

# Oviposition behaviour and response of *Monochamus scutellatus* (Coleoptera: Cerambycidae) to conspecific eggs and larvae

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- Abstract**
- 1 The oviposition behaviour of white-spotted sawyer beetle *Monochamus scutellatus* (Say) (Coleoptera: Cerambycidae) females was studied under laboratory and field conditions.
  - 2 Females walked over the bark surface and stopped to palpate it with their labial and maxillary palpi. Once a potential oviposition site was located, the female excavated a scar in the bark with her mandibles, deposited an egg and brown plug in the scar and inserted her mandibles again into the scar prior to leaving the area.
  - 3 Female *M. scutellatus* preferred to lay eggs on bolts containing no eggs (control) to those containing eggs from other females, but did not show this preference when provided with control bolts and those containing their own eggs. When females were provided with bolts containing their own eggs and bolts containing eggs from other females, they laid more eggs on bolts containing their own eggs. Females laid more eggs on control bolts than on bolts containing their own larvae or larvae from other females.
  - 4 The brown plug in the oviposition scar may provide a protective barrier to the egg, a chemical message that the site is occupied, or both.

**Keywords** Cerambycidae, choice bioassay, oviposition behaviour, oviposition deterrence.

## Introduction

The white-spotted sawyer beetle *Monochamus scutellatus* (Say) (Coleoptera: Cerambycidae) is found throughout most of North America (Yanega, 1996) and attacks recently killed, weakened and dying conifers, or fresh logging debris. Males arrive first at mating sites and guard territory until arrival of the female. Males copulate repeatedly with females and often disrupt oviposition (Hughes & Hughes, 1985). Eggs are deposited in scars excavated in the bark. Larvae feed in the phloem and eventually tunnel into the xylem, where they pupate after one or two years (Gardiner, 1957). Upon emergence, adults feed on young twigs and foliage of conifers during a maturation period before mating (Rose, 1957).

Oviposition behaviour has been examined in several species of *Monochamus* in North America and Japan (Shibata, 1984; Walsh & Linit, 1985; Edwards & Linit, 1991; Jikumaru *et al.*, 1994; Anbutsu & Togashi, 1996, 1997a, 2000; Zhang & Linit, 1998; Akbulut & Linit, 1999a, b), but there has been no detailed examination of oviposition behaviour of *M. scutellatus*. In the Japanese pine sawyers, *Monochamus alternatus* Hope and *M. saltuarius* (Gebler), females are deterred from ovipositing in the presence of conspecific eggs or larvae (Anbutsu & Togashi, 1996, 1997a, 2000). In some species of *Monochamus*, larvae consume conspecific eggs or larvae, or engage in combat resulting in death of larvae if they encounter each other in the phloem (Victorsson & Wikars, 1996; Anbutsu & Togashi, 1997b). The site chosen for oviposition therefore may be important to reduce larval competition and cannibalism. Our objective was to describe the sequence of oviposition behaviour in female *M. scutellatus*, and to examine how the presence of her own or conspecific eggs or larvae affects oviposition choices.

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## Methods

### Insects

Adults of different age used in 1998 were hand-collected in June and July from red pine (*Pinus resinosa* Ait.) trees cut in the winter, c. 25 km NE of Thessalon, Ontario, Canada (46°20'N 83°33'E). Beetles were also hand-collected in July and August 1999 from recently felled jack pine (*P. banksiana* Lamb.) trees at a clear-cut site in Lawlor Township, c. 140 km NE of Thessalon (47°05'N 82°50'E). The sex of beetles was determined by antennal length (Yanega, 1996) and verified by examination of the internal genitalia of 30 adults. Insects were held individually in screened plastic cages (12 cm long × 7 cm wide × 4 cm high) in environmental chambers (20 °C, LD 16:8 h, 70% RH) and provided a jack pine twig and a 15% aqueous sugar solution on cotton batting for nourishment 2–3 days prior to the experiments.

