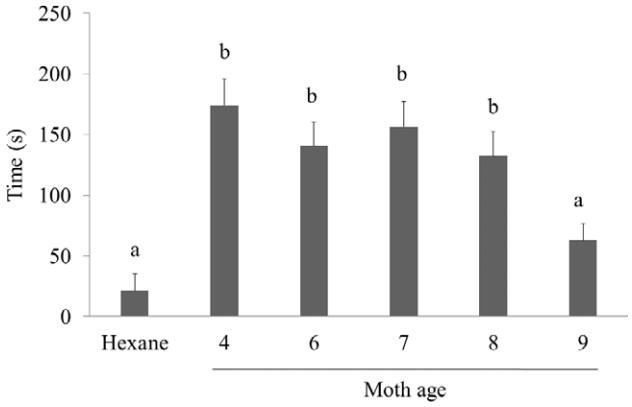

Fig. 5. Time (mean ± SE) *Telenomus remus* females spent on filter papers impregnated with hexane (control) and extracts of 1-day-old eggs laid by *Spodoptera frugiperda* of different ages. Bars with different letters indicate significant differences between treatments (n = 20; Dunn $P < 0.05$).

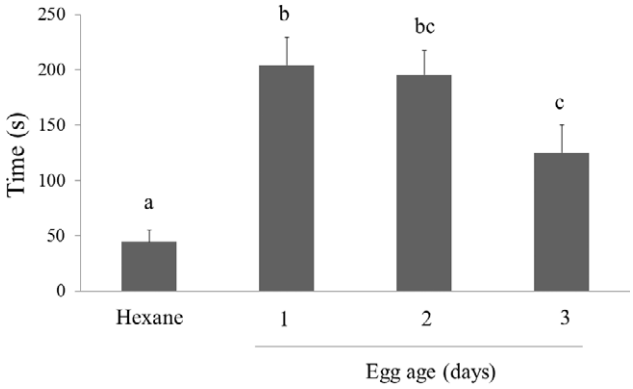

Fig. 6. Time (mean ± SE) *Telenomus remus* females spent on filter papers impregnated with hexane (control) and extracts of 1-, 2- and 3-day-old eggs of *Spodoptera frugiperda*. Bars with different letters indicate significant differences between treatments (n = 20; Duncan $P < 0.05$).

This study revealed that the parasitoid *T. remus* prefers to parasitize young hosts (1- and 2-day old eggs). The old hosts (3-day-old eggs) were not only less preferred than young hosts for parasitism, but also less acceptable as the parasitoid parasitized fewer old eggs in no-choice assays (Figs 2 and 3). Percentage of adults emerging from 2- and 3-day old eggs was less than from 1-day old eggs (Fig. 4). These results suggest that *T. remus* females are able to discriminate between the most (1-day-old eggs) and the least suitable (3-day-old eggs) hosts, but are unable to recognize the unsuitability of intermediately aged eggs. These findings are not consistent with the predictions of optimal foraging theory, which predicts that parasitoids prefer hosts that provide the best conditions for offspring performance (Pyke et al., 1977), since *T. remus* does not discriminate 2-day-old eggs, which are not as good as 1-day-old hosts in terms of offspring performance. However, *T. remus* avoids parasitizing 3-day-old eggs, which were the least suitable of the different ages of eggs tested. In this case, *T. remus* behaviour agrees with optimal foraging theory.

On the other hand, egg aging did not affect the sex ratio of *T. remus* (Fig. 5) or its developmental time. Although a reduction in the proportion of males emerging from old eggs is reported (Sousa & Spence, 2001), this effect is not recorded for other species of Scelionidae, such as *Gryon gallardoi* (Brethes) (Da Rocha et al., 2006) and *Telenomus isis* (Hymenoptera: Scelionidae) (Bruce et al., 2009).

Suitable egg age depends on host species as embryo development may vary among species (Pak et al., 1986; Monje et al., 1999; Chabi-Olaye et al., 2001). This may account for the differences between the results obtained in this and other studies in which *T. remus* parasitized the eggs of other species of *Spodoptera* (Gerling & Schwartz, 1974; Dass & Parshad, 1983).

