OVIPOSITION BEHAVIOR OF *Trichogramma platneri* NAGARKATTI (HYMENOPTERA: TRICHOGRAMMATIDAE) [1]

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RESUMO

Comportamento de *Trichogramma platneri* Nagarkatti (Hymenoptera: Trichogrammatidae) durante o processo de oviposição

O comportamento de *Trichogramma platneri* Nagarkatti, durante o processo de oviposição, foi estudado usando como hospedeiro ovos de *Trichoplusia ni* (Hübner). A duração das etapas que compreendem o processo de parasitização ("drumming", penetração e oviposição) foi altamente variável: 15,7 ± 8,62 17,3 ± 9,42; e 74,0 ± 61,00 segundos, respectivamente. O número máximo de progênie de *T. platneri* que emergiu de um ovo do hospedeiro foi três (2 fêmeas e 1 macho), ocorrendo em 7% do número total de ovos parasitados. Progênie constituída de uma fêmea, emergiu de 36% dos ovos parasitados. Vinte e seis por cento dos hospedeiros parasitados deram origem a duas fêmeas, 19% a uma fêmea e um macho, e 12% produziram apenas um macho. Sessenta por cento do total da progênie constituída por machos, produzida por parasitóides criados em ovos de *Sitotroga cerealella* (Olivier), emergiram dos primeiros ovos parasitados. Quando se utilizaram fêmeas criadas em *T. ni*, este nível atingiu 73%. O tempo gasto durante a etapa de penetração do hospedeiro e o processo de alimentação sobre o hospedeiro foi influenciado pela idade das fêmeas. De um total de 10 fêmeas (3-10h de idade), criadas sobre ovos de *S. cerealella*, quatro

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fêmeas se alimentaram em comparação com duas fêmeas criadas em ovos de *T. ni*. Quando fêmeas mais velhas foram utilizadas (27-34 h de idade), seis fêmeas criadas em ovos de *S. cerealella* e 10 fêmeas em *T. ni* se alimentaram no hospedeiro.

ABSTRACT

The oviposition of *Trichogramma platneri* Nagarkatti was studied, using eggs of *Trichoplusia ni* (Hübner) as the host. When provided with host eggs, most female parasitoids responded by ovipositing therein. However, some females showed no interest, even when walking among the eggs. Other females appeared to recognize the host eggs, walked on them, and even tried to penetrate the chorion, but soon left the eggs without ovipositing. The time the females spent in the ovipositional process was highly variable. The mean duration of drumming, drilling, and stinging was 15.7±8.62, 17.3±9.42, and 74.0±61.00 seconds, respectively. The maximum number of progeny emerging from a single egg was three (2 females and 1 male), occuring in 7% of the total number of eggs parasitized. One female progeny emerged from 36,0% of parasitized eggs. Twenty-six percent of the host eggs yield two females, 19% yielded one female plus one male, and 12% produced on male. Sixty percent of the total male progeny produced by parasitoids reared from *Sitotroga cerealella* (Olivier) eggs emerged from the first eggs exposed compared to 73% of the male progeny produced by female parasitoids reared from *Sitotroga cerealella* (Olivier) eggs emerged from the first eggs, exposed compared to 73% of the male progeny produced by female parasitoids reared from *T. ni* eggs. The time spent in the drilling process and the host feeding response was influenced by the age of the female parasitoid. Of ten females (3-10 hr old) reared from *S. cerealella* eggs, four host fed compared to two females reared from *T. ni* eggs. When older females (27-34 hr old) were used, six females from *S. cerealella* and 10 from *T. ni* cultures fed on the host exudate.

INTRODUCTION

The ovipositional behavior of *Trichogramma* involves a sequence of events which culminates in the parasitization of the host egg by the female parasitoid. This biological process consists of a series of responses by the female to the environment. These responses are not fully understood as the ovipositional behavior of females vary somewhat among individuals of the same species.

The host parasitoid relationships have important implications in the morphology, behavior, and physiology of *Trichogramma* (SALT, 1940). In order to study the behavior of *Tricho*

gramma platneri Nagarkatti in the process prior to, during, and following insertion of the ovipositor, a series of behavioral experiments were conducted. Experiments also were conducted to determine the effects of biological factors such as different hosts, female age, and host feeding on ovipositional behavior and progeny production of the parasite.

MATERIALS AND METHODS

Eggs of the cabbage looper, *Trichoplusia ni* (Hübner), and the Angoumois grain moth, *Sitotroga cerealella* (Olivier) were used as hosts. To obtain *T. ni* eggs, a culture was established and maintained as described by PAK and OATMAN (1982). *S. cerealella* eggs were obtained from Foothill Insectaries, Corona, California.