### Oviposition behaviour

Preliminary observations of oviposition behaviour were made in 1998 at field sites in early to mid-afternoon, when insects were most actively mating and females were laying eggs. In the laboratory, behaviour was usually observed in early to mid-afternoon, under fluorescent lighting (900–950 lux) at 25 °C. Male and female pairs were placed separately in plastic cages (30 cm long × 20 cm high × 11 cm wide) containing a red pine log (10 cm long × 10 cm diameter, hereafter referred to as bolts) for oviposition, and provided a jack pine twig for feeding. Behaviour was divided into components based on the movement and use of various body parts by the female; these components were timed with a stopwatch. The oviposition behaviour of some females was observed more than once after a rest period of 24 h.

### Response of females to eggs and larvae in choice tests

Five experiments were conducted to determine how the abundance and distribution of eggs of an ovipositing female were affected by the presence of eggs or larvae. In the first experiment, a female was given a choice between a bolt containing her own eggs (treatment) and one without eggs (control). Experiment 2 consisted of a choice between a control bolt and one that contained eggs from a different female. In experiment 3 a female was given a choice between a control bolt and a bolt containing her own larvae. In the fourth experiment, a female was given a choice between a control bolt and one that contained larvae from a different female. In experiment 5, a female was given a choice between a bolt containing her own eggs, and one containing eggs from a different female. Experiments 1–4 were conducted in 1998 and experiment 5 in 1999.

Red pine trees cut in June prior to the adult flight season were held about 4 weeks in the laboratory at 25 °C prior to use in choice tests. Bolt sections (10 cm long × 10 cm diam) were cut from these as needed and labelled. The bolts used in each choice test were contiguous from the same tree so as

to provide similar bark thickness, phloem quality and moisture.

To obtain the treatment bolts (i.e. those with eggs or larvae), individual bolts were randomly assigned to 'own eggs' (Experiments 1 and 5), 'conspecific eggs' (Experiments 2 and 5), 'own larvae' (Experiment 3) or 'conspecific larvae' (Experiment 4). For each bolt a single female was allowed to oviposit for 24 h and then removed. The bolts with eggs (Experiments 1, 2 and 5) were used within 3–5 days of initial oviposition for the choice tests and those with larvae (Experiments 3 and 4) were used after 2–3 weeks when first instars were present. For experiments 1, 2 and 5, we examined the treatment bolts for larvae, 5, 7 and 10 days after eggs were deposited and found none. In the field, Rose (1957) found larvae 9–14 days (mean 12 days) after oviposition.

Prior to the choice tests, the treatment bolts were examined to determine the number of oviposition scars (scars cut in the bark by a single female to facilitate placement of the egg underneath the bark) and eggs present. Once located, each scar was marked with a small dot with a permanent ink marker (Anbutsu & Togashi, 1996). In preliminary work, we did not observe an apparent effect of the marker on host choice. Because not all oviposition scars result in egg deposition, the scars were examined under a stereomicroscope for the presence of the brown jelly-like plug. Preliminary studies indicated that 96% (51 of 53) of scars containing an egg also contained the brown plug. This allowed determination of the presence of an egg in an oviposition scar without destroying the oviposition site for the choice tests. Thus, if a plug was visible, the scar was assumed to contain an egg, whereas any scar without this plug was assumed to be empty. Anbutsu & Togashi (2000) found that 94% of *M. alternatus* oviposition scars contained a plug; all of these contained eggs, whereas those without plugs had no eggs.

