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Appl. Ent. Zool. **22** (4): 456–464 (1987)

Characteristics of the Oviposition of a Parasitoid, *Chrysis shanghaiensis* (Hymenoptera: Chrysididae)

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(Received February 7, 1987)

Observations and experiments were carried out indoors to clarify some features of the oviposition of *Chrysis shanghaiensis*. The behavior of oviposition was described. It took 62.5 min on an average to lay an egg. The female wasp laid at most three eggs a day, and 28.7 eggs during her whole life. She did not attack host cocoons on days when the maximum temperature in the rearing room was less than 22°C. When the host inside the cocoon was dead, the female laid no egg in the cocoon. There was no difference between cocoons with a prepupa and those with a pupa in the probability of the wasp's laying an egg, the survival rate of the wasp during the egg to pupal stages, or the body size of the adult wasp which emerged.

INTRODUCTION

Chrysis shanghaiensis (Hymenoptera: Chrysididae, Chrysidinae) is an ectoparasitoid specific to the oriental moth, *Monema flavescens* (Lepidoptera: Heterogeneidae). Most of the chrysidid wasps lay their eggs inside the nests of wasps or bees, and the species attacking moth cocoons is rare in the Chrysididae.

C. shanghaiensis was apparently introduced by chance into Japan around 1900 (OYA, 1914), and is now distributed throughout the country except the northern part (KAJI, 1979). The wasp is believed to suppress the oriental moth population to a low level in many places in Japan (IWATA, 1963, 1975). Field studies in Uji City, Kyoto (YAMADA, 1987), revealed that the wasp had the ability to produce a high rate of parasitism and to avoid superparasitism. The rate of parasitism was influenced by the relative density of the wasp to the host cocoon rather than by the wasp density itself.

In spite of these interesting features, there is not detailed information about fecundity, though PIEL (1933), PARKER (1936), and IWATA (1963, 1975) disclosed some biological characteristics of *C. shanghaiensis*. In this paper, observations and experiments in the laboratory clarify ecological features in oviposition, including the egg-laying capacity.

LIFE CYCLES OF THE INSECTS

In Uji, the oriental moth and the chrysidid wasp have one and part of a second generation a year. Overwintered moth cocoons produce adults of the moth in late June and those of the wasp in early July (Fig. 1). Moth cocoons of the first generation appear in late July to early August, and are subjected to parasitization by the wasp.

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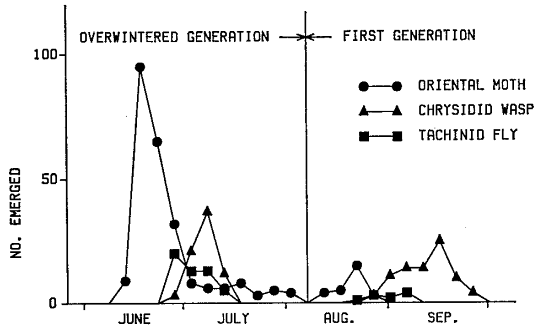

Fig. 1. Emergence curves of the oriental moth and its two parasitoid species from moth cocoons collected in Uji City in the spring and summer of 1978. The value of each point represents the total number of emerged adults in a five-day period.

Some moth cocoons of the first generation give rise to adults of the moth in late August and those of the wasp in September, which produce the respective second generations.

Besides the chrysidid wasp, *Chaetexorista eutachinoides* (Diptera: Tachinidae) emerges from the moth cocoon. This parasitic fly attacks the final instar larvae of the oriental moth, and the life cycle is similar to that of the chrysidid wasp.

MATERIALS AND METHODS

Adult wasps used for the study were those which emerged from host cocoons collected in Uji in 1982 and 1983. In 1982, experiments for overwintered generation wasps were carried out in a laboratory, and those for first generation wasps in a greenhouse where the temperature was over 25°C when the weather was fine. In both experiments the windows were kept open and the direct rays of the sun were kept off the plastic rearing cages. In 1983 experiments for both generations were conducted in an incubator of 25°C and 16L–8D.