A culture of *T. platneri* was started in July, 1979, using parastioids reared from codling moth, *Cydia pomonella* (L.) eggs collected from and apple tree in Riverside, California, by Dr. E.R. Oatman. The culture was maintained in polyethylene containers (0.47 l), the open ends being covered with filter paper disks. The disks were secured by polyethylene lids from which the centers had been removed. Twenty-four-hours-old parasitoids, which had been fed on honey, were exposed to a large supply of host eggs (24 hr old) for one day. The host eggs then were held for progeny development. Cultures were started on different days to provide material for the experiments as needed.

To determine the time females spent drumming, drilling and ovipositing in host eggs, mated female parasitoids (24-36 hr old) with acess to honey were placed individually in Petri dishes, containing large numbers of *T. ni* eggs (24-36 hr old). The females were observed with a dissecting microscope.

Glass shell vials (9.5 x 2.5 cm) were used as oviposition units, as described by OATMAN & PLATNER (1973). All experiments were conducted at room conditions (24 ± 1°C, RH 50±15%).

A series of experiments also were conducted with starved females to study the influence of *T. platneri* size on the time required to penetrate *T. ni* eggs, as well as other behavioral characteristics of the female during oviposition. Ten females 3-10 hours old, and 10 females 27-34 hours old were selected from both *S. cerealella* (small *T. platneri)* and *T. ni* eggs (large *T. platneri)*. The females were placed individually in Petri dishes, containing large numbers of *T. ni* eggs (24-36 hr old), and allowed to attack five eggs each. The time required for each female to penetrate the host egg and its attack sequence was recorded. The eggs were held for progeny emergence. The progeny number and sex were also recorded.

RESULTS AND DISCUSSION

Once the host egg was perceived, the female either tapped the egg with her antennae or immediately climbed on top of the egg and started the drumming process. Drumming was characterized by back and forth movements on the egg surface, tapping the egg with the antennae, specially along the margins. The time spent inspecting the egg varied, but averaged 15.7 ± 5.27 seconds (Table 1).

As soon as the egg was accepted, the drilling process began. The female stood perpendicularly to the egg surface and touched it with the tip of the ovipositor, with remained sheathed until an insertion site was selected. When she decide on a suitable place, she unsheathed the ovipositor, adjusted it perpendicularly to the egg, and began inserting it. Sometimes after probing, the female either rejected the egg or moved to another site in the same egg. The average time spent drilling was 17.3±9.42 seconds (Table 1). Most of the females observed in the drilling process penetrated the chorion of the host egg with a jerky downward movement of the abdomen. Others drilled through the egg chorion without such obvious movements.

The time spent by a female penetrating the host egg apparently is unrelated to size (Table 2). Small females (3-10 hr old), reared from *S. cerealella* eggs, penetrated the host egg as rapidly as the females, reared from *T. ni* eggs, independendent of their age or size. Older females (27-34 hr old), reared from *S. cerealella* eggs, however, took more time to penetrate the host egg than the younger ones that were reared from the same host.

The female usually remained still during the period after insertion of the ovipositor, except for an occasional vibration of the antennae, and movement of the tip of the abdomen at intervals before and after oviposition. After insertion of the ovipositor, the wings of *T. platneri* female remained folded and the antennal club was pointed downward. The ovipositor remained inside the host eggs from as few as 10 seconds to as many as 388 second ($\bar{X}$ = 74.0 ± 61.0 seconds) (Table 1). In most cases, eggs were not deposited in the host if the ovipositor remained inside the egg less than 50 seconds When a single parasitoid emerged from the host, the parental female's ovipositor had remained in the host egg from 27 to 160 seconds. When two parasitoids emerged from the host, her ovipositor had remained in the host egg from 60 to 220 seconds. The maximum number of progeny emerging from a single host egg was three. However, the time that the female spent ovipositing in this case was not recorded.

The amount of time the female spent successfully ovipositing was highly variable. She sometimes spent 10 to 15 minutes inserting her ovipositor several times, followed by host feeding. Parasite progeny still emerged from these eggs. In other situations, no progeny emerged. Instead, a host larva emerged or the host egg collapsed.

Table 1 - Average time (seconds) *T. platneri* females spent during various activities associated with the parasitization of *T. ni* eggs.*

	Drumming		Drilling		Ovipositing	
	Mean	(Sd)	Mean	(Sd)	Mean	(Sd)
	15.7	± 8.62	17.3	± 9.42	74.0	± 61.0
n	102		192		209	

* *T. ni* eggs used as host.

Table 2 - Average time (seconds) required by *T. platneri* females (reared from two different hosts) to penetrate *T. ni* eggs.