For each experiment, a replicate consisted of a single female in a cage with a pair of bolts (i.e. control and treatment), together with a jack pine twig and sugar water solution. The screened plastic cage was 30 cm long × 11 cm wide × 20 cm high, with the two bolts placed along two adjacent sides with their ends about 5 cm apart. The jack pine twig was placed in the far corner away from the logs and the sugar solution was placed in the middle of the cage. A single male was included with each female because mating pairs are often observed in the field (Hughes & Hughes, 1985; personal observation) and the absence of the male may or may not influence oviposition behaviour or choice. The female was allowed access to the bolts for 48 h, after which both bolts were removed for examination of the number of new oviposition scars and eggs. Some females were used again but only for another experiment. These females were numbered and after a rest period of 24 h, where they were not exposed to eggs or larvae, they were assigned randomly to the new experiment.

A Mann–Whitney Rank Sum test was used to determine if the total duration of oviposition by females differed under field and laboratory conditions. For the choice tests, the numbers of scars cut, eggs laid and subsequent oviposition

success (the number of eggs deposited/number of scars excavated) in each bolt were compared using the Wilcoxon signed rank test at  $\alpha = 0.05$  (Zar, 1999) calculated with SigmaStat<sup>®</sup> (1997, version 2.03, SPSS Inc., Chicago, IL) software.

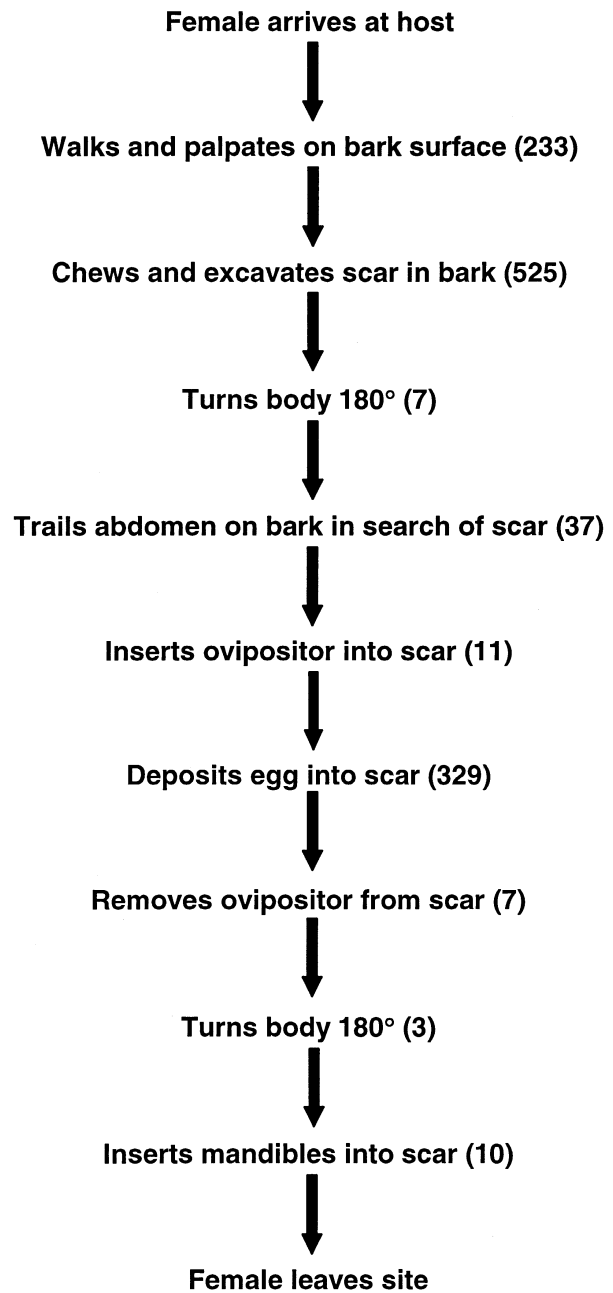
## Results

### Oviposition behaviour

Observations were made of 35 oviposition events involving 14 females over a total of 13 h in 1998, and of 23 oviposition events involving 13 females over a total of 22 h in 1999. Of the 58 observations, 10 were of females in the field and the remaining 48 were of females in the laboratory. The sequence of oviposition behaviour was observed and divided into 11 components (Fig. 1). The components of the sequence were identical and stereotypic in both the field and the laboratory, and there was no significant difference between total amount of time spent on oviposition for females under field or laboratory conditions ( $T = 216$ ,  $P = 0.106$ ).