The experiments for first generation wasps were started on the day the wasp emerged, while the experiments for overwintered generation wasps were started several days after emergence as no host cocoons were available. However, the data of the overwintered generation of 1982 was not used to estimate lifetime fecundity, since host cocoons had not been provided for more than a month after the emergence.

A mated female (a virgin female in the overwintered generation of 1982) was transferred at night into a transparent plastic cage, 20×36×28 cm, with many ventilation slits in the lid. The cage contained ten host cocoons reared in the laboratory from the egg stage. The cocoons remained glued to twigs and were kept off the floor and the wall of the cage. A piece of absorbent cotton soaked with honey containing fresh pollen and another piece of absorbent cotton soaked with water were supplied for the wasp. As resting sites at night, one sheet of paper, 24×16 cm, which was folded in fourths, was put on the floor and another attached to the ceiling.

Every night parasitized cocoons (strictly speaking, cocoons with oviposition holes on the surface) were replaced by unparasitized cocoons. The former cocoons were dissected to examine the parasitoid eggs and host condition. After dissection the parasitoid eggs were reared in individual glass vials (10 m*l*) plugged with cotton till adults emerged.

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Table 1. Time spent in laying an egg (min)

Inspection	Perforation[a]	Oviposition	Sealing	Time after sealing[b]	Total
2.66±3.00[c]	42.72±23.83	9.45±3.62	7.27±2.51	0.38±0.73	62.47±25.88

[a] Including the time spent in turning around and inserting the ovipositor a few times before actual laying of an egg.

[b] Time between completion of sealing the hole and leaving the cocoon.

[c] Mean±S.D. (the number of observed cases=8).

The maximum temperature was measured near the rearing cages every day in 1982. Adult behavior was visually observed at intervals of several days.

RESULTS

The female wasp searched for host cocoons only in the daytime, and stayed still at night in the folded paper sheets or on a twig. She searched mainly by walking.

For a few minutes after encountering a host cocoon, the female wandered on and around it while stroking and tapping the surface with her antennae. It seemed that she was examining whether the cocoon was already parasitized and finding a suitable site to chew an oviposition hole in it. Then she stationed herself on the twig with her mouth in contact with the cocoon surface and chewed a small hole, which was usually located around the cephalic end. At this time she pressed her body against the cocoon surface using the five pointed teeth on the terminal of her abdomen as spikes. Perforation lasted about 43 minutes (Table 1). The powder of the cocoon shell which was produced during the perforation was mixed with the saliva and attached to the cocoon surface around the hole. This powder was used later for sealing the hole.

After chewing the hole the wasp female turned around and inserted her long ovipositor through the hole into the cocoon. She often laid no egg at the first try, then turned around and began enlarging the hole. After a few repeats of the ovipositor insertion and the hole enlargement, the wasp succeeded in depositing an egg inside the cocoon. The egg was not glued to a particular site in the cocoon, but placed on one of various parts of the host or the lining of the cocoon. The diameter of the oviposition hole ranged from 0.5 to 0.7 mm. After an ovipositing operation which lasted for about 10 min, the wasp turned around to plug the hole. In contrast to her chewing of the hole, while plugging it she did not use the teeth on the abdominal end as spikes and often kept her abdomen off the twig. Some wasps wandered around the cocoon for tens of seconds after plugging.

The overall time spent in laying an egg ranged from 31 min and 30 sec to 107 min and 16 sec, averaging 62.5 min (Table 1). This time was not related to the thickness of the cocoon shell around the hole, which ranged from 0.15 to 0.26 mm and averaged 0.20 mm.