Parasite source (host egg)	Parasite age (Hr)	Tibia length (mm)		Penetration time Men	(Sd)	% Females host fed
S. cerealella	3-10	0.141a*	46	15.8	5.27 b	40
S. cerealella	27-34	0.142a	50	21.1	13.80a	60
T. ni	3-10	0.171b	50	16.3	7.03 b	20
T. ni	27-34	0.196c	46	16.0	6.09 b	100

* Column means followed by the same letter are not significantly different at 5% level.

When the female withdrew the ovipositor, its proximal part was withdrawen gently, followed by lateral movements of the body, whereas the tip of the ovipositor was released from the egg by a quick pull. Withdrawl may be followed by host feeding on the exudate from the ovipositor puncture. The female occasionaly pierced and fed as many as twelve times at the same site on the same host egg. Host feeding was preceeded by different kinds of movements. The most frequent ones were back and forth, and lateral movements of the body. The female apparently was trying to enlarge the puncture wound in order to extract more exudate as she fed eagerly thereafter. After spending time at one site, she moved to another site on the same

egg, tapped the chorion with the ovipositor sheath, and then started drilling and feeding until she apparently became satiated. Before starting the insertion process, the female occasionally touched the chorion of the egg with her mouth parts. As the area touched was not a drilling site, she apparently was using her mouth parts for either selecting a place to insert her ovipositor or was softening or piercing the chorion to facilitate drilling. This observation has not been recorded for other *Trichogramma* species.

The time the female spent feeding apparently was related to the amount of food obtained from drilling. When the exuding fluid seemed to be adequate, she remained still for about one minute while feeding before leaving the feeding site. However, if the exudation was inadequate, she continued to drill and feed eagerly until she apparently was satiated. The female usually feed on the first egg attacked, and her ovipositor remained inserted in the egg longer than in subsequent eggs. Some females fed on more than one egg. Of the five host eggs attacked up to three were fed on. Although most females host fed on the first host egg, sometimes they attacked several eggs before feeding.

Four of ten younger females (3-10 hr old), reared from *S. cerealella*, host fed while two of ten reared from *T. ni*, did so. In comparison to younger females, six of ten older females (27-34 hr old), reared from *S. cerealella* eggs, host fed while ten of ten older females, reared from *T. ni* eggs, host fed (Table 3).

After host feeding, the female left the egg and started walking and tapping the substrate with her antennae. If she could not find another egg nearby, she either returned to the egg already attacked or continued to search the surrounding areas until one was found. The female usually did not move far from the area where she discovered the first egg.

The maximum number of parasitoids that emerged from a host egg was three (2 females and 1 male), representing 7% of the total oviposition (Fig. 1). The most frequent sex allocation, however, was one female per host, occurring in 36% of the eggs parasitized. Twenty-six percent of hosts yielded two females whereas, one female plus one male and 1 male per host occurred in 19 and 12% of the cases, respectively. Each value represents the mean of four treatments. Fig. 1 also shows that the host on which the parasitoids were reared and the parental female age affected progeny and sex allocation. Considering only the effect of rearing, females reared from *T. ni* eggs usually preferred to allocate one female per host egg whereas, females reared from *S. cerealella*, usally allocated either one or two females per host. The allocation of one male plus one female per host was more frequent when the females were reared from *S. cerealella*, while one male per host egg was allocated mainly by females reared from *T. ni* eggs.

Although the overall sex ratio was female-biased (76%), the gender of progeny that emerged from the first host egg of

the sequence was male-biased, especially those parasitized by older females reared from *T. ni* eggs (Table 3). Of the total number of male progeny produced by parasitoids reared from *S. cerealella* eggs, an average of 60% was allocated in the first host egg the female oviposited in. For parasitoids reared from *T. ni* eggs, the figure was 73%.

When accepting a *T. ni* egg, the behavior of *T. platneri* females was similar to that described by TAYLOR (1969) for *Trichogramma semifumatum* (Perkins).

Host size appeared to be important to females of *T. platneri*. When provided with large numbers of *T. ni* eggs, large female parasitoids rejected the small ones after abrief examination. Other females spent some time tapping the areas beyond the margin of the host egg. According to SALT (1940), the animal host size acceptable to a parasitoid depends upon the parasitoid size.

TAYLOR (1969) noted that it is not known whether drumming by the female parasitoid determines the state of the host (i.e. parasitized or not), or if she is searching for a suitable oviposition site. KLOMP & TEERINK (1962) suggested that female *Trichogramma embryophagum* Hartig use drumming to measure the size of the host egg, and that the duration of this process is related to the number of eggs laid.

