Arrestment of *Telenomus remus* (Hymenoptera: Scelionidae) by a Kairomone Associated with Eggs of Its Host, *Spodoptera frugiperda* (Lepidoptera: Noctuidae)

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Telenomus remus Nixon females, but not males, were arrested after contacting a kairomone(s) extracted from eggs of *Spodoptera frugiperda* (J. E. Smith). Bioassays were used to characterize the retention of the wasp in an area treated with the kairomone(s). The retention time in the treated area was affected by dose of the kairomone and also by the dimensions of the treated area. Female wasps were most sensitive to the kairomone, and were arrested for a longer period, at the beginning of the scotophase. Maximal response was exhibited by young, 2- to 4-day-old wasps. The wasps also were arrested by a kairomone(s) extracted from whole bodies of adult male or female moths.

**Key Words:** *Telenomus remus*; *Spodoptera frugiperda*; contact kairomones; egg parasitoid; fall armyworm; photoperiod; semiochemicals.

**INTRODUCTION**

The scelionid *Telenomus remus* Nixon, a wasp endemic to Sarawak and New Guinea, is a solitary egg parasitoid which has been successfully established in Barbados and Montserrat on several *Spodoptera* species (Wojcik et al., 1976). It was introduced into Florida 20 years ago to control the fall armyworm *Spodoptera frugiperda* (J. E. Smith), but apparently was not established (Waddill and Whitcomb, 1982).

The success of egg parasitoids as well as other natural enemies is enhanced by their tendency to remain in an area infested by host insects. This retention is governed largely by their ability to locate their hosts. Egg parasitoids locate hosts by using a variety of signals. However, semiochemicals play a major role in their host foraging strategy (for review see Tumlinson et al., 1992).

Chemicals used by parasitoids of lepidopterous eggs in their search for hosts include both volatiles, with a long-range effect and nonvolatile compounds detected upon contact. Adult and egg stages of the host, as well as the plants on which the moths oviposit, have been investigated as potential sources for these semiochemicals (for review see Noldus, 1989). Volatile stimuli (synomones) from certain plants were preferred by *Trichogramma pretiosum* Riley in an olfactometer and increased its parasitism rate (Nordlund et al., 1985). Host volatiles emitted from female moths increased parasitism by *Trichogramma* spp. (Lewis et al., 1982). These volatiles were thought to be sex pheromones of the host moth. In field tests, a synthetic blend of *Helicoverpa zea* (Boddie) sex pheromone doubled the rate of parasitization by native *Trichogramma* spp. (Lewis et al., 1982). In olfactometer tests synthetic sex pheromones affected the walking behavior of *T. remus* (Nordlund et al., 1983) and *Trichogramma* spp. (Noldus et al., 1991) and increased the wasp's tendency to stay in their odor field. Synthetic sex pheromone also increased the landing rate of *T. pretiosum* in wind tunnel tests (Noldus et al., 1990). However no parasitoid of moth eggs has been observed to be attracted to volatiles emitted by host adults or eggs.

Laing (1937) demonstrated that *Trichogramma evanescentia* Westwood failed to find its host eggs from a very short distance. On the other hand, Laing (1973) clearly demonstrated the presence of a kairomone which was detected upon contact. Contact kairomones were involved in the specific behavioral response performed by a wasp prior to parasitization. Upon contact with host eggs, or within their immediately surrounding area, the parasitoid begins an examination behavior. This behavior includes an arrestment response, followed by host recognition, leading to host accep-

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tance. Several investigations have been conducted on the role of kairomones involved in that examination behavior (Lewis et al., 1972; Jones et al., 1973; Beevers et al., 1981; Gross et al., 1984; Noldus and van Lenteren, 1985; Gardner and van Lenteren, 1986; Zaborski et al., 1987; Thomson and Stinner, 1988; Shu et al., 1990).

