

KAIROMONES AND THEIR USE FOR MANAGEMENT OF ENTOMOPHAGOUS INSECTS: II. MECHANISMS CAUSING INCREASE IN RATE OF PARASITIZATION BY *Trichogramma* spp.^{1,2,3}

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Abstract—When the effect of the kairomone, tricosane, on parasitization by *Trichogramma achaeae* Nagaraja and Nagarkatti of eggs of *Heliothis zea* (Boddie) was studied in petri dish tests, the greatest percentage parasitization ($\bar{X} = 64\%$) was obtained if the entire filter paper was treated. Treatment of smaller areas (about the eggs) resulted in decreased parasitism. In the greenhouse, highest parasitization ($\bar{X} = 71\%$) by *T. pretiosum* (Riley) of *H. zea* eggs placed on pea seedlings grown in pie pans was obtained if the whole pan was treated; lowest parasitism ($\bar{X} = 29\%$) occurred when the pans were untreated. Parasitization was intermediate ($\bar{X} = 52\%$) in other pans treated only at selected spots. Dissections of *H. zea* eggs collected from kairomone-treated and untreated field plots revealed that eggs of *Trichogramma* spp. were more efficiently distributed (less superparasitism) among host eggs in treated plots. These kairomones increase parasitization of *Trichogramma* spp. by releasing and continuously reinforcing an intensified searching behavior rather than by attracting and guiding the parasite directly to the host.

Key Words—*Trichogramma achaeae*, *Heliothis zea*, biological control, kairomones, pest management, parasitoids, host finding, insect behavior, pheromones, behavior chemicals.

¹ Hymenoptera: Trichogrammatidae.

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INTRODUCTION

The results of the previous report in this series demonstrated that field plot application of tricosane or similar appropriate kairomone(s) resulted in increased rates of parasitization by certain *Trichogramma* spp. (Lewis et al., 1975). It was also demonstrated that the kairomone did not have to be limited to the immediate vicinity of the host eggs, but increased parasitization when applied by blanket spraying of the material throughout the plot. These data suggested that the kairomone functioned primarily as a releaser to elicit a more intensified search pattern in treated areas rather than as a trail substance or attractant which might guide parasites to host eggs. The present studies were designed to elucidate the behavior modification(s) causing increased parasitization.

METHODS AND MATERIALS

Petri Dish Test

Comparative evaluations were made of rates of parasitism by *T. achaeae* Nagaraja and Nagarkatti of *Heliothis zea* (Boddie) eggs in petri dishes with different treatment patterns. The bottom of each 150 × 15-mm petri dish was covered with a piece of 13.8-cm Whatman No. 1 filter paper which was marked with a pencil at 6 different locations in a pattern which would allow maximum separation of the eggs. The kairomone, tricosane, was applied to the paper at the rate of 50 ng/cm² using a hypodermic syringe. Each piece of filter paper was treated according to 1 of 4 patterns: circles of 1.2 cm, 2.0 cm, or 3.7 cm in diameter around each designated egg location, or treatment of the entire piece of paper. Eggs were attached to the papers at each of the 6 locations using a spot of rubber cement. Two freshly emerged *T. achaeae* females were introduced into each dish and allowed to search for 45 min, after which the eggs were dissected to determine parasitization according to the method described by Lewis and Redlinger (1969). For each treatment pattern 10–20 replications of this test were conducted.

Greenhouse Studies

A comparison was made in the greenhouse of the parasitization rates by *T. pretiosum* (Riley) of the eggs of *H. zea* placed on plants having different treatment patterns. Crowder pea seedlings grown in 22.8-cm pie pans were used. The 3 treatment patterns evaluated were (1) complete coverage application of the kairomone (blanket treatment), (2) application at restricted locations (partial treatment), and (3) untreated controls. An aerosol chroma-

tograph spray device was used as described by Lewis, Jones, and Sparks (1972) to apply the kairomone. The blanket treatment was accomplished by putting 10 pans of peas in a group and spraying them all at once at a rate of $10 \mu\text{g}$ of tricosane in 1 ml hexane/pan (ca. 26 ng/cm^2). The partial treatment was accomplished by using wrapping paper as a shield. The paper shield was designed so that it could be held over a group of 10 pans. There were 10 groups of 5 holes (3 cm in diam) in the shield arranged so that each group of holes would be directly above 1 of the 10 pans. The 5 holes were evenly spaced over the pan. The area under each hole was marked with a small piece of masking tape. The spraying was done in the same manner as with the blanket spraying, except that the shield allowed the treatment to occur only at the 5 designated locations for each pan. Thus, partially treated pans received the same amount of kairomone per unit of treated area as the blanket-treated pans.

