The Ovipositional Behavior in *Euplectrus kuwanae* CRAWFORD (Hymenoptera: Eulophidae), a Parasitoid of *Argyrogramma albostriata* (BREMER et GREY) (Lepidoptera: Noctuidae)

Hideo UEMATSU

*Institute of Biological Control, Faculty of Agriculture, Kyushu University, Fukuoka 812, Japan*

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The ovipositional behavior of a gregarious external parasitoid, *Euplectrus kuwanae*, was studied in the laboratory. The parasitoid females began oviposition on the third day after emergence. An adult female attacked seven to nine host larvae for oviposition and laid an average of 96 eggs during its life time. However, the fecundity decreased considerably when the female parasitoid was given only already parasitized hosts. Number of eggs deposited on a single host varied with host size. When the host was large, 18 or more eggs were usually laid as a cluster by a female parasitoid; for a host lighter than 10 mg, on the contrary, the cluster size was as small as six eggs. The parasitoid had an ability to modify the sex ratio of the progeny according to the host size, i.e., the larger the host size, the larger the proportion of fertilized eggs to all the eggs laid by the female became. These abilities allowed *E. kuwanae* to utilize the host resources efficiently. When healthy and parasitized hosts were exposed to the parasitoid at the same time, the parasitoid sometimes attacked the parasitized host and destroyed the eggs existing on it before laying its own eggs.

INTRODUCTION

Many insect parasitoids are known to possess two different abilities, the ability to discriminate between healthy and parasitized hosts and that to refrain from depositing eggs on the latter. Solitary parasitoids possessing such abilities are able to distribute progeny evenly in the host population to avoid intraspecific competition. However, gregarious parasitoids are faced with a more complex problem. In addition to the above-mentioned abilities, they have to be able to estimate the host capacity in order to avoid competition and to exploit their host resource efficiently. It is well known that the number of eggs deposited on a single host by gregarious parasitoids depends upon the stage or size of the host (SALT, 1934; KLOMP and TEERINK, 1962; WYLIE, 1967; NESER, 1973).

BASHIR and VENKATRAMAN (1968) have reported an interesting behavioral aspect of *Euplectrus laphygnae* FERRIÈRE. When a parasitoid female finds eggs existing on a host, she often destroys them before depositing her own eggs. I observed a similar behavior in the female of *E. kuwanae* CRAWFORD. The purpose of the present study is to analyze the ovipositional behavior of *E. kuwanae* and to obtain some basic information of its host utilization.
As described previously (Uematsu, 1981), E. kuwanae is a gregarious external parasitoid of lepidopterous larvae. It deposits 3 to 30 eggs in a cluster on the dorsum of the host caterpillar. The parasitoid larvae develop externally and do not leave the original position until they develop into the mature larval stage. The duration of development from egg to adult is 13.3 days at 25°C.

MATERIALS AND METHODS

Eggs and larvae of E. kuwanae parasitizing on larvae of Argyrogramma albostrata (Bremer et Grey), a common host in Fukuoka, were collected in the autumn of 1979 and 1980 and reared at an insectary to obtain adult parasitoids. The third to fifth instar larvae of A. albostrata, which had developed by feeding on leaves of Solidago altissima L., were used as hosts of the parasitoids. Throughout the experiments, fresh leaves of Solidago were placed in the container since the hosts feeding on them were easily attacked by the parasitoids. The experiments were carried out at a temperature of 25°C±1°C.

Ovipositional sequence and fecundity. Eight newly emerged female parasitoids were used for this experiment. Each of the females paired with a male was put into a test tube (30×200 mm) with a host larva (fourth or fifth instar). A droplet of honey was given as food for the parasitoid. The host larvae were examined every 12 hr and when there were individuals which had been attacked by the parasitoid or were going to molt, they were replaced with new ones. The experiment was continued until the parasitoids died.