The first reaction of an egg parasitoid when encountering a host site is arrestment, that is, a change from random walking to an intense directed examination. Several investigations have characterized this response. Both moth scales and eggs have been investigated as the sources of the arrestment kairomones. Scales of several moth species are abundant in the vicinity of the deposited eggs. T. pretiosum was retained on a surface treated with an extract of H. zea scales, and its retention was related to the area of the treated surface (Beevers et al., 1981). No long-range attractant has been found in scales of three lepidopteran hosts of T. evanescens, indicating that these kairomones may act mainly through physical contact (Noldus and van Lenteren, 1985). Gardner and van Lenteren (1986) demonstrated that T. evanescens significantly decreased its activity and walking while increasing its turning behavior upon contacting an area treated with scale kairomone. Similar results were obtained with Trichogramma minutum Riley (Zaborski et al., 1987). Thompson and Stinner (1988) found that the anatomical origin of moth scales does not affect the response of T. pretiosum and Trichogramma exiguum Pinto and Platner. It was found that extract of scales contained a kairomone that increased parasitism rates by Trichogramma, both in the laboratory and in the field (Lewis et al., 1972; Gross et al., 1984). Chemical analysis revealed that tricosane, isolated from H. zea scales, is the most effective compound directing T. evanescens to its host's eggs (Jones et al., 1973). Scales of Ostrinia nubilalis (Hubner) contain 13,17-dimethylnonatriacon- tane which arrests Trichogramma nubilale Ertle and Davis (Shu et al., 1990).

Parasitoids modify their biology according to that of their host. Many aspects of insect biology are governed by the photoperiod and appear to be under control of a circadian rhythm (Saunders, 1982). In most of the studies on kairomones, host location by egg parasitoids has been considered to be a diurnal activity and thus bioassayed during the photophase. Recently, several studies have demonstrated a circadian activity and an existence of biological clocks in egg parasitoids. Idoine and Ferro (1990) demonstrated diurnal rhythm of oviposition in the eulophid, Eovum putti Grissel. A circadian locomotion rhythm, with a diurnal activity, was found in Trichogramma brassicae Bezdekenko (Allemand et al., 1994). This evidence suggests the possibility that the foraging behavior may also be restricted to a circadian rhythm, which is synchronized to that of the host. Thus, in the case of moth egg parasitoids, nocturnal host foraging should be considered.

This research focused on the arrestment response of T. remus caused by a contact kairomone associated with eggs of S. frugiperda. A bioassay was developed to examine the response and to study: (a) the sensitivity of the wasp to its host's kairomone; (b) the effect of the photoperiod on the arrestment response; (c) the response as a function of wasp age; and (d) the origin of the arrestment kairomone.

MATERIALS AND METHODS

Insects

Hosts. S. frugiperda eggs and pupae were obtained from a culture reared on an artificial diet (Burton, 1969) in the Insect Attractants, Behavior, and Basic Biology Research Laboratory, USDA-ARS, Gainesville, Florida. Pupa were sexed and females and males were placed in separate 20 × 20 × 20 cm³ plexiglass cages at 26 ± 1°C and 80 ± 2% RH, under a 10:14 h dark:light regime. Moths were supplied with a 10% sugar solution.

Parasitoids. T. remus were cultured on eggs of S. frugiperda. One to three hundred wasps were introduced into 20 × 2 cm glass tubes containing 1500–3000 eggs, 3 to 30 h old. Small strips of paper towel, soaked with honey, were provided as a food source. The tubes were plugged with cotton and incubated at 25 ± 2°C and 70 ± 5% RH, under a 10:14 h dark:light regime. Prior to bioassays, naive wasps with no previous experience of oviposition or contact with host eggs or related substances were placed in a 260-ml Nunc disposable tissue culture flask, supplied with honey and water. After 2–4 h, the females used for bioassays were collected with an aspirator under a stereomicroscope.

Bioassays

For bioassays, a 1 × 1 cm² filter paper (Whatman, No. 1) served as the treated surface. The square was prewashed with hexane and held horizontally in the air by a microalligator clip, attached to one of its corners. Twenty microliters of the investigated substance, dissolved in hexane, was applied to the paper. After drying for 15 min at room conditions, it was placed in an open cover of a petri dish (9.5 cm), on the center of a circular filter paper (Whatman, No. 1). All bioassays were performed using naive female wasps. One individual was placed with the aid of a camel's hair brush on the treated surface. The arrestment response was determined by monitoring the retention of the wasp on the treated surface, using a stopwatch. The measurement began when the wasp touched the treated surface and
was terminated when it left. If the wasp returned to the treated surface within 20 s, this period of time was included in the response and the timing was continued. Only wasps which remained on the treated surface for at least 2 s were scored. If a wasp stayed on the treated surface for less than 5 s it was introduced two more times and the longest retention time was recorded. Each treatment was tested with 6–9 individual wasps.

