

Mating behavior of the pine sawyer, *Monochamus saltuarius* (Coleoptera: Cerambycidae)

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Abstract:

We observed the mating behavior of *Monochamus saltuarius* (Cerambycidae: Lamiinae) and confirmed the following behavioral actions. The male reacted to the female with his antennae or tarsi, the male dashed to the female and mounted her back. Copulation consisted of three phases: First, while bending at the abdomen, the male inserted his penis into the female's genitalia, second, the male is motionless with the female's genitalia being pulled out from her abdomen by the male's penis, outside of both body cavities, finally, the male tries to pull out his penis from the female genitalia. The copulation was shown to take place mostly for one and a half minutes, with a significant tendency to be slightly shortened as the pair progressed from the first through the third copulation. The violent fight between two males took place in the presence of a female and sometimes she changed her mate. The male did not differentiate between dead and live females, because the male mounted dead females as same as live them.

Key words: *Monochamus saltuarius*; mating behavior; copulating duration; fighting; sex pheromone

INTRODUCTION

In Japan, pine tree damage is caused by the pine wood nematode, *Bursaphelenchus xylophilus* (Steiner et Buhner). It is one of the most serious problems in Japanese forestry. Two species of longicorn beetles, *Monochamus alternatus* Hope and *M. saltuarius* (Gebler), are known to be the vectors of the pine wood nematode in Japan. *M. alternatus*, the most critical factor of the pine mortality in Japan, has been repeatedly documented to reveal all aspects of its biology (Kishi, 1995). Among several studies on the mating behavior of *M. alternatus*, those by Fauziah et al. (1987) and Kim et al. (1992) are important since they verified the existence of a volatile male sex pheromone and a non-volatile female sex pheromone.

On the other hand, the biology of another vector species, *M. saltuarius*, has been made clear to a lesser extent. Mating behavior of *M. saltuarius* also has not been reported in detail. As one of the ecological aspects of *M. saltuarius*, we studied and analyzed its mating behavior. In the present investigation, we describe the sequence of its mating behavior and verify how males react toward dead males and female individuals in *M. saltuarius*. In this trial

we paid particular attention to the male behavior of continued mounting on the female's back. The detailed sequence of the male's behavior was recorded. We also observed the male behavior toward a dead individual as well as a live one.

MATERIALS AND METHODS

Insects. Adult beetles of the parent generation of the insects used in this study were field-collected at Tateiwa Village, Minamiaizu District, Fukushima Prefecture from June to July in 1999. These beetles were allowed to copulate on and oviposit on 1 m logs of Japanese red pine, *Pinus densiflora* Sieb. et Zucc., in a field cage at Nihon University Shonan Campus, Fujisawa.

The progeny adults, which emerged from the logs in May of the following year, were used for experiments I and III. The adults were collected from the field cage every morning. They were kept individually in polyethylene containers in which twigs of Japanese red pine were added as food. These containers were kept at a constant temperature of 15°C and photoperiod of 14L–10D (lights on, 6 a.m.; lights off, 8 p.m.). The beetles used for observations were kept for more than 20 days after

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their emergence, during which time they became sexually mature. Each male and female beetles were checked as to whether they had mating potential. Only beetles that showed mating potential were used for the observations. Some of the individuals used in Experiment I were also used in Experiment III.

The beetles for Experiment II were collected at Tateiwa in 1995. The adults were kept individually in the same manner as above. The containers were kept in the laboratory.

Observations of mating behavior in a large petri dish (Experiment I). Mating behavior was observed from June to July 2000 using a large petri dish, 14.6 cm inside diameter and 2.8 cm high, into which a beetle pair was introduced. Observations in the laboratory were conducted from 10 a.m. to 6 p.m. Laboratory temperature during observation was about 25°C. The petri dish was lit with a fluorescent lamp (28 W), located about 1 m above. One male and one female, held by tweezers, were released from opposite sides of the petri dish at the same time. The petri dish and the two pairs of tweezers used for the experiment were wiped with 75% alcohol prior to each observation. The detailed sequence of the male's behavior was recorded.

