

Host-tree Conditions Affecting the Oviposition Activities of the Woodwasp, *Sirex nitobei* Matsumura (Hymenoptera: Siricidae)

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Experiments were conducted to elucidate how the oviposition activities of *Sirex nitobei* Matsumura could be affected by different conditions of the host trees, using logs from felled healthy trees and the dead and living trees of *Pinus densiflora* Sieb. et Zucc. According to days elapsed after tree-felling, the proportions of oviposition, defined as the proportion of eggs laid to the potential fecundity of a female during her lifetime, could be divided arbitrarily into three groups. The proportions of oviposition on the logs within 0–3 days after felling, *i.e.* fresh logs, varied greatly from log to log, and about half of female adults showed proportions of oviposition under 50% (mean \pm SD: $39 \pm 32\%$). However, all the females that oviposited on the logs 4–24 days after felling, *i.e.* intermediate logs, invariably showed proportions of oviposition over 50% ($88 \pm 15\%$). On the other hand, proportions of oviposition in most of the females that oviposited on the logs over 25 days after felling, *i.e.* old logs, were less than 50% ($26 \pm 17\%$). The proportions of oviposition were significantly different between intermediate logs and old logs. The mean proportion of oviposition on living trees and that for dead trees were 45 and 58%, respectively. Thus, *S. nitobei* in the field would exhibit its preference for weakened trees of *P. densiflora* as oviposition sites, as it did for the logs 4–24 days after felling in this study.

Key words: host-tree condition, oviposition activity, *Pinus densiflora*, *Sirex nitobei*, woodwasp

Woodwasps have a specific feeding habit in that their larvae feed exclusively on the sapwood of various coniferous and broad-leaved trees. Most species of woodwasp carry arthrospores of one of specific fungi, *Amylostereum* spp., as a symbiont in a pair of small intersegmental sacs in the body. Soon after a short dispersal flight following emergence, females make several oviposition holes through the bark deep into the sapwood of new host trees and then deposit arthrospores of the fungus, which are presumed to produce enzymes capable of decomposing cellulose and/or lignin of the wood tissue (Kukor and Martin, 1983), and “mucus,” an plausible phytotoxic secretion (Coutts, 1969b; Madden, 1988) or a suspected wetting agent (Sano, *per. com.*), together with eggs, in the holes (Madden, 1988; Morgan, 1968; Talbot, 1977).

In the 1960–1970s, a great number of trees of *Pinus radiata* D. Don in Australia were killed due to heavy infestations of *Sirex noctilio* Fabricius, and this incident has been known as a typical example of the damage to trees presumably due to coaction of the symbiotic fungus and mucus (Coutts, 1969a, b; Madden, 1988). In Japan, *Sirex nitobei* Matsumura attacks various coniferous species, mostly pine trees (Kanamitsu, 1978). This species may be responsible for the larger part of the local mortality of pine trees than has ever been considered (Kobayashi *et al.*, 1978).

S. nitobei is distributed all over Japan except for Hokkaido Island. The life cycle of this species is usually completed in one year (Kanamitsu, 1978; Takeuchi, 1962), and the adult longevities are about four days for each sex (Fukuda *et al.*, 1993).

S. nitobei is symbiotically associated with the specific fungus, *Amylostereum areolatum* (Terashita, 1970). This wood-

wasp species constructs single or multiple drills in the xylem through a oviposition hole through the phloem when it lay eggs on the trunk of a tree. When a single drill is made, only the arthrospores of the fungus and mucus are deposited, whereas in the case of multiple drills, the fungus and mucus are deposited into one drill, and one or more eggs is laid into each of the other drills (Fukuda *et al.*, 1993; Kanamitsu, 1978). Madden (1974) emphasized that the tendency of a female adult of *Sirex noctilio* to make single or multiple drill(s) was closely related to the physiological status of the host tree at the drilling site measured in terms of its osmotic pressure, *i.e.*, female adults of this species changed the number of eggs laid per oviposition hole according to the osmotic pressure of the living host trees.