Unless otherwise indicated, bioassays were conducted using 2.5-day-old females, 4 to 6 h into their photophase, at room temperature and under fluorescent lighting. Bioassays in the scotophase were performed under a dim red light.

Statistical analysis was performed by analysis of variance (ANOVA). Differences between means were tested using Fisher’s least significant difference (LSD) test at P = 0.05 or by a two-sample t-test, with the Number Cruncher Statistical System (Version 5.1) statistical analysis package.

Extracts

Host eggs. Clutches of 3- to 12- h-old S. frugiperda eggs deposited on a paper towel were collected by cutting the paper around each clutch. Eggs were weighed and placed in a 20-ml glass vial containing hexane at a concentration of 150 mg eggs/ml. The hexane was collected by a pipette after 6 min, and the extraction repeated with the same volume of hexane for another 6 min. The combined extracts were concentrated under nitrogen to 1.5 mg egg equivalents/ml.

Moths. Adult S. frugiperda (1.5- to 2.5-day-old) 2 to 4 h into the photophase, were placed in a 125-ml Erlenmeyer flask containing hexane for 15 min at a concentration of 3 moths/ml. The hexane was collected by pipette and filtered through filter paper (Whatman, No. 1). The extraction was repeated with the same volume of hexane for another 6 min. The combined extracts were concentrated under nitrogen to 10 moth equivalents/ml. Female and male moths were extracted separately.

Abdominal tips. S. frugiperda females (1.5- to 2.5-day-old) were dissected 5 h into their photophase. Their eighth and ninth abdominal segments, containing the sex pheromone glands, were excised and placed for 15 min in hexane, 10 gland/ml. One gland equivalent of the extract contained 3.4 ng of the major component (2)-9-tetradecen-1-ol acetate. This was determined by GC analysis, following the procedure described by Tumlinson et al. (1986), using hexadecan-1-ol acetate as an internal standard.

Synthetic Sex Pheromone

A blend of the five synthetic components of the sex pheromone of S. frugiperda was dissolved in hexane at a concentration of 50 µg of total blend per milliliter. The proportion of the components in the blend was the same as that loaded on rubber septa to obtain a release ratio of the compounds similar to that released by calling females: dodecan-1-ol acetate (0.4%); 11-dodecen-1-ol acetate (0.5%); (2)-7-dodecen-1-ol acetate (0.5%); (2)-9-tetradecen-1-ol acetate (84.4%), and (2)-11-hexadecen-1-ol acetate (14.2%) (Tumlinson et al., 1986). These components were obtained from commercial sources and were purified in the Insect Attractants, Behavior, and Basic Biology Research Laboratory, USDA-ARS, Gainesville, Florida (Tumlinson et al., 1986).

RESULTS

Females of T. remus were arrested by a hexane extract of S. frugiperda eggs. The response of a wasp began with a complete halt of movement while vibrating the antennae on the treated surface. After a few seconds, the female began to walk, slowly at first, within the treated surface while tapping its antennae on the paper. Eventually the wasp would begin to “give up,” by departing for brief periods, each less than 1 s, to search the immediate surrounding area. Progressively, its departures increased in duration and distance and the parasitoid walked up to 4 cm away, turned, and walked back. If the wasp did not relocate the treated surface, it continued to turn and walk for up to 20 s until it encountered the treated surface again. This response was terminated when the wasp walked away, began to hop around, and subsequently flew away.

Female wasps were retained on a 1-cm² filter paper, treated with a hexane extract of an average egg clutch (14.7 mg) of S. frugiperda for an average of 195.5 ± 18.9 s (mean ± S.E., n = 11). The retention time on a control filter paper treated with hexane only was 4.8 ± 1.0 s (n = 9). Male wasps were not affected by the extract and remained on the treated area for 2.7 ± 0.4 s (n = 9). The moth’s larvae hatched normally from eggs extracted with hexane. This suggests that the extracted substances were associated mainly with the outer surface of the eggs or their surroundings.