The first series of observations (Experiment Ia) lasted for less than 40 min and only one complete sequence of mating, involving contact, copulation and detachment, was observed for each pair. Forty new pairs were prepared as replicates and if mounting did not take place within 20 min, this pair was discarded.

After the beetles were used in the first experimental series, we carried out a second series of observations (Experiment Ib), in which up to 3 complete sequences of mating were followed for each pair. In some cases, the female refused by shaking off the male after the first sequence of mating, resulting in failure of the second mating. If the break of contact after such a refusal lasted for 5 min, the observation was terminated. Thirty pairs plus another 30 pairs with different partners were observed as 60 replicates. If mounting did not take place within 20 min, the pair was discarded.

Observations on mating behavior in a large breeding container (Experiment II). Another series of observations on mating behavior were carried out from June to August, 1995 in the labora-

tory, using a breeding container made of plastic with an site of 35 cm×60 cm×30 cm. One Japanese red pine log (8–10 cm in diameter, 50 cm long) and two twigs (30 cm long) were placed in the container as an ovipositing and clinging matrix, on which two males and two females were released. Observation time, lighting and release into the large breeding container were the same as in Experiment I. This time the container wasn't covered with a lid to allow for easy observation of the insects' behavior. There were no cases of beetles' flying away due to the flight-inactive nature of this species. The observation time in this study was 2 h. Five replications were done by preparing new partners and a competitor for each of the beetles employed in the first replication.

Observation of male behavior against a dead individual (Experiment III). Observations on the males' mating behavior toward dead female and male beetles was carried out from 29 May to 1 June, 2000 in the laboratory. A virgin male beetle and a virgin female beetle, more than 20 days after emergence, were killed by freezing at about -30°C for 30 min. The dead individuals about 10–180 min after removal from the freezer, as well as one normal living male, were put into a large petri dish similar to Experiment I. Observation time, lighting and release into the petri dish were the same as for Experiment I. The living male walked around the petri dish and touched the dead individuals very quickly. Then, the male's reaction was observed toward the dead individuals. The observation lasted for 20 min, at most. It terminated if the male did not show any reaction toward the dead individual within this time. Twenty-five living males were used for the experiment as the searching individuals.

Dead individuals used for the experiments were kept in a polyethylene container at room temperature in the laboratory and were sensed for the same experiment 24, 48 and 72 h after the first trial. If the male didn't move or it didn't touch the dead individual while walking, the data male was discarded.

RESULTS

Mating behavior of *Monochamus saltuarius* (Experiment I)

Immediately after the male and the female were

put in a large petri dish, they were not ready to mate. They remained motionless for a moment or walked rather sluggishly. Then, began to walk quite irrespective of the partner. As soon as the male touched the female, with his antenna or foretarsus, he attempted to mate with her. Of the 100 pairs employed for these observations, males reacted to the female by touching her with his antenna in 65 pairs, by touching her with his foretarsus in 28 pairs, and motionless male's reacted to a walking female when the female's antenna touched the male's elytron in 2 pairs. The older male of *M. saltuarius* tended to react less to the female.

After the male dashed to the female, the male mounted her back and repeatedly licked around her scutellum. Then the male inserted his penis into the female's genitalia. The copulation from insertion to withdrawal of penis consisted of the following three phases.

I. The male bent his abdomen. Then the male penis was inserted into the female's genitalia. (Insertion Phase; IP)

II. The male was motionless with the female's genitalia pulled out of her abdomen by the male's penis, which was probably engaged in sperm delivery. (Sperm Delivery Phase; SDP)

III. The male tried to pull his penis out from the female genitalia by violently jerking his abdomen, terminating copulation. (Disconnection Phase; DP)

In the first phase (IP), neither in pairs with a virgin female nor in those with a non-virgin female could we detect any "sperm removal action," which Yokoi (1990) observed in another lamiine cerambycid, *Psacotha hilaris* (Pascoe).

Throughout the process, the female remained still or walked rather sluggishly. This is consistent

with the observations by Nakayama et al. (1998).