The parasitoid *T. remus* was arrested by hexane extracts of *S. frugiperda* eggs (Fig. 6). Although all the hexane egg extracts invoked arrestment behaviour, *T. remus* spent longer on filter paper impregnated with extracts of 1- and 2-day old than with 3 day-old eggs (Fig. 6). This arrestment response was equal to the preference of *T. remus* for 1- and 2-day-old eggs. Therefore, it is possible that the egg kairomones associated with 3-day-old eggs were altered or reduced.

Gazit et al. (1996) report a residence time for *T. remus* on extracts derived from 1-day-old *S. frugiperda* eggs of 195 ± 19 s (mean ± SE). We obtained similar averages for extracts of 1- and 2-day-old eggs, which were 204 ± 24 s and 195 ± 22 s, respectively. The residence time was significantly lower, 125 ± 24 s, on extracts of 3-day-old eggs.

Qualitative or quantitative changes in the chemical composition of the surface of 3-day-old *S. frugiperda* eggs may be the cue used by *T. remus* to avoid ovipositing in old hosts. That is, the lower percentage parasitism of 3-day-old eggs by *T. remus* could be partly due to the detection of chemicals on the surface of eggs.

Chemicals associated with eggs are well known to induce arrestment behaviour in Scelionidae parasitoids (Strand & Vinson, 1983; Bin et al., 1993). They may play a role in host recognition and act as short-range attractants (Norlund et al., 1987; Boo & Yang, 2000).

Hexane extracts may not contain the host recognition kairomone from *S. frugiperda* eggs as they consist of heavy proteins that are associated with moth scale compounds, which are arrestants (Strand & Vinson, 1983; Gazit et al., 1996). A preliminary bioassay of the arrestment recorded for 1-day-old eggs laid by 9-day-old moths did not induce arrestment in *T. remus* (Fig. 5). We suppose that the lack of arrestment in this case is due to the reduction in the number of scales on old moths. Hence, 3-day-old egg extracts may contain fewer moth scale residues and are therefore less effective at inducing arrestment behaviour in *T. remus*.

Nevertheless, not only contact chemical cues are important for egg parasitoids in recognizing suitable hosts, but also physical characteristics, such as the hardening of the chorion, which hampers the penetration of a parasitoid's ovipositor (Leibee et al., 1979; Irvin & Hoddle, 2005).

The ability to parasitize eggs of a wide range of ages is one attribute that might confer a higher potential for controlling pests in the field. In the case of *T. remus*, results suggest that location of *S. frugiperda* eggs can be critical for eggs older than 2 days, and may also limit percentage of parasitism and emergence.

Furthermore, the results of this study may help in improving the mass rearing of *T. remus*. We show that in order to maintain a high productivity in mass rearing it is important to offer 1-day-old *S. frugiperda* eggs to *T. remus*.

ACKNOWLEDGEMENTS. We are grateful to V.W. Wekesa for reviewing the English and INCT – Semioquímicos para a Agricultura, CNPq and Fapesp for financial support.

REFERENCES

Bai B., Luck R.F., Forster L., Stephens B. & Janssen J.A.M. 1992: The effect of host size on quality attributes of the egg parasitoid, Trichogramma pretiosum. *Entomol. Exp. Appl.* **64**: 37–48.

Barret M. & Schimdt J.M. 1991: A comparison between the amino acid composition of an egg parasitoid wasp and some of its hosts. *Entomol. Exp. Appl.* **59**: 29–41.

Beevers M., Lewis W.J., Gross H.R. & Nordlund D.A. 1981: Kairomones and their use for management of entomophagous insects: X. Laboratory studies on manipulation of host-finding behavior of Trichogramma pretiosum Riley with a kairomone extracted from Heliothis zea (Boddie) moth scales. *J. Chem. Ecol.* **7**: 635–648.

Bin F., Vinson S.B., Strand M.R., Colazza S. & Jones Jr. W.A. 1993: Source of an egg kairomone for Trissolcus basalis, a parasitoid of Nezara viridula. *Physiol. Entomol.* **18**: 7–15.