The female wasp had four ovarioles per ovary. The egg, 2.18±0.16 mm long and 0.55±0.04 mm wide (mean±S.D., n=136), was sausage-shaped, usually with a very short petiole about 0.01 mm long at the cephalic end, though in some eggs no petiole was found. Four gravid females, which were reared for 14 days without a supply of host cocoons, had 2, 2, 3, and 4 mature eggs, respectively.

The female wasp did not lay any eggs for two or three days after emergence. This

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Table 2. Influence of temperature on oviposition. The proportion of oviposition occurrence was significantly different between days with a maximum temperature of less than 22°C and the others (Fisher's exact probability test, $p<0.001$)

Daily maximum temperature (°C) <21	21–22	22–23	23–24	24–25	25–26	26–27	27–28	28≤
0/12[a]	1/13	4/9	2/2	2/7	4/10	5/9	8/9	35/64

[a] A total of 45 days from the first day of oviposition were categorized according to the daily maximum temperature. The denominators are the number of days on which each range of temperature was experienced, and the numerators the number of days on which at least one egg was laid. Each figure in the table is the sum of three first generation wasps of 1982.

was due to the fact that she had no mature eggs in her ovaries at emergence. Oviposition seldom occurred on the days when the maximum temperature remained below 22°C (Table 2). Observation on October 17, when the maximum temperature was 20.7°C, revealed that the wasp rarely wandered but spent most of the time staying still between the paper sheets.

The wasp encountered host cocoons many times a day, but almost all of the encounters resulted in her leaving the cocoon without starting to gnaw a hole on the surface. She made a hole at most three times a day.

Only one oviposition hole was usually perforated in a cocoon except for three of 331 cocoons, which had two holes. (The number 331 is larger than the total of the figures for the individuals shown in Table 3, because the former includes the number for the overwintered generation wasps of 1982.) In 114 of these 331 cocoons no eggs were laid; and 85 of these 114 cocoons had live hosts inside. When an egg was laid in the cocoon, the oviposition hole was almost always plugged neatly (Table 3). Meanwhile, of the 116 oviposition holes through which no eggs were laid, 28 were not neatly plugged and 51 were abadndoned in the course of perforation. The number of oviposition holes without eggs varied considerably from individual to individual (Table 3).

The lifetime fecundity, which averaged 28.7 eggs, varied greatly with the individuals (2–47 eggs), but was not influenced by body size or rearing conditions (Table 3). The average of eggs laid per female per five days never exceeded five. The number reached maximum (4.2) during the 5 to 10 days after emergence, and after that it decreased gradually (Fig. 2). An adult over 60 days old rarely laid eggs. The female lived long after the last oviposition.

The wasp usually laid one egg or no eggs in a day, but sometimes laid two. The laying of three eggs in a single day took place only three times: Two cases occurred when an overwintered generation wasp was supplied with hosts for the first time after emergence and the other on the day after a first generation wasp had not attacked cocoons for three days due to low temperature.

When the host was not alive, the wasp tended to avoid laying an egg on it (Table 4). Since there was no difference in the probability of the wasp's abandoning the cocoon in the course of perforation between live and dead hosts (χ^2-test, $p>0.4$), the discrimination was considered to be made after insertion of the ovipositor.

The oriental moth overwinters in the prepupal stage so that the first generation wasp encounter only prepupae, while the overwintered generation wasp encounters prepupae and pupae. There was no significant difference in the probability of egg-

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Table 3. Fecundity, longevity, and body size of individual wasps

Year	Generation[a]	Rearing conditions[b]	No. of eggs laid[c]	No. of oviposition holes without eggs[d]			Width of mesothorax (mm)	Longevity (days)	Age of the last oviposition[e] (days)
				A	B	C			
1982	F	G	12 (3)	3	1	4	4.10	83	60
1982	F	G	32 (0)	4	1	10	3.99	82	58
1982	F	G	34 (0)	1	3	3	3.71	84	56
1983	O[f]	I	47 (2)	1	1	5	3.86	86	69
1983	F	I	45 (2)	11	3	10	3.64	166	54
1983	F	I	29 (1)	10	9	13	3.86	155	59
1983	F	I	2 (0)	2	3	0	3.83	191	6