The copulation duration was measured in the pairs whose copulation process was complete in terms of the above 3 phases. If the male could not perform DP, he immediately retried copulation by repeating IP. After the male finished the process of copulation, from IP to DP, he didn't try another copulation immediately, but only remained on the female's back. In the present observations, males didn't try a second copulation within five minutes after finalizing the first. Figure 1 shows the variation in the copulating durations of 100 pairs of *M. saltuarius* adults. In many cases copulation lasted for one to one and a half minutes. There was not different between females that were motionless and those walking sluggishly. Figure 1 also shows that the duration of copulation may be bimodal, as was seen in another Lamiine cerambycid, *Acalolepta luxuriosa* (Bates), by Akutsu and Kuboki (1983).

After copulation, a so-called "post-copulatory mounting" occurred in which the male always remained mounted on the female's back if the female did not refuse. In such a case, the male tried copulation again after a while.

Of the above 100 pairs, multiple copulations were observed in 60 pairs. As a result, 54 pairs (90.0% of the 60) carried out a second copulation and 45 pairs (75.0% of the 60) a third. The second copulation was observed to take place 6–43 min after the first. If we let the interval between the first and the second copulation be a , and that between the second and the third be b , we can determined the correlation between a and b as shown in Fig. 2. There is a large correlation between these two parameters ($r=0.5879$, $p<0.001$).

The durations of the first through the third

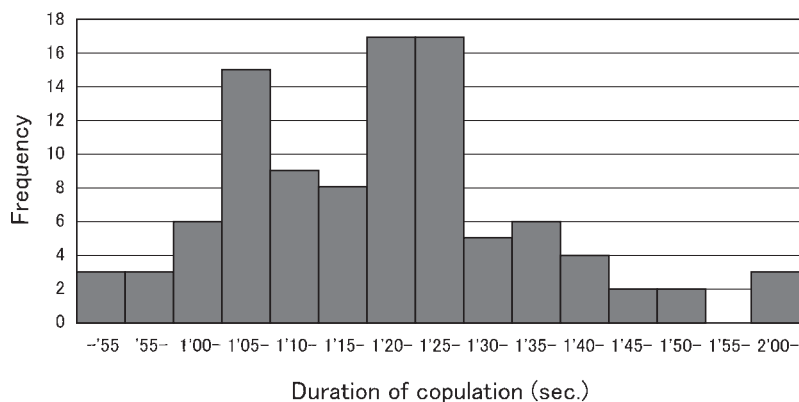


Fig. 1. Frequency of copulation durations for *Monochamus saltuarius* in a petri dish.

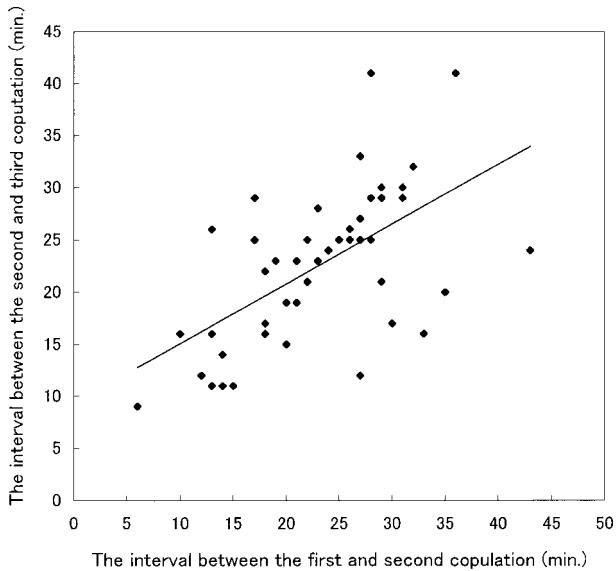


Fig. 2. Interval time difference in multiple copulations for *Monochamus saltuarius*.

copulations are comparatively shown in Fig. 3. Although no drastic differences are seen among the durations of the three actions, the duration tended to be shorter in the three consecutive copulations progressed and was significant (Kruskal-Wallis test; $H=8.5214$, $p=0.0142<0.05$). In the first copulation of the three, the duration of copulation again is possibly bimodal as in Fig. 1.

When the male maintained his mount on the female's back for an extended period, the female tried to remove the male in the following manner:

(i) Hind legs of the female used to shake off the male's mid legs.

(ii) The female shakes her body.