It is known that *S. nitobei* usually produce about 40–400 eggs, and the proportions of eggs actually deposited by the woodwasp into host trees were suggested to vary greatly with host-tree conditions (Fukuda *et al.*, 1993). Thus, we conducted an oviposition experiment to elucidate how the oviposition activities of *Sirex nitobei* could be affected by different conditions of the host trees, using logs from freshly felled trees and dead and living trees of *Pinus densiflora* Sieb. et Zucc.

Materials and Methods

1 Collection of infested sample trees and emerging adults of *S. nitobei*

Sample trees were taken from the following two mixed stands: 1) the Tokyo University Forest in Aichi, Seto City, situated about 20 km east of Nagoya City, denoted as “Seto,” and 2) Nagoya University Campus in Nagoya City, denoted as “Nagoya.”

On the Seto plot, a total of 22 1-m long logs infested by *S. nitobei* were collected: 10 logs from a tree of Japanese red pine, *Pinus densiflora*, in August 1992 (abbreviated as Seto-92 logs) and 12 logs from another red pine in July 1993

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Table 1 Sample trees of *Pinus densiflora* and emergence periods of *Sirex nitobei*.

| Tree No. | Tree height (m) | No. of logs* | Site | Date of tree-felling | Period of emergence | Population code of woodwasps |
|----------|-----------------|--------------|--------|----------------------|---------------------|------------------------------|
| 1 | 18 | 10 | Seto | Aug. 1992 | Aug.-Nov. 1992 | Seto-92 |
| 2 | 17 | 12 | Seto | July 1993 | Aug.-Nov. 1993 | Seto-93 |
| 3 | 8 | 4 | Nagoya | May 1993 | Aug.-Nov. 1993 | Nagoya-93 |

* Number of logs (1-m long) taken from each sample tree.

(Seto-93 logs) (Table 1). Both pine trees had probably been infested with the woodwasp while they had been alive. On the Nagoya plot, four logs from a tree of *P. densiflora* were collected in May 1993 (Nagoya-93 logs) (Table 1). All logs were transferred to an outdoor cage on the Nagoya University Campus.

During the period from August to November in 1992 and 1993, we collected new adults of *S. nitobei* emerging from the logs every day and measured their fresh body-weights soon after emergence. The body-weight of females in this study includes the weight of their eggs because most eggs have already been matured at the time of emergence.

2 Estimation of realized fecundity

It is difficult to determine the exact number of eggs actually laid in the wood because females of the woodwasp drill and oviposit through the bark deep into the sapwood of host trees. Thus, the potential fecundity of a female (N_P) was estimated using the regression that had previously been constructed (Fukuda *et al.*, 1993). The regression is given by the formula:

$$N_P = 1.86 W^{0.92} (n = 42, r^2 = 0.94, p < 0.01). \quad (1)$$

From the body-weight (W) of a female determined before oviposition and the number of eggs remaining in the female body after oviposition (N_R), the number of eggs actually laid by the female (N_L) and the proportion of oviposition (P_E) (defined as the proportion of eggs laid to the potential fecundity of a female during her lifetime) were estimated as follows (Fukuda *et al.*, 1993):

$$N_L = N_P - N_R, \quad (2)$$

$$P_E = (N_L/N_P) \times 100 [\%]. \quad (3)$$

3 Relationship between condition of host trees and oviposition activity

1) Effect of days elapsed after tree-felling (Experiment 1). One experiment was conducted to elucidate the relationship between a host-tree condition of *P. densiflora*, evaluated in terms of days elapsed after tree-felling, and the proportion of oviposition.

A total of 43 newly-emerging female adults, eight from the Seto-92 population, four from the Seto-93 population and 31 from the Nagoya-93 population were randomly selected from each population for the experiment. After weighing on a microbalance at the time of emergence, all of the females were allowed to mate with males emerged on almost the same day from the same population. One day after emergence, they were individually placed in a clear cylindrical container made of polyvinyl chloride (30 cm in diameter and 1.1 m long) under a laboratory condition (about 25 °C) and were allowed to oviposit on a total of 43 1-m long logs (8–15 cm

in diameter) taken from 6 felled healthy trees of *P. densiflora* in the Seto plot, 0–63 days after felling at the beginning of woodwasp oviposition. All the logs were kept in the outdoor cage on the Nagoya University Campus until the oviposition experiment after applying silicone paste to the cross section of each log to prevent desiccation. None of logs with a bark thickness 2 mm and over were used in order to exclude the influence of bark thickness on the oviposition behavior.