Boo K.S. & Yang J.P. 2000: Kairomones used by Trichogramma chilonis to find Helicoverpa assulta eggs. *J. Chem. Ecol.* **26**: 359–374.

Borges M., Costa M.L.M., Sujii E.R., Cavalcanti M., Redígolo G.F., Resck T.S. & Vilela E.F. 1999: Semiochemical and physical stimuli involved in host recognition by Telenomus podisi (Hymenoptera: Scelionidae) toward Euchistus heros (Heteroptera: Pentatomidae). *Physiol. Entomol.* **24**: 227–233.

Bruce A.Y., Schulthess F. & Mueke J. 2009: Host acceptance, suitability, and effects of host deprivation on the west African egg parasitoid Telenomus isis (Hymenoptera: Scelionidae) reared on east African stemborers under varying temperature and humidity regimens. *Environ. Entomol.* **38**: 904–919.

Cave R.D. 2000: Biology, ecology and use in pest management of Telenomus remus. *Biocontrol News Inf.* **21**: 21–26.

Chabi-Olaye A., Schulthess F., Poehling H.M. & Borgemeinster C. 2001: Factors affecting the biology of Telenomus isis (Polaszek) (Hymenoptera: Scelionidae), an egg parasitoid of Cereal stem borers in West Africa. *Biol. Control* **21**: 44–54.

Da Rocha L., Kolberg R., Mendonça Jr M.S. & Redaelli L.R. 2006: Effects of egg age of Spartocera denticentris (Berg) (Hemiptera: Coreidae) on parasitism by Gryon gallardoi (Brethes) (Hymenoptera: Scelionidae). *Neotrop. Entomol.* **35**: 654–659.

Dass R. & Parshad B. 1983: Rearing of important lepidopterous pests on known artificial diet and screening for preferred hosts of parasite, Telenomus remus Nixon (Hymenoptera: Scelionidae). *Entomol. Res. (B)* **8**: 89–92.

Gazit Y., Lewis W.J. & Tumlinson J.H. 1996: Arrestment of Telenomus remus (Hymenoptera: Scelionidae) by a kairomone associated with eggs of its host, Spodoptera frugiperda (Lepidoptera: Noctuidae). *Biol. Control* **6**: 283–290.

Gerling D. & Schwartz A. 1974: Host selection by Telenomus remus, a parasite of Spodoptera littoralis eggs. *Entomol. Exp. Appl.* **17**: 391–396.

Greene G.L., Leppla N.C. & Dickerson W.A. 1976: Velvetbean caterpillar. A rearing procedure and artificial medium. *J. Econ. Entomol.* **69**: 447–448.

Hilker M. & Meiners T. 2002: *Chemoecology of Insect Eggs and Egg Deposition*. Blackwell, Berlin, 390 pp.

Irvin N.A. & Hoddle M.S. 2005: Determination of Homalodisca coagulate (Hemiptera: Cicadellidae) egg ages suitable for oviposition by Gonatocerus ashmeadi, Gonatocerus triguttatus, and Gonatocerus fasciatus (Hymenoptera: Mymaridae). *Biol. Control* **32**: 391–400.

Jacob H.S., Joder A. & Batchelor K.L. 2006: Biology of Stethynium sp. (Hymenoptera: Mymaridae), a native parasitoid of an introduced weed biological control agent. *Environ. Entomol.* **35**: 630–636.

Kennedy J.S. 1978: The concepts of olfactory arrestment and attraction. *Physiol. Entomol.* **3**: 91–98.

Leibee G.L., Pass P.C. & Yeargan K.V. 1979: Development rates of Patasson lameerei (Hym.: Mymaridae) and the effect of host egg age on parasitism. *Entomophaga* **24**: 345–348.

Liu S.S., Zhang G.M. & Zhang F. 1998: Factors influencing parasitism of Trichogramma dendrolimi on eggs of the Asian corn borer, Ostrinia furnacalis. *BioControl* **43**: 273–287.