Effects of the host size on the egg cluster size and the sex ratio in the parasitoid. Fifty female parasitoids were put in a plastic cage (235×175×200 mm) with 70 host larvae (third to fifth instar) for 24 hr. The experiment was repeated 12 times. Parasitized caterpillars were individually weighed, and eggs deposited on them were counted using a binocular microscope. Sixty of the total 169 parasitized hosts were individually reared to clarify sex ratio in adult parasitoids. Of them, 9 were killed by the fungus, Nomuraea rileyi.

Ovipositional discrimination by parasitoid between healthy and parasitized hosts. Twenty-four female parasitoids were divided into 12 groups of two individuals each. Two hosts, one healthy and the other already parasitized, were exposed to each group in the test tube. When the parasitoid deposited eggs on either of the hosts, the host was immediately replaced with a new healthy or parasitized one. Thus, the female could always select either a healthy or parasitized host throughout the experiment. The experiment was ended when 40 cases of selection had been observed.

Reactions of female parasitoid to the eggs laid by another parasitoid on the surface of a host larva. Two female parasitoids were placed in a test tube with a host larva bearing a cluster of parasitoid eggs. Before the parasitized host was offered, the number of eggs existing on it was recorded. When a parasitoid was observed to be located on the host, the test tube was put under the binocular microscope to observe the parasitoid’s behavior minutely.

Oviposition to the already parasitized host. Eight newly emerged female parasitoids were used for this experiment. Each female paired with a male was placed in a test tube with a host larva bearing a parasitoid egg cluster. The host larvae were examined every 12 hr, and when one was ascertained to be attacked by the parasitoid,
it was replaced with an other parasitized host. The number of eggs newly deposited on the already parasitized host was counted using a binocular microscope. The test was continued until the parasitoids died.

Eleven host larvae bearing two parasitoid egg clusters were obtained in this experiment. They were individually reared to investigate the process of intraspecific competition between parasitoid larvae after hatching of the eggs.

RESULTS AND DISCUSSION

Ovipositional sequence, fecundity and host-feeding

The female parasitoid usually began oviposition on the third day after emergence, and deposited seven to nine egg clusters during 16.5 days of its average life span. The female deposited one or two egg clusters per day. The mean number of eggs deposited by a female during its lifetime was 96.5, 50% of them being deposited by the 8th day and 90% by the 14th day after emergence (Fig. 1, open-circles).

Swezey (1924) recorded that a female of *Euplectrus platypterus* (Howard) deposited 213 eggs in a period of two weeks. Although the fecundity of the present species was considerably lower than that of *E. platypterus*, it was not always low in comparison with the fecundity of several other *Euplectrus* species (Chatterjee, 1945; Bashir and Venkatraman, 1968). The number of egg clusters deposited by an *E. kuwanus* female was less than the 25 deposited by *E. parvulus* (Chatterjee, 1945).

Three of the 8 females used in this experiment exhibited host-feeding behavior on the 7th to the 8th day after the first oviposition. One of them fed three times at intervals of five or six days, and deposited as many as 179 eggs. The host-feeding behavior seems to be common to members of the genus *Euplectrus* since it has also been observed in *E. parvulus* (Chatterjee, 1945) and *Euplectrus* sp. near *laphysmae* Ferrière (Neser, 1973). As Chatterjee (1945) and Neser (1973) pointed out, feeding on the body fluid of the host is necessary to obtain protein needed for oviposition.

![Cumulative percentage ovipositional curves in *E. kuwanus*. Open and solid circles refer to oviposition on healthy and parasitized hosts, respectively.](image-url)
Effect of host size on the egg cluster size and the sex ratio in the parasitoid

The body weight of host larvae varied greatly even within the same instar. In the third instar, it ranged from 2 to 14 mg; in the fourth instar, 12–66 mg; and in the fifth instar, 60–243 mg. Therefore, the parasitized hosts whose body weight ranged 6–125 mg were classified into six classes according to their weight, and then the mean size of egg cluster in each class was calculated (Table 1). The smaller the host size was, the less number of eggs per cluster was observed.