The number and proportion of eggs laid actually into the logs were estimated using Eqs. (1)–(3). Moreover, the number of oviposition holes on each 1-m log was also determined in order to estimate the number of eggs laid per oviposition hole. Due to the great difficulties in locating oviposition holes, they were only counted in about two-thirds of all the logs (28/43 logs).

2) Effect of status of trees of *P. densiflora*: dead, alive or felled (Experiment 2). Another oviposition experiment was conducted during the period from September to October, 1994. In this experiment, the condition of the host trees of *P. densiflora* was evaluated according to three categories: dead, alive or felled. A total of 40 new female adults were randomly selected from the Nagoya-94 population, the next generation of the Nagoya-93 population. The females were treated in the same manner as in Experiment 1. Four living trees (L1–L4) and two dead trees, which died of pine wilt disease between the summer and fall of 1994 in the Nagoya plot, were used for this oviposition experiment. Five females per tree were released into a 1-m long net (34 × 32 mesh per inch) wrapped around the stem at the breast height of each tree with a bark thickness under 2 mm at that position and were allowed to oviposit one day after emergence.

For the experiment using felled trees, one living tree of *P. densiflora* was cut in late September, 1994 in the Inabu Town situated about 70 km east of Nagoya City and divided into 1-m long logs. All these logs were transferred and kept in the outdoor cage on the Nagoya University Campus after applying silicone paste to the cross section of each log to prevent desiccation. Of them, only two logs with a bark thickness under 2 mm (8–12 cm in diameter) were used about 10 days after tree-felling at the beginning of woodwasp oviposition. Five females from the Nagoya-94 population were released for each log in same manner as in Experiment 1.

Results

1 Effect of days elapsed after tree-felling (Experiment 1)

1) The proportion of oviposition. Based on days elapsed after tree-felling, the status of the logs used for the

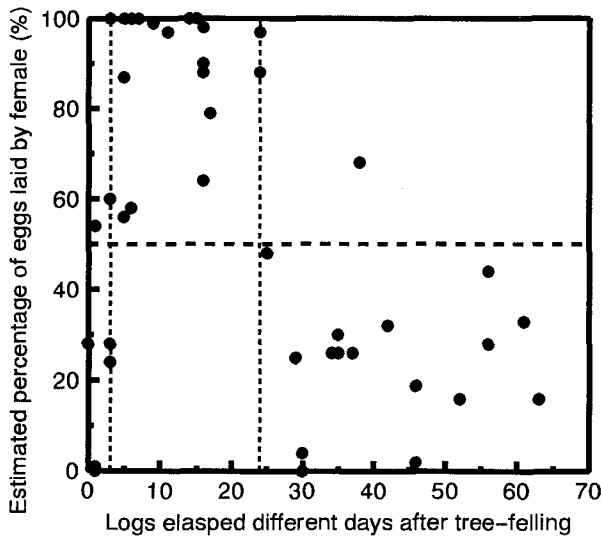


Fig. 1 Relationship between logs elapsed different days after tree-felling and estimated percentage of eggs laid per female of *S. nitobei*.

experiment could be arbitrarily divided into three groups: 0–3, 4–24 and over 25 days after tree-felling (Fig. 1). The proportions of oviposition during their lifetime on the logs within 0–3 days after felling at the beginning of woodwasp oviposition (denoted as “fresh” logs) varied greatly from log to log, and about half of the female adults (56%) showed proportions of oviposition under 50% (mean \pm SD: $39 \pm 32\%$, $n = 9$) (Fig. 1). However, all the females that oviposited on the logs 4–24 days after felling, *i.e.*, “intermediate” logs, invariably showed proportions of oviposition over 50% ($88 \pm 15\%$, $n = 17$). On the other hand, proportions of oviposition in most of the females (94%) that oviposited on the logs over 25 days after felling (“old” logs) were less than 50% ($26 \pm 17\%$, $n = 17$) (Fig. 1). The proportions of oviposition were significantly different between intermediate logs and old logs (Scheffe’s multiple range test; $p < 0.05$).