The fact that older females reared from *S. cerealella* eggs required more time to penetrate the host eggs than females of the same age reared from *T. ni* eggs (Table 2) might be attributed to starvation. The females reared from *S. cerealella* eggs may have been less vigorous than the larger females reared from *T. ni* eggs by the second day, and thus took more time to drill through the egg chorion. Although host feeding is a common occurrence in many species of parasitoids, it apparently has little effect as a source of energy. It pays a major role supplying protein needed for oogenesis (DOTTEN, (1911). BARTLETT (1964) stated that the widespread occurrence of host feeding by adults in parasitic Hymenoptera suggests that such activity is indicative of dietary deficiencies.According to FLANDERS (1953), adults of many hymenopterous parasitoids are unable to reproduce to their full capacity without feeding on the host fluids. He noted that host feeding by the female indicates that oogenesis is about to begin or is already underway, and that cessation of host feeding in the presence of the host indicates that oogenesis has ceased.

Trichogramma females exhibited different patterns of progeny and sex allocation when reared from different hosts. *T. platneri* reared from *T. ni* eggs usually allocated one female per host egg whereas, those females reared from *S. cerealella* eggs allocated about the same number of one and two female eggs per host (Fig. 1). Male eggs were allocated mainly in the first host egg parasitized. Hence, the sex ratio in these eggs were more male-biased (Table 3). WAAGE & MING (1984) also reported this pattern of gender allocation for *T. evanescens*. WAAGE (1982) hypothesized that parasitoids with female-biased sex

TABLE 3 - Comparison between the overall sex ratio and the sex ratio in the first egg *T. platneri* females (reared from different hosts) oviposited in.*

Parasite source (host egg)	Parasite age (Hr)	Overall sex ratio (%)		Sex ratio/first egg (%)		Males/first egg of total males (%)
		Females	Males	Females	Males	
S. cerealella	3-10	79.0	21.0	73.4	26.6	50
S. cerealella	27-34	78.3	21.7	59.0	41.0	70
T. ni	3-10	71.5	28.5	61.6	38.4	70
T. ni	27-34	77.0	23.0	42.0	58.0	77

*T. *ni* used as host.

ratio often lay male eggs first in a succesion of eggs laid consecutively. Parasitic Hymenoptera are thought to be able to regulate the number and sex ratio of their progeny and to produce only males necessary to made her daughters (CHARNOV, 1982). *T. platneri* appear to follow this pattern.

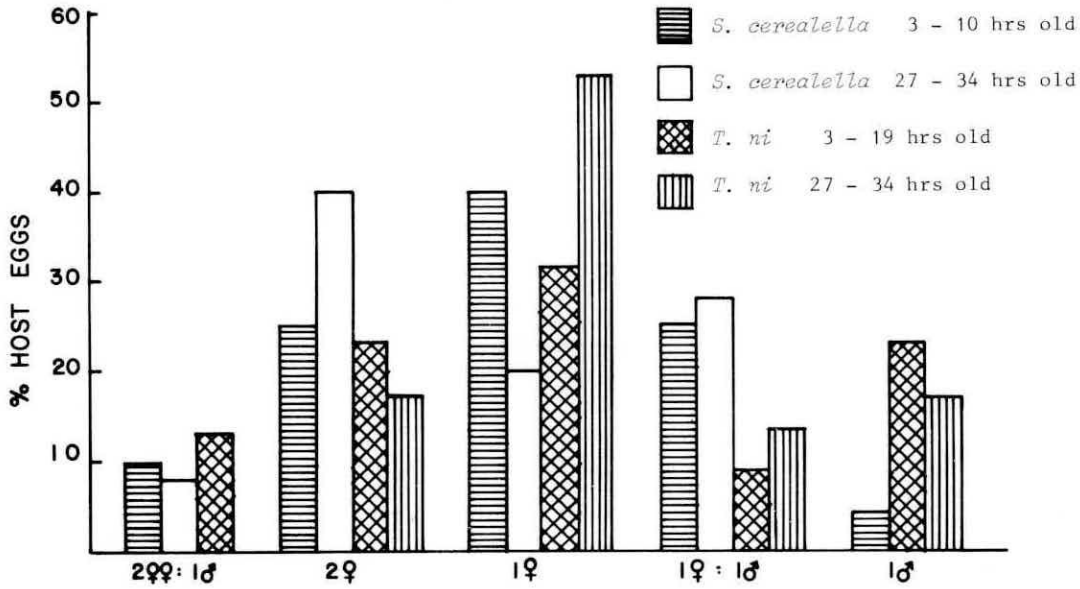

FIGURA 1 - Sex allocation (%) per host when *T. platneri* was reared from *S. cerealella* or *T. ni* eggs of different ages.

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