This indicates that *E. kuwanae* females are able to regulate the number of eggs to be deposited according to the host size. Since host larvae on which *E. kuwanae* deposits eggs have a wide range of size, such ability of the parasitoid distinctly allows it to utilize the host resources efficiently.

KLOMP and TEERINK (1962) observed the oviposition behavior of the egg parasitoid, *Trichogramma embryophagum* (HARTIG), and stated that the number of eggs deposited on a host was correlated with time spent for drumming. However, the relationship which was observed between *E. kuwanae* and *A. albostriata* was quite different. When the female of *E. kuwanae* jumped on a host caterpillar, *A. albostriata*, for oviposition, the host wriggled violently and sometimes shook its head and disgorged some green secretion to protect itself from the attacker. Under such circumstances, no drumming by the female parasitoid took place prior to oviposition.

WYLIE (1967) suggested that piercing by the ovipositor of a parasitoid would bring about gradual chemical and/or physical changes in the host and they would be perceived by another female parasitoid which inserted her ovipositor into the host later. It is guessed that a similar phenomenon may also appear in the process of oviposition by *E. kuwanae*, for it was observed that the female, in spite of external parasitoid, pierced the host body with her ovipositor before fastening her eggs on the host with pedicels. However, this does not seem to be decisively important for *E. kuwanae*, since its ability to estimate the host size does not disappear even when it attacks a parasitized host in which chemical or physical changes are supposedly progressed.

When the female of *E. kuwanae* encountered a host caterpillar feeding on a leaf, she performed a peculiar “dance” mainly consisting of walking sideways, keeping a constant distance from the host. During this dance the female frequently directed her antennae towards the head of the host without touching it, and then she jumped on the host caterpillar. This inspection of the host by the parasitoid may be related to her ability to estimate host size. The same behavior has also been observed by NESER (1973) on *Euplectrus* sp.

In the experiment for clarifying sex ratio in the parasitoid, 438 adults emerged and 279 of them were females. As seen in Fig. 2, the percentage of females emerging

<table>
<thead>
<tr>
<th>Host weight Class</th>
<th>No. of egg clusters examined</th>
<th>No. of eggs per cluster (mean±s.e.)</th>
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<tbody>
<tr>
<td>&lt;10 mg</td>
<td>15</td>
<td>5.9±0.4</td>
</tr>
<tr>
<td>10–30</td>
<td>68</td>
<td>9.0±0.3</td>
</tr>
<tr>
<td>30–50</td>
<td>44</td>
<td>11.7±0.5</td>
</tr>
<tr>
<td>50–70</td>
<td>17</td>
<td>12.9±1.2</td>
</tr>
<tr>
<td>70–90</td>
<td>10</td>
<td>16.5±0.9</td>
</tr>
<tr>
<td>&gt;90</td>
<td>15</td>
<td>18.3±1.8</td>
</tr>
</tbody>
</table>
Fig. 2. Relationship between host size and sex ratio in emerged parasitoids. Vertical lines show ranges of sex ratio for 95% C.L.

Fig. 3. Relationship between host weight per parasitoid egg and sex ratio in emerged parasitoids. For explanation of vertical lines see Fig. 2.

from hosts in the smallest size class was extremely low, the average being only 9.4%. On the contrary, in all of the larger classes it was more than 50%.

Relationships between host weight per parasitoid egg and sex ratio in emerged adult parasitoids are shown in Fig. 3. Percentage of females was significantly lower in the lowest class of host weight per parasitoid egg than in any of the other classes.