Upon arrival on the pine bolt, a female began walking and intermittently palpating the bark surface with her maxillary and labial palpi. Antennal preening was observed prior to searching behaviour but was not here considered as part of oviposition behaviour. Females spent a mean of 233 s ( $\pm 24$  SE), or about 20% of the total time, walking over the surface of the bolt before finding an oviposition site (Fig. 1). The female then excavated a scar in the bark with her mandibles, taking about 525  $\pm 61$  s to complete the scar. After excavating, the female turned 180° ( $7 \pm 1$  s), trailed her abdomen along the surface until the scar was found ( $37 \pm 7$  s) and then inserted the ovipositor into the newly excavated scar ( $11 \pm 1$  s). Oviposition lasted 329  $\pm 38$  s and included rubbing the scar with the tip of abdomen. Once the ovipositor was removed from the scar ( $7 \pm 1$  s), the female turned 180° ( $3 \pm 0.5$  s) and inserted her mandibles into the scar for about 10  $\pm 2$  s before walking away. After depositing the egg, the female deposited a light brown jelly with her abdomen that plugged the oviposition scar cut into the bark. In total, females spent about 19 min in searching for an oviposition site, excavating and laying an egg in each scar.

When males were not in the vicinity of females, the oviposition sequence showed little variation for all females observed. When males were nearby or half-mounted on the females just prior to copulation (Hughes, 1979), the oviposition sequence was sometimes altered or interrupted. The majority of females completed the sequence without interruption by the male (49 of 58 oviposition events). In one event, the female did not complete oviposition, and in the other eight events, the male slowed the progress of oviposition. At indeterminate intervals during oviposition, some males copulated with their female partner, a process that lasted *c.* 30–45 s. In one instance, the male directly interfered with oviposition by mounting a female in the process of ovipositing and immediately forcing her abdomen up out of the scar to copulate.



**Figure 1** Sequence of oviposition events (mean time in seconds) by female *Monochamus scutellatus*.

### Choice tests

When females were offered a choice between a bolt with no eggs and a bolt containing their own eggs, there was no significant difference in the number of scars excavated ( $W = 2.0$ ,  $P = 0.922$ ) or in the number of eggs deposited ( $W = 18.0$ ,  $P = 0.465$ ) (Experiment 1, Table 1). Slightly more than half (56%) of the total number of eggs (based on the number of new eggs deposited) occurred on control bolts and oviposition success did not differ among treatments ( $W = 29.0$ ,  $P = 0.160$ ; Table 1). When females were offered a choice between a bolt with no eggs and a bolt

**Table 1** Response of female *Monochamus scutellatus* to red pine bolts with or without her own eggs or larvae or those from a different female in laboratory choice tests

Experiment	Treatment <sup>1</sup> (N)	No. of scars or eggs on test bolts prior to experiment (mean ± SE) <sup>2</sup>		No. of new scars (mean ± SE)	No. of new eggs (mean ± SE)	Oviposition success (%) (mean ± SE)
		Scars	Eggs			
1	Same female egg (11)	8.4 ± 1.8	6.3 ± 1.6	5.1 ± 1.1a	3.2 ± 0.8a	52.3 ± 9.5a
	Control (11)	0	0	4.7 ± 1.0a	3.5 ± 0.7a	70.6 ± 9.8a
2	Different female egg (27)	18.8 ± 2.2	12.2 ± 1.5	1.7 ± 0.4a	0.8 ± 0.2a	35.3 ± 8.2a
	Control (27)	0	0	8.1 ± 1.1b	5.7 ± 1.0b	62.3 ± 6.1a
3	Same female larvae (10)	11.9 ± 1.6	8.8 ± 1.3	3.9 ± 1.3a	2.3 ± 0.7a	47.1 ± 12.6a
	Control (10)	0	0	9.5 ± 2.2a	4.0 ± 0.6a	61.4 ± 10.8a
4	Different female larvae (28)	19.8 ± 1.5	14.0 ± 1.4	3.5 ± 0.6a	1.8 ± 0.5a	38.3 ± 7.5a
	Control (28)	0	0	8.9 ± 1.4b	5.4 ± 1.0b	53.9 ± 6.8a
5	Same female egg (75)	11.2 ± 0.7a	9.9 ± 0.7a	7.7 ± 0.7a	6.6 ± 0.6a	82.6 ± 3.1a
	Different female egg (75)	12.6 ± 0.7a	10.9 ± 0.7a	6.3 ± 0.6a	5.1 ± 0.5b	69.4 ± 3.7b