Eggs were applied to the plants by hand, using a camel's hair brush moistened with saliva. 2 eggs were placed in each of 5 treated and 5 untreated locations in the partially treated pans, resulting in a total of 20 eggs/pan. 20 eggs were placed in similar areas of the blanket-treated and control pans. 20 replications (pans) were prepared for each of the 3 treatments, and the pans were arranged in a randomized complete block design with interspacings of ca. 15.2 cm within replications and ca. 0.6 m among replications.

Newly emerged females of *T. pretiosum* (6/pan) were released from 2-dram shell vials placed in the center of each pan.

The eggs were collected after 1 h exposure to the parasites and dissected to determine percent parasitization. Arcsin transformations were made for the percentages, and an analysis of variance was conducted. The means were separated by Duncan's multiple range test.

Distribution of Parasite Eggs, Small Plots

When dissecting host eggs to determine parasitization, a record was kept of the number of parasite eggs per host egg. Occasionally as many as 12 parasite eggs were found in a single host egg, leading us to believe that a significant increase in the percent of parasitization could be obtained simply by achieving a more efficient distribution of the parasite eggs. Subsequent experiments were conducted to determine whether kairomones affect the distribution of parasite eggs.

Plots, 1 row \times 3.0 m, were selected in a soybean field. Pairs of plots were arranged on 2 parallel rows separated by 2 interspacing rows (50.8-cm rows). A 1.5-m space was left between plots on the same row. Plots in each pair were designated as treated or control in an alternating pattern. A total of 10 pairs of plots were used.

The treatment consisted of a 1/1000 dilution of a standard moth scale hexane extract eluant (Jones et al. 1973) applied at the rate of 1 ml/30.5 cm of row using a pneumatic sprayer (Nordlund et al. 1974). *H. zea* eggs were applied by hand at the rate of 40 eggs/plot, using Plantgard as an adhesive. Control plots were not sprayed, but eggs were applied in the same manner. All parasitization was by naturally occurring parasites.

The eggs were collected after ca. 20 h and dissected to determine parasitization. The experiment was repeated on the following day. The data for both days were combined to give a total of 10 replications.

The levels of parasitization which would have occurred with a random parasite egg distribution was calculated on the basis of the mean number of stings observed per host egg, as described by Wadley (1967). Based on unpublished personal observations that *Trichogramma* spp. most frequently deposit 2 eggs/sting per *H. zea* egg, the number of stings was considered to be 1/2 the total number of parasite eggs. The ratio of percent random parasitization to percent observed parasitization (*R/O*) was taken as a measure of the efficiency of the distribution. The lower the *R/O*, the more efficient the distribution. Significance was determined by a paired *t* test.

Distribution of Parasite Eggs, Large Plots

Plots 15.2 m long and 40 rows wide were marked in a soybean field using plastic flagging. There were 6.1-m spacings between plots. Treated plots were blanket-sprayed with a 1/1000 dilution of the hexane eluate of the moth scale extract (Jones et al. 1973) at a rate of 2 ml/30.5 cm of row using a pneumatic sprayer (Nordlund et al. 1974). Control plots received no treatment. Eggs were placed on 10 sample subplots, 3.0 m × 1 row, randomly distributed about the plot. The eggs were placed by hand using Plantgard (Nordlund et al. 1974). There were 4 replications of each treatment, and parasitization was evaluated on 3 different days. Eggs were collected after ca. 20 h exposure to the naturally occurring parasites and dissected to determine degree of parasitization. The data were totalled for the 3 days, and the *R/O* was calculated as above. Significance was determined by a paired *t* test.