[a] F, First; O, Overwintered.
[b] G, Greenhouse; I, Incubator of 25°C.
[c] The numbers in parentheses mean the numbers of cases in which the oviposition hole was not plugged neatly.
[d] Oviposition holes without eggs were divided into three categories: A, the hole was plugged neatly; B, the hole was not plugged at all, or a chink was left in the plug; C, abandoned before the hole pierced the cocoon shell.
[e] The age of the adult when it laid the last egg.
[f] Cocoons were first supplied 11 days after the wasp's emergence.

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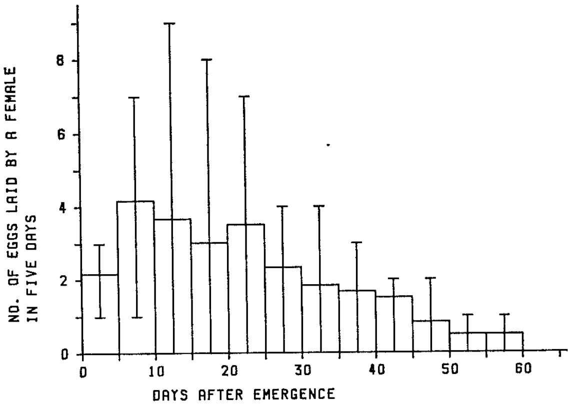

Fig. 2. Ovipositional trend of *C. shanghaiensis*. The figure was drawn on the basis of data of six first generation wasps. The histogram shows the averages of eggs laid by a female in a five-day period and the vertical bars show the ranges between the maximum and minimum.

Table 4. Avoidance of dead hosts

Host condition	No. of cocoons attacked (A)	No. of cocoons in which an egg laid (B)	No. of cocoons abandoned before completion of perforation	Probability of egg-laying (B/A)
Alive	160	119	24	0.744***
Dead	30	4	3	0.133

*** There was a significant difference between live and dead hosts (Fisher's exact probability test, $p<0.001$).

Table 5. Influence of the developmental stage of host on the probability of egg-laying

Developmental stage of host	No. of cocoons attacked[a] (A)	No. of cocoons in which an egg was laid (B)	No. of cocoons abandoned before completion of perforation	Probability of egg-laying (B/A)
Prepupa	50	41	4	0.820
Pupa	33	22	5	0.667

[a] Dead hosts were excluded.

Table 6. Influence of the developmental stage of host on the survival of the parasitoid during the egg to pupal stages and on the body size of the adult parasitoid

Developmental stage of host	No. of cocoons in which an egg was laid	Survival ratio	Width of mesothorax (mm)[a]	
			Female	Male
Prepupa	41	0.610	3.48±0.08 (7)	3.55±0.05 (17)
Pupa	22	0.636	3.61±0.12 (5)	3.48±0.06 (8)

[a] Mean±S.E. (sample size).

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laying between the prepupae and the pupae (χ^2-test, $p>0.1$; Table 5). Venom injection by the wasp usually caused a swelling on the ventral side of the host prepupa, while it caused a few black spots on the pupal abdomen. The host stage on which the wasp egg was laid had no relevance to the survival rate of the parasitoid during the egg to pupal stages or the body size of the parasitoid adult (χ^2-test for the former, $p>0.4$; two-sample t-test for the latter, $p>0.3$; Table 6). This survival rate in the rearing experiment, however, was lower than that among the cocoons with one oviposition hole which were collected in Uji in August, 1978 (87.8%) (Y. YAMADA, unpublished), probably because the latter cocoons were not dissected.