 Arrestment of T. remus occurred in a dose-dependent manner (Fig. 1). A significant arrestment of 44.1 ± 27.6 s (n = 8) was caused by a dose of 0.06 mg egg equivalents, a concentration equal to a single egg (0.0611 ± 0.0111 mg). Higher doses increased the response and 1 mg egg equivalents induced maximal arrestment of 193.1 ± 18.5 s (n = 8). Higher concentrations did not significantly increase this response.

The possibility that wasp arrestment could be affected by differences in the dimensions of the treated surface was examined (Table 1). Wasps were introduced to different sizes of filter papers, treated with a constant dose of 0.5 mg eggs/cm². Their response differed
significantly with the various dimensions. Among treatments with the same area, the retention time increased as the diagonal of the treated paper increased, suggesting that the significant parameter affecting the response was the diagonal of the treated surface and not its area.

These results established the conditions of the bioassay for further characterization of the arrestment response. For convenience, the treated surface's dimensions were $1 \times 1$ cm$^2$, and the concentrations used ranged from 0.1 to 0.5 mg eggs/cm$^2$. Under these conditions, the arrestment of the wasps was significant and yet not maximal, providing the ability to inspect variations. This bioassay was then used to determine: (a) if the response of *T. remus* varied during the photoperiod; (b) if the response depends on the wasp age; and (c) whether the kairomone is located on eggs only.

Wasps were more aggregated and motionless within the rearing tubes during the scotophase than in the photophase. However, activity increased upon transfer from the tube, and a marked arrestment was evoked by exposure to the egg kairomone, as described under Materials and Methods. Thus, the objective of the following experiment was to determine whether the arrestment response of *T. remus* varied during the photoperiod.

The response of *T. remus* to 0.1-mg egg equivalents/cm$^2$ was monitored every 2 h during the photoperiod (Fig. 2). At the beginning of the scotophase, 0 to 30 min after the lights turned off and 2 to 2.5 h later, the arrestment was maximal, with retentions of 327.0 ± 46.5 and 324.4 ± 40.9 s, respectively. During the remainder of the photoperiod, the wasps were retained for less than 200 s. Since the response later into the scotophase was significantly lower, it is unlikely that these differences were caused by the dim red light under which the wasps were assayed. Throughout the entire photoperiod, the retention of the wasps with the control (not shown) was for less than 10 s.

Significant differences in wasp responses during the photophase and the scotophase were further supported by dose–response analysis. Wasps were exposed to serial concentrations of the extract at two times: (a) at 0–2 h into scotophase, when maximal response was exhibited, and (b) at 4–6 h into the photophase, when the least response was shown (see Fig. 2). The results (Fig. 3) indicated a difference between the two time periods. At early scotophase, arrestment was higher in every dose tested. At both times the retention with the control was for less than 10 s (not shown).

Comparison of the doses of *S. frugiperda* egg extract

### TABLE 1

<table>
<thead>
<tr>
<th>The treated surface</th>
<th>Wasp retention time</th>
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<tbody>
<tr>
<td><strong>Dimensions</strong> (mm)</td>
<td><strong>Diagonal</strong> (mm)</td>
</tr>
<tr>
<td>2 × 2</td>
<td>2.83</td>
</tr>
<tr>
<td>4 × 4</td>
<td>5.66</td>
</tr>
<tr>
<td>7 × 7</td>
<td>9.90</td>
</tr>
<tr>
<td>10 × 10</td>
<td>14.14</td>
</tr>
<tr>
<td>20 × 0.5</td>
<td>20.62</td>
</tr>
<tr>
<td>20 × 20</td>
<td>28.28</td>
</tr>
<tr>
<td>40 × 2.5</td>
<td>40.80</td>
</tr>
<tr>
<td>80 × 1.25</td>
<td>80.01</td>
</tr>
</tbody>
</table>

Means with a common letter do not differ significantly according to Fisher's LSD test (P = 0.05).
required to elucidate the minimal and the maximal wasp responses between the two time periods indicated that they were more sensitive to the kairomone during early scotophase. The minimal dose required to induce the response was 0.0125 mg at early scotophase and 0.05 mg at photophase, causing retentions of 23.4 ± 6.127 and 19.0 ± 7.8 s, respectively. Maximal response was induced with a concentration of 0.1 mg at scotophase and 1.0 mg at photophase.