Monje J.C., Zebitz C.P. & Ohnesorge B. 1999: Host and host age preference of Trichogramma galloi and T. pretiosum (Hymenoptera: Trichogrammatidae) reared on different hosts. *J. Econ. Entomol.* **92**: 97–103.

Moreno F., Pérez-Moreno I. & Marco V. 2009: Effects of Lobesia botrana (Lepidoptera: Tortricidae) egg age, density, and UV treatment on parasitism and development of Trichogramma cacoeciae (Hymenoptera: Trichogrammatidae). *Environ. Entomol.* **38**: 1513–1520.

Narváez C.E.G. & Zocco J.L. 1996: Control integrado de Spodoptera frugiperda (Smith) utilizando Telenomus remus (Nixon) em Zea mays L. *Invest. Agric*. **1**: 1–5.

Norlund D.A., Strand M.R., Lewis W.J. & Vinson S.B. 1987: Role of kairomones from host accessory gland secretion in host recognition by Telenomus remus and Trichogramma pretiosum, with partial characterization. *Entomol. Exp. Appl.* **44**: 37–43.

Pak G.A., Buis C.E.M., Heck I.C.C. & Hermans M.L.G. 1986: Behavioural variations among strains of Trichogramma spp.: Host-age selection. *Entomol. Exp. Appl.* **40**: 247–258.

Pyke G.H., Pulliam H.R. & Charnov E.L. 1977: Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.* **52**: 137–154.

Reznik S.Y. & Umarova T.Y. 1990: The influence of host's age on the selectivity of parasitism and fecundity of Trichogramma. *Entomophaga* **35**: 31–37.

Romeis J., Shanower T.G. & Madhuri K. 2000: Biology and field performance of Gryon clavigrallae (Hymenoptera: Scelionidae), an egg parasitoid of Clavigralla spp. (Hemiptera: Coreidae) in India. *Entomol. Res. (B)* **90**: 253–263.

Ruberson J.R. & Kring T.J. 1993: Parasitism of developing eggs by Trichogramma pretiosum (Hymenoptera: Trichogrammatidae): host age preference and suitability. *Biol. Control* **3**: 39–46.

Schmidt J.M. & Smith J.J.B. 1985: Host volume measurement by the parasitoid wasp Trichogramma minutum: the roles of curvature and surface area. *Entomol. Exp. Appl.* **39**: 213–221.

SCHWARTZ A. & GERLING D. 1974: Adult biology of Telenomus remus (Hymenoptera: Scelionidae) under laboratory conditions. *Entomophaga* **19**: 482–492.

SOUZA J.M. & SPENCE J.R. 2001: Host age and parasitism by Tiphodytes gerriphagus (Hymenoptera: Scelionidae), an egg parasitoid of water striders (Heteroptera: Gerridae). *Ann. Entomol. Soc. Am*. **94**: 681–685.

STRAND M.R. & VINSON S.B. 1983: Analysis of an egg recognition kairomone of Telenomus heliothidis (Hymenoptera: Scelionidae). Isolation and host function. *J. Chem. Ecol.* **9**: 423–432.

STRAND M.R., MEOLA S.M. & VINSON S.B. 1986: Correlating pathological symptoms in Heliothis virescens eggs with development of the parasitoid Telenomus heliothidis. *J. Insect Physiol.* **32**: 389–402.

TUNÇBILEK A.S. & AYVAZ A. 2003: Influences of host age, sex ratio, population density, and photoperiod on parasitism by Trichogramma evanescens Westw. (Hym., Trichogrammatidae). *J. Pest. Sci.* **76**: 176–180.

VINSON S.B. 1976: Host selection by insect parasitoids. *Annu. Rev. Entomol.* **21**: 109–134.

VINSON S.B. 1984: Parasitoid-host relationships. In Bell W.J. & Cardé R.T. (eds): *Chemical Ecology of Insects*. Chapman and Hall, London, pp. 205–233.

VINSON S.B., BIN F. & VET L.E.M. 1998: Critical issues in host selection by insect parasitoids. *Biol. Control* **11**: 77–78.

Received June 14, 2011; revised and accepted July 29, 2011