Many insect parasitoids are known to lay more fertilized eggs, which are able to develop to females, in larger hosts (Assem, 1971; Aubert, 1959; Brunson, 1937; Sandlan, 1979; Neser, 1973; Salt, 1934). Such maternal regulation in oviposition is profitable because female progeny usually require more nutrition for development
than males. It can be said that in *E. kuwanae*, females not only lay fertilized eggs in high proportion on large hosts, but also manipulate the size of egg cluster to allocate sufficient food resource for female progeny.

**Ovipositional discrimination by parasitoid between healthy and parasitized hosts**

When healthy and already parasitized hosts were offered side by side, a female parasitoid selected the former in significantly higher frequency (Table 2). At the same time, it should be noted that the parasitoid attacked the already parasitized hosts at a rate of almost one of four times. These results indicate that the parasitoid is able to distinguish between healthy and already parasitized hosts, though the distinction is not perfect.

**Reactions of female parasitoid to the eggs laid by another parasitoid on the surface of a host larva**

After jumping upon the thoracic segments of a host larva, the parasitoid female immediately inserted her ovipositor into the body of the host to paralyze it completely, and then usually moved to the abdominal segments without folding her ovipositor. In the course of her movement, if the female encountered parasitoid eggs which had already been deposited by another female, she always persistently destroyed them by stinging them with her ovipositor. If such an encounter did not take place, the previously deposited eggs were left intact. Table 3 shows frequency of the destruction behavior shown by the second attacker.

**Oviposition to the already parasitized host**

As seen in Fig. 1 and Table 4, previpositional period and the number of eggs deposited per female were significantly different between healthy and already parasitized hosts. These results suggest that an *E. kuwanae* female has a faculty of refraining to a certain extent from attacking the already parasitized host which she has encountered.

It was often observed that when a female parasitoid laid her eggs without destroying all the eggs which had already been laid by another female, the second at-

<table>
<thead>
<tr>
<th>Host condition</th>
<th>Frequency</th>
</tr>
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<tbody>
<tr>
<td>Healthy</td>
<td>29\textsuperscript{*}</td>
</tr>
<tr>
<td>Parasitized</td>
<td>11\textsuperscript{*}</td>
</tr>
</tbody>
</table>

\textsuperscript{*} \chi^2=8.1, P<0.01

<table>
<thead>
<tr>
<th>Reaction</th>
<th>Frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>Failure to encounter</td>
<td>16\textsuperscript{*}</td>
</tr>
<tr>
<td>Destruction of some of the eggs</td>
<td>6 \textsuperscript{*}</td>
</tr>
<tr>
<td>Destruction of all the eggs</td>
<td>64 \textsuperscript{*}</td>
</tr>
</tbody>
</table>

\textsuperscript{*} \chi^2=33.9, P<0.01
Ovipositional Behavior in *Euplectrus* 449

<table>
<thead>
<tr>
<th>Host</th>
<th>Preovipositional period (days)</th>
<th>Mean no. of egg clusters</th>
<th>Mean no. of eggs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Healthy</td>
<td>3.0a</td>
<td>8.4a</td>
<td>96.5b</td>
</tr>
<tr>
<td>Parasitized</td>
<td>4.4a</td>
<td>6.1a</td>
<td>62.8b</td>
</tr>
</tbody>
</table>

* Significant difference at 5% level.
* Significant difference at 1% level.

tacker’s progeny were seriously affected by those of the first attacker. The following example can be regarded as extreme. A parasitized host larva bearing 17 eggs was attacked by a second attacker. She destroyed 16 of the first attacker’s eggs before laying her own six eggs on the host. Then, the remaining undestroyed first attacker’s egg successfully developed to the adult stage, while all the progeny derived from the second attacker died out during the larval stage without showing any physical combat between them. This was probably caused by the death of the host or a physiological deterioration in the host prior to the maturation of the second attacker’s progeny. In this connection, it is guessed that the degree of time lag between oviposition of the first and second attackers would be of the most importance for determining whether the second attacker’s progeny are able to develop or not.

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REFERENCES


The paper marked with an asterisk was cited from Clausen (1962).