The second objective was to determine whether arrestment depends on wasp age. Wasps of different ages were assayed at the two time periods mentioned above with a low dose of 0.1 mg egg extract (Fig. 4). The wasps were 2.5 to 17.5 days old at the photophase and 2 to 32 days old at scotophase (under our laboratory conditions the average life span of T. remus was ca. 25 to 30 days).

The results indicated that maximal arrestment occurred at early scotophase. At the age of 3 and 4 days, the wasps responded for 288.1 ± 56.2 and 323.1 ± 55.2 s, respectively, when 2 of 10 wasps did not respond and remained on the treated surface less than 10 s. At 6 days the wasp arrestment dropped significantly to 74.1 ± 34.7 s, and only 4 of 10 wasps responded. That response decreased further with age. These results suggest that the sensitivity of wasps to the kairomone is age dependent. During photophase wasp response was significantly lower than during scotophase and with every age tested, only 5 of 10 wasps responded. Wasps 2.5 and 3.5 days old at photophase were arrested for 89.6 ± 20.3 and 71.6 ± 29.6 s, respectively.

The possibility that the moth of a host species is the origin of the arrestment kairomone for egg parasitoids was investigated using the bioassay. Two possible origins were examined: (a) moth scales and (b) moth sex pheromone. Observations of the wasp behavior indicated that female wasps were arrested on a paper towel on which adults S. frugiperda had walked. Therefore, T. remus responses to egg extract was compared with their response to hexane extracts of the paper towel surrounding the host eggs. The results indicated that 1-mg egg extract arrested the wasps for 138.9 ± 23.7 s (n = 8) while the paper towel extract of similar area induced a retention of 77.4 ± 22.9 s (n = 8). No significant response (4.2 ± 1.1 s, n = 6) to an extract of a clean paper towel was observed. Hence, it appears that the kairomone comes from moths and is adsorbed on eggs and the substrate on which they are deposited. That possibility was further examined with hexane extracts of the whole moth body (Fig. 5). The wasps were arrested by a concentration equivalent to 0.0002 male and female moths for 108.4 ± 13.9 and 144.6 ± 32.6 s, respectively. Activity also was found in extracts of the abdominal tip of the female moths, where the sex pheromone gland is located. A crude hexane extract, equivalent to 0.01 gland at photophase (containing 0.034 ng of the major component, (Z)-9-tetradecen-1-ol acetate), elicited a response of 89.4 ± 20.1 s. The five-component blend of S. frugiperda sex pheromone (Tumlinson et al., 1986) was bioassayed in serial doses, ranging from 10⁻⁵ to 1000 ng. Only 10⁻¹ ng caused a limited though not significant retention of 22.8 ± 13.2 s (see "Blend" in Fig. 5).

**DISCUSSION**

Females of T. remus were arrested by a kairomone(s) associated with their host's eggs. The females were
that males wait on parasitized eggs for females to filterpaper.

while the bioassay in this study was performed on flat to the moth egg, was present (Nordlund response occurred only when a spherical object, similar described in this study. In addition, the recognition extract with hexane by the extraction procedure Nordlund et al., (1987). The egg recognition kairomone consists of heavy proteins, secreted from the accessory glands of the moth (Strand and Vinson, 1982, 1983; Nordlund et al., 1987) and these proteins could not be extracted with hexane by the extraction procedure. The arrestment kairomone investigated in this study was probably not related to the egg recognition kairomone for T. remus, found on the eggs of S. frugiperda by Nordlund et al. (1987). The egg recognition kairomone consists of heavy proteins, secreted from the accessory glands of the moth (Strand and Vinson, 1982, 1983; Nordlund et al., 1987) and these proteins could not be extracted with hexane by the extraction procedure described in this study. In addition, the recognition response occurred only when a spherical object, similar to the moth egg, was present (Nordlund et al., 1987), while the bioassay in this study was performed on flat filter paper.