DISCUSSION

Dissection of the field-collected cocoons showed that one oviposition hole on the surface generally meant that one egg had been laid through it, except in cocoons with dead hosts (Y. YAMADA, unpublished). In the field the number of eggs laid was only slightly smaller than that of oviposition holes, since cocoons with dead hosts were very few. On the contrary, in the present study the wasp often made a meaningless oviposition hole even when the host in the cocoon was alive. This must have been because of a superabundant supply of host cocoons.

PIEL (1933) reported that the female of *C. shanghaiensis* laid 8–10 eggs indoors during her lifetime and PARKER (1936) reported she laid 11.3 eggs. These values are much smaller than the value obtained in the present study, i.e., 28.7 eggs. Though the above authors did not mention the rearing methods, they must have been less favorable for the oviposition of the wasp.

Pupae of the oriental moth are as suitable for the development of the parasitoid larvae as prepupae, and hence each host is available to parasitoids for a long period. Rearing at constant temperature (Y. YAMADA, unpublished) revealed that the periods of the prepupal and pupal stages were respectively 7.4 days and 20.5 days at 25°C, and 5.5 days and 16.4 days at 30°C. These figures are so large that the overwintered generation wasps can lay most of their eggs by the time first generation moths start emerging.

The fecundity in *C. shanghaiensis* (or the number of mature eggs per gravid female, which seems to be closely correlated with the fecundity) is rather low (small) compared with that in other parasitoids (IWATA, 1955, 1960, 1962; PRICE, 1975). PRICE (1974, 1975) mentioned that the main factor promoting low fecundity was the high survival rate of the parasitoid during the egg to pupal stages. This idea holds for *C. shanghaiensis*, but it does not explain the extremely small number of eggs laid per day and the long ovipositional period. This type of ovipositional trend seems to be closely related to the long handling time and the long period during which the host is vulnerable.

In addition to *C. shanghaiensis*, some chrysidines are equipped with teeth on the abdominal end, but there are no reports on how the teeth are used. IWATA (1978) observed in Taiwan that *Stilbum cyanurum splendidum* arched its body when chewing a small hole in a nest of the host wasp, and this suggests that the wasp used its teeth as spikes to press its mouthparts against the host nest.

The Cleptinae, which are the most primitive Chrysididae and attack cocoons of sawflies (KROMBEIN, 1957, 1983; KIMSEY, 1981), are not equipped with teeth on the abdominal end. Though the ovipositional habit of cleptines is known only in two species, *Cleptes* sp. (CLAUSEN, 1940) and *Cleptes fudzi* (OKAMOTO and NAITO, 1963), it

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closely resembles that of *C. shanghaiensis*. The female of *Cleptes fudzi* takes only about five minutes to chew a small hole, lay an egg, and seal the hole, probably because the cocoon shell of sawflies is not so hard as that of the oriental moth. The teeth on the abdominal end seem to have evolved as equipment for chewing holes in hard shells or walls protecting the hosts.

Besides the ovipositional habit of making an oviposition hole (type A), some species of the Chrysidinae in Japan have another type of ovipositional habit; they lay an egg inside a nest cell which is not yet sealed while the owner of the nest is absent (type B) (IWATA, 1978). For wasps of type B the teeth on the abdominal end are unnecessary. In fact, some species of type B, such as *Chrysis japonica* and *Chrysis hirsuta*, lack these teeth (TSUNEKI, 1970). Moreover, *Chrysis lusca* and *Chrysis fasciata daphne*, which have the ovipositional habit of type B (IWATA, 1978), show a wide variation in the shape of the teeth among individuals, and in some individuals a few teeth are short and blunt (TSUNEKI, 1955, 1963). This suggests that type A is more primitive than type B, and with the change in ovipositional habit, the teeth on the abdominal end seem to have degenerated in some species of type B or to be in the process of degeneration.

ACKNOWLEDGEMENTS

The author wishes to thank Dr. R. KISIMOTO for his critical reading of the manuscript. Special thanks are due to Dr. H. SHIMA for identification of the tachinid fly.

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