RESULTS

Petri Dish Test

The results of the laboratory test (Table 1) indicated that the heaviest parasitization ($\bar{X} = 64\%$) occurred when the entire piece of filter paper had been treated. Progressively lower rates of parasitization occurred as the area

TABLE 1. PERCENT PARASITIZATION OF *H. zea* EGGS BY *T. achaeae* IN PETRI DISHES WITH DIFFERENT TREATMENT PATTERNS WITH TRICOSANE (\pm SE)^a

Day	Diameter of treated circle, 6 locations/dish			Whole dish treatment
	1.2 cm	2.0 cm	3.7 cm	
1	25 \pm 12	30 \pm 9	40 \pm 12	
2		39 \pm 11	49 \pm 8	64 \pm 10

^a 10 replications of each test on each day.

of treatment was decreased, with a mean of 25% parasitization being recorded when the treated areas consisted of circles only 1.2 cm in diameter. The test results demonstrate that the kairomone stimulated a more effective searching behavior rather than acting as an attractant, guiding parasites directly to the host. Treating the entire substrate would be detrimental in the case of an attractant.

Greenhouse Test

The data from this experiment (Table 2) supported those from the petri dish test. Best parasitization ($\bar{X} = 71\%$) was obtained with treatment of the entire pan, while the lowest parasitization ($\bar{X} = 29\%$) occurred in the control pans. Parasitization in the partially treated pans ($\bar{X} = 52\%$) was intermediate between that of the untreated and fully treated pans. Comparison of parasitization of eggs located on the treated and untreated areas of the partially treated pans showed higher parasitism in the treated areas of these pans

TABLE 2. MEAN PERCENT PARASITIZATION OF *H. zea* EGGS BY *T. pretiosum* ON PANS OF PEA SEEDLINGS COMPLETELY, PARTIALLY, OR UNTREATED WITH A MOTH SCALE EXTRACT

Complete	Partial		Control
	Treated areas	Overall	
71 ^a	57 ^b	52 ^a	29 ^a

^a Means are significantly different ($P = 0.01$).

^b Means are significantly different ($P = 0.05$).

($\bar{X} = 57\%$; $\bar{X} = 47\%$). The average parasitization within the treated areas of the partially treated pans was lower than the parasitism recorded for the completely treated pans. However, parasitization in the untreated areas of the partially treated pans was higher than that in the control pans.

These relationships are exactly those that would be expected with a host-seeking stimulant. Treatment of the entire pan should result in the quickest activation of the maximum number of females, and the response should be reinforced and maintained throughout the pan. Parasitism in untreated pans would be expected to be very poor because the parasites receive no stimulation except that derived from random contact with eggs. The number of females activated and the rapidity with which activity occurs in the partially treated pans should be proportional to the amount of treated to untreated area in the pans and the rate at which the wasps come into contact with the treated surfaces. Therefore, fewer parasites are activated and the activation rate is slower in the partially treated than completely treated pans. Also, the stimulated parasites do move into and search the surrounding untreated areas. As a result the level of parasitization in the treated areas is lower than that of fully treated pans, while parasitization in the untreated areas is higher in the control pans.

TABLE 3. EFFECT OF A MOTH SCALE EXTRACT ON THE EGG DISTRIBUTION OF *Trichogramma* spp. AMONG HOST EGGS IN SMALL PLOTS OF SOYBEANS

Replication no.	<i>R/O</i> ratio ^a	
	Treated	Control
1	1.20	1.18
2	0.95	1.24
3	1.04	1.25
4	0.92	1.40
5	1.05	1.40
6	1.06	0.90
7	1.92	2.89
8	0.80	1.58
9	0.93	1.00
10	0.89	1.00
Mean ^b	1.08	1.34

^a *R/O* ratio is the ratio of percent parasitism that would have occurred in a random distribution of parasite eggs to the observed percent parasitism.

^b Means are significantly different at the 5% level as determined by a paired *t* test.

Distribution of Parasite Eggs, Small Plots

The hexane eluate of the moth scale extract apparently caused an increase in the efficiency of egg distribution by ovipositing females of *Trichogramma* spp. (Table 3). The *R/O* was significantly lower ($P = 0.05$) in the treated plots (1.08) as compared to the control plots (1.34). This is apparently one mechanism by which the increase in parasitization was achieved as a result of the kairomone influence. The presence of the kairomone on the surrounding plant surfaces probably induces the ovipositing females to depart more rapidly from host eggs than they have stung and to go in search of other hosts, thereby reducing superparasitism. On the other hand, the absence of the kairomone from the surrounding substratum would result in the wasps lingering on and repeatedly stinging each host that is found.