The fresh body-weight of female adults was not correlated with estimated number of eggs laid on fresh logs ($r = 0.47$, $p > 0.05$), but was highly correlated with those on intermediate and old logs. The linear regressions for the relationships between fresh body-weight of female adults (W) and estimated number of eggs laid (N_L) on intermediate and old logs are given by Eq.(4) and Eq.(5), respectively.

$$N_L = 1.04 W - 2.20 \quad (n = 18, r^2 = 0.87, p < 0.01), \quad (4)$$

$$N_L = 0.34 W - 1.14 \quad (n = 17, r^2 = 0.67, p < 0.01). \quad (5)$$

However, the gradients of the regression lines were significantly different between intermediate logs and old logs (t -test, $p < 0.01$) (Fig. 2). This means that for the same body size, female adults could oviposit more eggs on intermediate logs than on old logs.

2) The number of eggs laid per oviposition hole. The estimated number of eggs laid per oviposition hole averaged about 1.5, ranging from 0.8 to 2.2 (Fig. 3). Although there were no correlations between fresh body-weight of a woodwasp and number of eggs laid per oviposition hole, the mean number of eggs laid per oviposition hole was significantly dif-

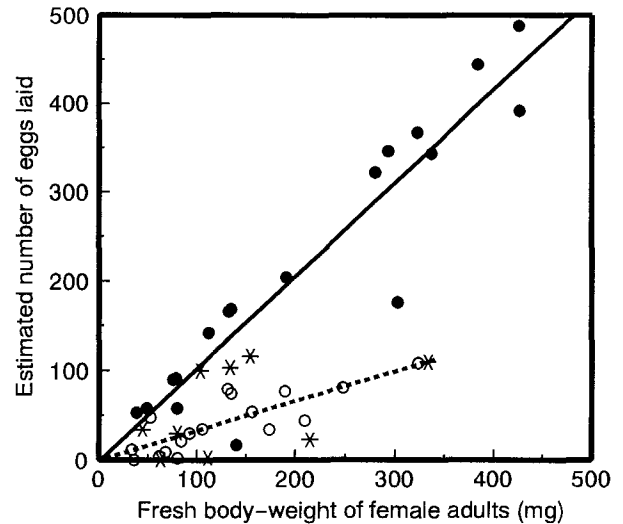


Fig. 2 Relationship between fresh body-weight of a female adult and estimated number of eggs laid per female of *S. nitobei*. *, Host trees within three days after tree-felling; ●, host trees 4–24 days after tree-felling; ○, host trees felled more than 25 days before. Note: Linear regressions are given by Eq. (4) (—●—) and Eq. (5) (---○---) in the text.

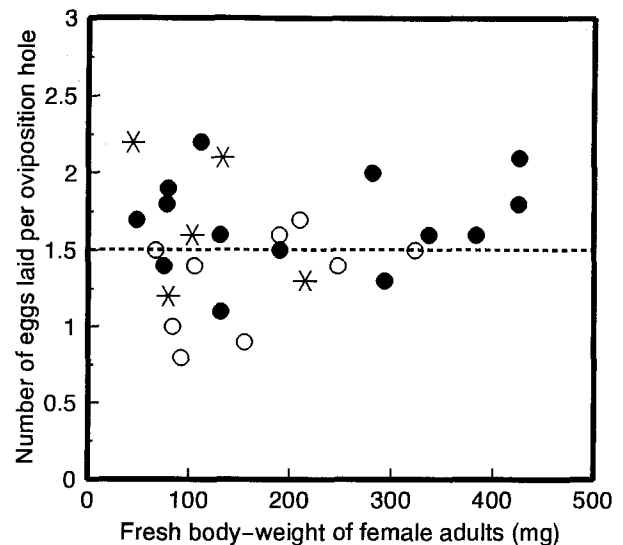


Fig. 3 Relationship between fresh body-weight of a female adult and estimated number of eggs laid per oviposition hole constructed by a female adult of *S. nitobei*. *, Host trees within three days after tree-felling; ●, host trees 4–24 days after tree-felling; ○, host trees felled more than 25 days before. Note: A broken line indicates the mean (1.5).

ferent between intermediate logs and old logs (Scheffe’s multiple range test; $p < 0.05$) (Fig. 3).