<sup>1</sup>Control = no eggs for experiments 1 and 2 and no larvae for experiments 3 and 4.

<sup>2</sup>Means followed by the same letter within a column and experiments are not significantly different at  $P \leq 0.05$ , Wilcoxon Signed Rank Test.

containing eggs from another female, there were significantly more scars ( $W = 334.0$ ,  $P < 0.001$ ) and eggs ( $W = 285.0$ ,  $P < 0.001$ ) laid on the control bolt (Experiment 2, Table 1). Oviposition success was not significantly higher ( $W = 146.0$ ,  $P = 0.051$ ) on the control bolts. About 87% of the total number of eggs were laid on the control bolts.

For Experiment 3, which tested the response of females to their own larvae, the number of oviposition scars cut and eggs laid was not significantly higher ( $W = 29.0$ ,  $P = 0.160$  for scars and  $W = 22.0$ ,  $P = 0.148$  for eggs) in the control bolt than in bolts containing larvae from the same female (Table 1). Similarly, there was no significant difference between these two treatments in oviposition success ( $W = 10.0$ ,  $P = 0.570$ ). About 63% of the total number of eggs were laid on control bolts. When females were offered a choice between a control bolt and a bolt containing larvae from another female, significantly more oviposition scars were cut and eggs were laid on the control bolts ( $W = 245.0$ ,  $P = 0.002$  for scars and  $W = 209.0$ ,  $P = 0.003$  for eggs) (Experiment 4, Table 1). Oviposition success was not significantly different between the two treatments ( $W = 121.0$ ,  $P = 0.127$ ). About 75% of the total number of eggs were laid on control bolts.

When a female was given a choice between a bolt containing her own eggs or one containing eggs from another female, there was no significant difference in the number of scars excavated between the two bolts ( $W = -592.0$ ,  $P = 0.064$ ), but there was a significant difference in number of eggs deposited ( $W = -856.0$ ,  $P = 0.012$ ) and oviposition success ( $W = -846.0$ ,  $P = 0.002$ ) (Experiment 5, Table 1). Prior to the choice tests, there were no significant differences in the number of scars cut ( $W = 699.0$ ,  $P = 0.055$ ) or eggs laid ( $W = 415.0$ ,  $P = 0.245$ ) between treatments.

## Discussion

Females of *M. scutellatus* cut more scars than were used for oviposition. The highest oviposition success observed on control bolts was about 71% (Experiment 1) leaving 29%

of the scars cut but not used for egg deposition. This suggests that females need to excavate the bark before they can fully assess the site for egg deposition. We hypothesize that phloem thickness is critical to the survival of young larvae and that females assess phloem thickness during scar excavation.

The sequence of oviposition events by *M. scutellatus* is similar to that of *M. saltuarius* (Anbutsu & Togashi, 1997a) and *M. alternatus* (Anbutsu & Togashi, 2000). One notable difference is that female *M. scutellatus* inserts the mandibles into the scar after oviposition, whereas the Japanese sawyers *M. saltuarius* and *M. alternatus* apparently do not. The function of post-oviposition mandible insertion remains to be determined.