Distribution of Parasite Eggs, Large Plots

The results of this test (Table 4) were similar to those obtained in small plots. The calculated *R/O* in the treated plots (1.14) was lower ($P < 0.10$) than that of the control plots (1.27). The hexane eluate of the moth scale extract caused an increase in the parasitization efficiency of *Trichogramma* spp. Again, these results were indicative of an activator, not an attractant.

DISCUSSION

The studies all indicated that the primary process by which these kairomones function to increase parasitization rates of *Trichogramma* spp. is by releasing and maintaining the appropriate motor response in the wasp rather

TABLE 4. EFFECT OF A MOTH SCALE EXTRACT ON THE EGG DISTRIBUTION OF *Trichogramma* spp. IN HOST EGGS, IN LARGE PLOTS OF SOYBEANS

Replication no.	<i>R/O</i> ratio	
	Treated	Control
1	1.08	1.26
2	1.17	1.20
3	1.25	1.46
4	1.06	1.16
Mean ^a	1.14	1.27

^a Means are significantly different at the 10% level as determined by a paired *t* test.

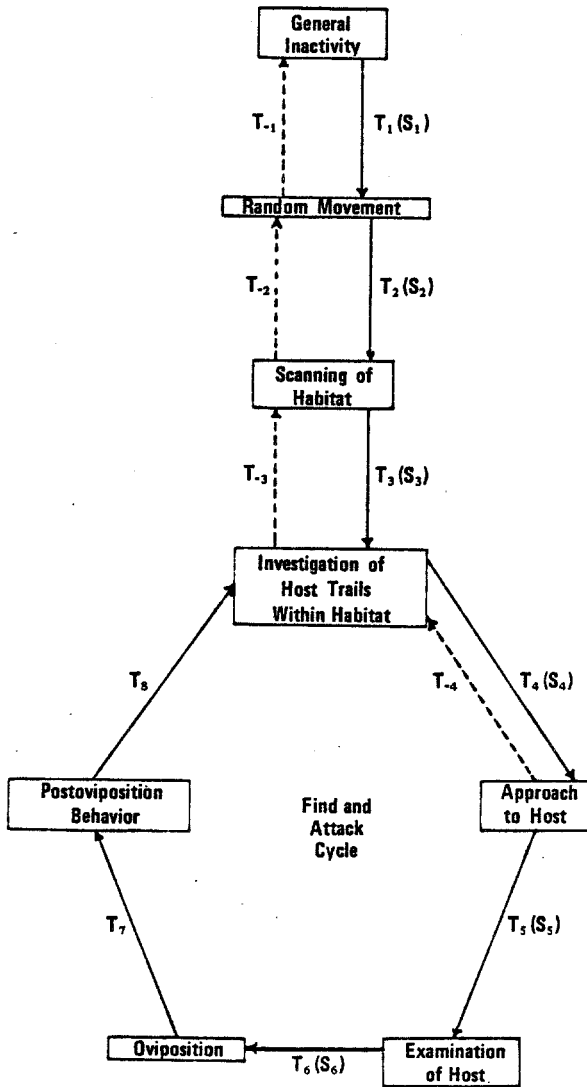


FIG. 1. Basic sequence of host-finding activities by females of parasitic insects: T_1 to T_8 and T_{-1} to T_{-4} —transitions among the indicated behavioral acts. S_1 – S_6 —stimuli releasing the indicated behavioral patterns. S_2 —olfactory, visual, and physical cues associated with host plants on other habitats. S_3 —primarily chemical cues from frass, moth scales, and decomposition products associated with the presence of host insects. S_4 —olfactory, visual, auditory, and other chemical or physical cues from host insect. S_5 and S_6 —olfactory, tactile, auditory, and/or combination of these cues from host individual.

than by attracting and serving as a steering mechanism. Treatment of the entire target area gave the best results. This treatment procedure apparently serves to elicit host-seeking response more quickly from more females and continuously reinforces this behavior throughout the area. The data also demonstrate that a more efficient egg distribution pattern is achieved in the treated areas, apparently as a result of the activation process.

The fact that these kairomones do not function as attractant has important implications for their use in pest-control programs, since such use will be less likely to adversely disrupt natural distribution patterns of the parasites. As they are understood at this point, it does not appear that use of these kairomones would be detrimental to *Trichogramma* populations since they function primarily to intercept and activate otherwise less productive *Trichogramma* females.