2 Effect of status of trees of *P. densiflora*: dead, alive or felled (Experiment 2)

The mean proportion of oviposition for 20 individuals on four living trees of *P. densiflora* and that for 10 individuals on two dead trees were 45 and 58%, respectively (Fig. 4). On the other hand, female adults showed high proportions of oviposition (86% on average) on the logs from the felled tree, as was the case on the intermediate logs in Experiment 1 (Figs. 1 and 4).

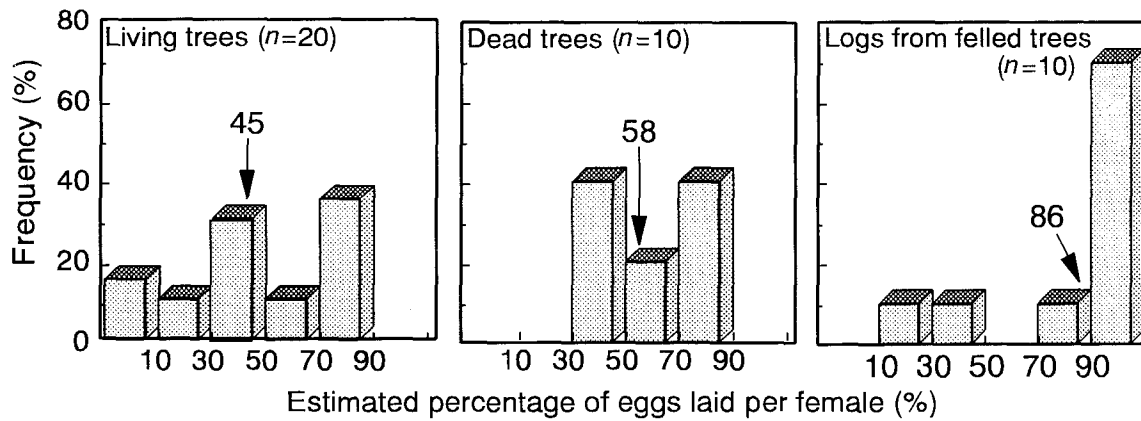


Fig. 4 Difference in the proportion of oviposition of *S. nitobei* on living trees, dead trees and logs from felled tree of *P. densiflora*. Note: Arrow indicates the mean %.

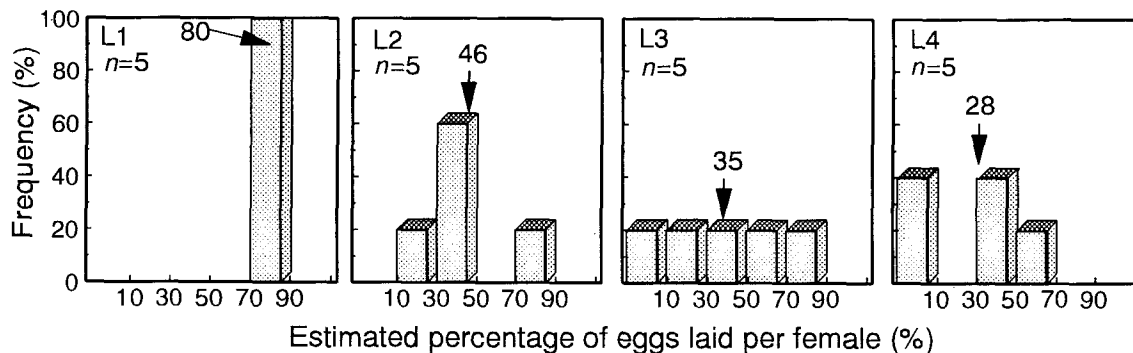


Fig. 5 Difference in the proportion of oviposition among four living trees (L1-4) of *P. densiflora*. Note: Arrow indicates the mean %.