T. remus males failed to respond to hexane extracts of moth eggs. This might be explained by the observation that males wait on parasitized eggs for females to emerge (Schwartz and Gerling, 1974). This occurs at least 10 days after the moth eggs were deposited. The females, on the other hand, must locate fresh eggs as suitable hosts (Gerling and Schwartz, 1974).

During the arrestment response of T. remus, and as reported for other wasps (Gardner and van Lenteren, 1986), the parasitoids usually leave the treated paper for short periods and find their way back by walking in a circular path. When T. remus responds to the kairomone, it occasionally continues its circular pathway even if it passes within 1 mm (one wasp body length) of the apex of the treated paper. This reduces the possibility of involvement of volatile attractants, suggesting that arrestment happens only upon a wasp's physical contact with the kairomone. One explanation for the turning locomotion is that it is the mechanism guiding the wasp back to its host. Beevers et al. (1981) showed that T. pretiosum is more likely to return to a treated surface as its area increases. The present study further supports this (Table 1). The response induced in T. remus by a treated, 80 × 1.25 mm rectangle was four times greater than the response caused by a treated 2 × 2 mm square. Wasps tended to lose small treated surfaces once they departed, probably because the turns they performed were too wide. When the treated area was enlarged to 20 × 20 mm² wasp responses increased, but only to 64% of the responses induced by the long rectangle. This suggests that the significant parameter affecting the response is the diagonal of the treated paper and not its area.

The response and sensitivity of T. remus to egg extract varied during the photoperiod, with a significant increase during the beginning of the scotophase (Figs. 2 and 3). This response varied with wasp age, with the greatest response exhibited by young (2- to 4-day-old) females (Fig. 4). It is not clear to what degree this response is correlated to host searching and oviposition activity in the field. Results from this study suggest the possibility that T. remus may forage for hosts at scotophase. One of the very few observations of nocturnal oviposition activity in an egg parasitoid was reported for another Telenomus sp. (Arakaki, 1990). This wasp has a phoretic relationship with a tussock moth Euproctis sp. It attacks its host eggs at the beginning of the scotophase, soon after they are deposited. Although phoresy in T. remus has not been reported, nocturnal host foraging in this wasp should be considered, since its host is a nocturnal moth.

T. remus responded to an extract of paper towel ing that was exposed to S. frugiperda moths. It also responded to a hexane body wash of moths (Fig. 5). Therefore, it is likely that its arrestment kairomone originated from the moth rather than from the eggs. Scales from several species of moths are known to contain contact kairomones that arrest egg parasitoids.

FIG. 5. Arrestment response of T. remus to the following extracts: 1 mg S. frugiperda egg equivalent (Eggs); whole body extract of S. frugiperda females and males 0.0002 moth equivalent (Female and Male); abdominal tip of female moth 0.01 pheromone gland equivalent, extracted at photophase and containing 0.034 ng/gland of the pheromone major component (Z)-9-tetradecen-1-ol acetate (PG); 0.1 ng of a five-component synthetic blend of the S. frugiperda sex pheromone (Blend), and hexane (Control). Each bar represents a mean ± SE of eight wasps tested.
(Jones et al., 1973; Shu and Jones, 1989). Since the wasps used in this study responded to a very low concentration of the moth body extract, it is possible that T. remus response was elicited by moth scales associated with S. frugiperda eggs. Also, it is possible that the same kairomone(s) from moth scales was adsorbed by the substrate surrounding the eggs.

Several studies have focused on the response of egg parasitoids to host sex pheromones and to calling female moths (Lewis et al., 1982; Nordlund et al., 1983; Noldus et al., 1990). However, these works have focused on the effect of these compounds as volatile cues and not as contact kairomones. In our study, extracts from the abdominal tip of female S. frugiperda moths and the male body evoked a high arrestment response in T. remus. These results and the fact that the synthetic sex pheromone blend failed to evoke a response exclude the possibility that the arrestment kairomone is restricted to the moth sex pheromone gland. However, it is possible that the moth sex pheromone affects other activities of T. remus not observed in our bioassays. Our results suggest the involvement of other substances which are present on the scales and the abdominal tip in the arrestment. It is not clear whether the kairomone found on the scales of both sexes of S. frugiperda, the abdominal tip of the female moths, and their eggs is the same compound.

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