Studies of these kairomones have helped in a better interpretation of the overall host-finding sequence of insect parasites in general. Although the sequence of activities to be noted here is fundamentally similar to generalized patterns described in previous reports (Salt, 1935; Flanders, 1953; Doutt, 1964), we shall attempt to analyze the sequence in a manner that better relates the behavioral patterns to the stimuli releasing the responses, so that we may identify key points for parasite manipulation in pest management programs.

A diagram of what we consider to be the basic pathways of host location and selection is presented in Figure 1. The solid lines show the processes that occur if the necessary stimuli are provided at each step. The dotted lines show the alternative processes that occur if the necessary stimuli for the subsequent steps are not present. This diagram is a generalization and includes the basic components. Additional substeps and minor alternative pathways are involved and can be incorporated with the discussion of an individual species.

The transition (T_1) from inactivity to initial random movement is initiated by an innate appetitive drive together with prevailing environmental conditions and the current physiological state of the parasite. The means of locomotion for most parasites is flight, but some walk or run in search of habitats (Wylie, 1972). The parasites make a transition (T_2) from random movement and scan selected habitats by orienting to certain olfactory, visual, or physical cues (S_2) associated with the plants or habitats where hosts occur (Arthur, 1962; Askew, 1961; Nishida, 1956; Read, Feeny and Root, 1970; Smith, 1943; Thorpe and Caudle, 1938; Ulyett, 1953; Varley, 1941; and Wylie, 1958; and others).

Upon detecting the appropriate stimuli indicating inhabitation by the host (S_3), the T_3 transition to a localized search within the habitat is released. Frass, moth scales, decomposition products, or some other cue(s) associated with the presence of hosts in the environment are the stimuli that elicit this response (Ulyett, 1953; Wylie, 1958; Lewis, 1970; Lewis, Jones, and Sparks,

1972; Flanders, 1947; Laing, 1937; Vinson and Lewis, 1965; Doutt, 1959; Mudd and Corbet, 1973; and Hendry, Greany, and Gill, 1973; and others). Two or three substeps are usually involved in the search of trails of the host, all of which apparently are released by these and other sources of stimuli from the host. Actual detection of the host results (T_4) in an orientation toward and approach to the host. Olfactory, visual, auditorial, and other chemical or physical cues (S_4) from the host individual release this behavioral act (Edwards, 1954; Laing, 1937; Lewis, 1970; and others). If the host is concealed, perception of noise, movement, or infrared radiation from the host may be the means of host detection (Labeyrie, 1958; Lathrop and Newton, 1933; Ryan and Rudinsky; 1962; Richerson and Borden, 1972; and others).

Upon reaching the host the female parasite examines it for acceptability for oviposition. Chemical, visual, and tactile cues (S_5 and S_6) have been demonstrated to be involved in releasing these responses (Salt, 1935; Jackson, 1968; Ulyett, 1936; Edwards, 1954; Richerson and Deloach, 1972; Salt, 1958; Simmonds, 1943; Arthur, Hegdekar, and Batsch, 1972; Hegdekar and Arthur, 1973; and others).

After ovipositing, parasites often innately make an intensive investigation of the area adjacent to that host (Laing, 1937; Jackson, 1966; Hokyō and Kiritani, 1966; and others). The female then reverts to search for other hosts within the habitat.

The T_3 and T_{-3} transitions and the associated stimuli (S_3) between scanning of the habitat and the more thorough investigation of host trails within the habitat are the processes of primary interest to us in our studies of kairomones and their use in pest management. In order to induce females of insect parasites to be retained and effectively search in a desired target area, necessary stimuli (S_3) for the T_3 transition must be provided. Contact with the mediator which releases this behavioral pattern must occur periodically to reinforce and maintain the process. Lack of sufficient reinforcement otherwise allows the T_{-3} reversion to general scanning and a loss of the parasite from the target area. Therefore, a sufficient quantity and distribution of the stimuli is important. A blanket distribution throughout the target area is perhaps optimal for the *Trichogramma* species studied.

The ability to manipulate the behavior of parasites at this point of the host-finding sequence is obviously of great potential importance for more effective utilization of parasites in pest-control programs.

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