On living trees, the frequency distributions for the proportion of oviposition were remarkably different in shape among the individual trees (Fig. 5).

Discussion

Figures 1 and 2 suggest that the oviposition success of the woodwasp would critically depend on the condition of a host tree at the time of oviposition, and may also suggest that the old logs used for the oviposition experiment (Experiment 1) were less acceptable to woodwasps for oviposition in physical and/or physiological status than those expected in the field where the woodwasps themselves can search for the most suitable host trees.

Considering their great efforts in the oviposition activity specific to woodwasp species, the average egg load of 1.5 per hole appears to be considerably low relative to the large potential fecundity (40–400 eggs per female) of this species. The oviposition system of this species is that a female adult drills many oviposition holes over the trunk of a host tree and then carefully oviposits a small number of eggs in each of oviposition holes so as to avoid intraspecific competition. It may be that such an oviposition system could guarantee comparatively high survivorship of this species under a parasite-free condition, as shown by Kanamitsu (1978).

Although the numbers of eggs laid per oviposition hole on the fresh logs varied greatly, those on the intermediate logs

were significantly larger than those on the old logs (Fig. 3). This fact suggests that the female adults of this species altered the number of eggs laid per oviposition hole on logs according to days elapsed after tree-felling, similarly on living trees according to the osmotic pressure (Madden, 1974). Female adults may have a tendency to deposit more eggs on suitable sites.

The averaged proportion of oviposition of *S. nitobei* on living trees of *P. densiflora* was lower than that on the logs from felled trees (Fig. 4), and varied greatly among the four sample trees (Fig. 5). The variance in the proportion of oviposition on the dead trees was smaller than that on the living trees, and moreover, the averaged proportion of oviposition on the dead trees was lower than that on the logs from the felled tree of *P. densiflora* (Fig. 4). These results were similar to those of Experiment 1; the proportions of oviposition varied greatly on the within-3-day logs, were high on the 4–24-day logs, but were low on the over-25-day logs. Thus, the host-tree preference in oviposition by *S. nitobei* for the living trees and for the dead trees would correspond with the preference for the within-3-day logs and that for the over-25-day logs, respectively. The greater variance in the proportion of oviposition on the living trees might reflect the differences in tree vigor among individual trees.

S. nitobei had a lower preference for oviposition sites in both living trees of *P. densiflora* with higher vigor and dead

trees that had already been invaded by decay fungi and/or other boring insects, both of which were markedly different in physical and biochemical qualities from intermediate or optimum logs. Lower preference for vigorous trees is probably because ovipositing females will have diminished oviposition behavior or deposited eggs will be covered over with resin or because the growth of inoculated fungus into the wood could be prevented by polyphenol formation (Coutts and Dolezal, 1966; Madden, 1988).

On the other hand, in dead trees, the growth of inoculated *Amylostereum* fungus could be restrained due to antagonism with other fungal species or physical and biochemical changes in the wood. Actually in the field, the host-tree preference for oviposition sites of *S. nitobei* would be judged from the activities of resin flow and/or volatile components (e.g. α - and β -pinene) of the host trees (Simpson, 1976). Thus, *S. nitobei* in the field would exhibit its preference for weakened trees of *P. densiflora* as oviposition sites, as it did for the logs 4–24 days after felling in this study. Also, in another woodwasp species, *Sirex juvencus*, chiefly attacks trees weakened by insect attack and newly killed trees (Stillwell, 1960, 1966). Even *S. noctilio*, considered to be a primary insect, is also attracted to physiologically stressed trees (Madden, 1977).

Clarification of the reproductive success of *S. nitobei* will require further information on its survival after the egg stage presumably affected by parasitism and/or physiological resistance and by changes in the physical and/or biochemical qualities of host trees after oviposition. The conditions of host trees after oviposition, in particular, would be closely related with the propagation success of the fungal symbiont injected in the wood tissues, which may be a critical factor affecting the fitness components of *S. nitobei*.

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