(iii) The female raises the tip of her abdomen and tries to lift the mounting male.

A female, which is larger than the male, was observed to remove the male by carrying out actions (ii) and (iii) alternately. In the present observation, the male individual was removed by the female before the second copulation trial in two cases, and before the third copulation trial in six cases.

Violent fighting between males (Experiment II)

The observation of *M. saltuarius* mating behavior in the large breeding container included 5 trials of 2 pairs, showing not only the normal process of mating and copulation as above, but also violent struggles among males. When a male and a female were in a post-copulatory mounting posture, a sec-

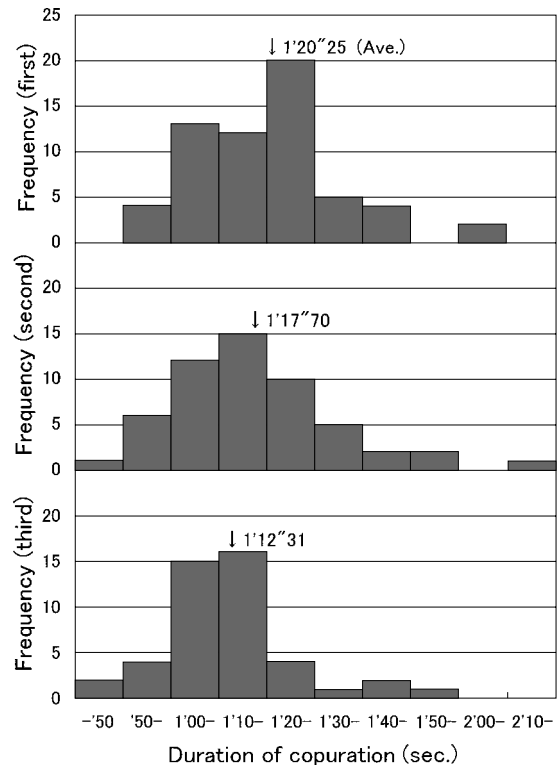


Fig. 3. Frequency of the first through the third copulation durations for *Monochamus saltuarius*.

ond male by chance came to interact with the pair by touching them with his antenna or fore leg. The second male dashed to the female and violent fighting between the males occurred (Fig. 4). When fighting occurred, the larger male robbed the smaller male of his mate in two cases of the five. It was also observed that the larger male, with the female having escaped, bent his abdomen down during the fighting to hold the other male. When a male happened to encounter just another male, fighting was observed but it was not as violent. Otherwise, an encounter of two males led to a simple repulsion to each other, with neither fighting nor homosexual mating trials occurring. Even if a single male approached a pair during mounting and he happened to touch the mounting male, the single male ran away. In preliminary trials with only two males in a petri dish, slight fighting and repulsion was observed.

Mating behavior of females on the red pine log (Experiment II)

As was described in Experiment I, the female, while being mounted by the male, was either mo-

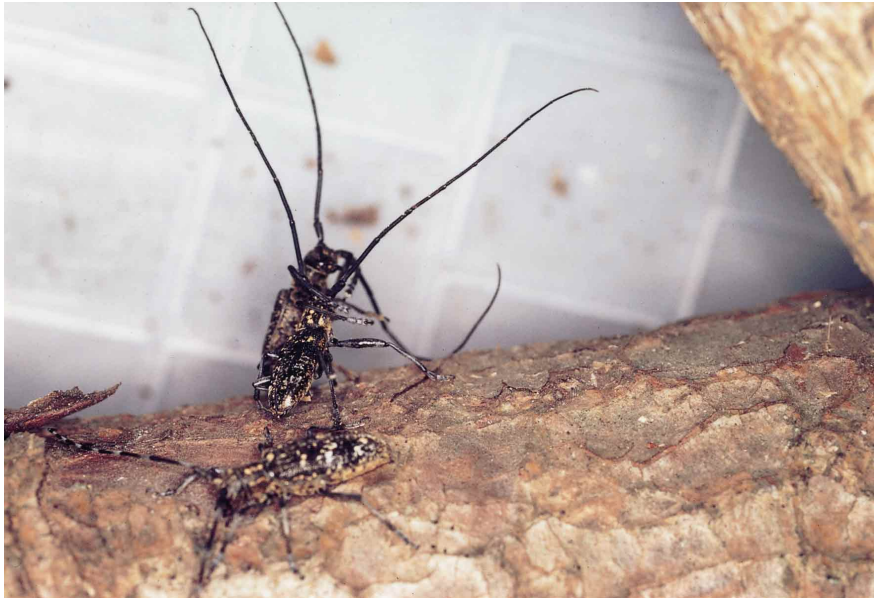


Fig. 4. Fighting of *Monochamus saltuarius* males in the large breeding container.