Female *M. scutellatus* preferred to lay eggs on bolts containing no eggs (control) to those containing eggs from other females (Experiment 1), but did not show this preference when provided with control bolts and those containing their own eggs (Experiment 2). It should be noted that the number of already-made scars and already-deposited eggs in Experiment 1 was about half of those in Experiment 2 and that this difference may have affected the outcome. Nonetheless, when the number of pre-treatment scars and eggs were similar between the two treatments (Experiment 5), females chose to lay more eggs on bolts containing their own eggs than on bolts containing eggs from other females. These data suggest that females can detect the presence of eggs but are also deterred somewhat by the presence of eggs from other females. These results are consistent with Anbutsu & Togashi (1996), who found that *M. alternatus* females were less likely to oviposit on bolts with pre-existing oviposition scars, especially those with scars from a different female. However, in later work Anbutsu & Togashi (2000) concluded that female *M. alternatus* did not discriminate between oviposition scars, either with or without eggs, made by themselves and those by others. Anbutsu & Togashi (1997a) also found no significant difference in behaviour by female *M. saltuarius* to its own eggs and to those of others.

It would seem that there is an adaptive advantage for a female to recognizing her own eggs. Anbutsu & Togashi (2000) found if an egg already occupied an oviposition scar, the survival of the second egg was less than 50%. Thus, we reason that if a female oviposits on a log containing her own eggs, the 50% of new eggs that are killed are actually food for her own first-born larvae. However, if the female oviposits on a log containing eggs from another female, the 50% of eggs that are killed are used to feed a competitor's larvae. Additional studies are needed to clarify the mechanisms by which female *M. scutellatus* respond differently to their own eggs and those from other females. It would also be interesting to determine the response of female *M. scutellatus* to eggs from sympatric and co-inhabiting *M. notatus* Drury and *M. mutator* LeConte, both boreal species coexisting with *M. scutellatus* within the study area.

Females of *M. scutellatus* chose to lay significantly more eggs on control bolts than on bolts containing larvae from other females, but bolts with her own larvae were not avoided as much. Clearly, it would be adaptive for females to avoid laying eggs in zones containing larvae, which are known to be cannibalistic and result in the primary cause of mortality of eggs and larvae (Rose, 1957; Victorsson & Wikars, 1996). Cues for females to avoid oviposition at sites occupied by larvae may include frass (personal observations), sound (Victorsson & Wikars, 1996) or deterioration of the phloem.

Many insects leave chemical markers after egg deposition to reduce the potential costs of intraspecific competition and thus increase their fitness by increasing the survival of offspring (Rauscher, 1979; Prokopy *et al.*, 1984; Roitberg & Prokopy, 1987). *Monochamus scutellatus* has all of the ecological characters that Roitberg & Prokopy (1987) identified as being correlated with host-marking systems, namely it is oligophagous, its hosts (trees) are permanent, larvae have low mobility, and have ephemeral and limited feeding sites. Our studies, and those of Anbutsu & Togashi (1996, 1997a, 2000), show that females palpate the bark surface prior to selecting an oviposition site. Furthermore, females that encountered scars with plugs left the area after palpation. Dyer & Seabrook (1978) observed prolonged periods of palpation by *M. scutellatus* females when they encountered oviposition scars, and suggested that contact chemoreception may play a role in site selection. The brown plug that we observed in scars containing eggs may be analogous to the plug produced by *M. saltuarius* and *M. alternatus* (Anbutsu & Togashi, 1997a, 2000). Recently, Anbutsu & Togashi (2001) showed that female *M. alternatus* recognize egg-containing scars by chemicals emitted from the plug and methanol extracts of female reproductive organs. Further examination of the chemical composition of the plug from *M. scutellatus* is required to determine if the plug acts as a chemical marker of occupancy, as protection from natural enemies or desiccation, or both.

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