Table 1. Responses of *Monochamus saltuarius* males to living females and dead individuals in a petri dish

Male's response	Living (♀)	Time elapsed (h) after taking out from the freezer							
		Dead (♀)				Dead (♂)			
		0 h	24 h	48 h	72 h	0 h	24 h	48 h	72 h
Dashing	37	23	22	14	9	12	11	12	3
Mounting	40	25	25	17	11	17	15	10	4
Bending the abdomen	40	25	25	17	11	15	15	9	4
Attacking	0	0	0	0	0	4	1	0	0
No response	0	0	0	5	12	6	9	9	19
No. of reacting insects tested	40	25	25	23	23	25	25	23	23

tionless or walked sluggishly in the petri dish. In the breeding container with a red pine log, the female having finished copulation but still mounted by the partner exhibited the action of biting the bark of the log, a process prior to egg-laying. Soon after the female had laid an egg, the mounting male again tried to copulate with her. In no case did the male try to copulate with the female when she was laying an egg, but in one instance the male tried copulate in vain when the female was biting the bark. After finalizing egg-laying and in search of another spot for the next egg-laying, the female mounted by the male tried to remove the male in the same manner as described in (i)–(iii) in Experi-

ment I.

Males' reaction toward dead individuals (Experiment III)

Responses of *M. saltuarius* males to living females and dead individuals is shown in Table 1. The male exhibited dashing, mounting and abdominal bending in the same manner toward the body of the female that had been dead for 24 h as toward living females. The body parts of the male used to detect the dead female body were antennae ($n=17$) and tarsi ($n=6$) (Table 2). On the other hand, the ratio of the male reactions with his antennae gradually decreased as the time after death of the female

Table 2. Male body parts that first touched other *Monochamus saltuarius* males, living females and dead individuals in a petri dish

First touched site	Living (♀)	Time elapsed (h) after taking out from the freezer							
		Dead (♀)				Dead (♂)			
		0 h	24 h	48 h	72 h	0 h	24 h	48 h	72 h
Antenna	29	17	15	6	0	5	7	3	0
Tarsus	8	6	8	9	11	9	2	6	3
Antenna+Tarsus	37	23	23	15	11	14	9	9	3
Other site	3	2	2	3	0	5	6	5	1
No response	0	0	0	5	12	6	9	9	19
No. of reacting insects tested	40	25	25	23	23	25	25	23	23

increased. The male did not react to the female body 72 h after death (Table 2).

The response of the male to dead males was in some cases the same as to dead females, although to a lesser extent. In other cases, males attacked the dead males. Sixty percent of the males still exhibited a mating response by bending their abdomen against the recently dead male corpse 0 and 24 h after death. On the other hand, 16% of the males exhibited aggression against the male corpse 0 h after death. These males bit the dead male's antennae and femora and even swung the corpse by grasping it. This behavior was not observed against corpses 48 h after death.

DISCUSSION

Observations on mating behavior

The results of the present investigation indicate that the mating behavior of *M. saltuarius* is quite typical among the family Cerambycidae and also among the subfamily Lamiinae. The recognition of females by males requires direct contact of male's antennae or tarsi.

Among some cerambycid species, whose mating behavior has been clarified, a lamiine species, *P. hilaris*, is probably the one that has been studied most intensively and seems quite typical among Lamiinae. In *P. hilaris*, as soon as the male recognizes the female with his antenna or tarsus, he dashes to and mounts the female (Fukaya and Honda, 1992). The male of *M. saltuarius* exhibited mating behavior similar to *P. hilaris*. Sexually mature, but younger males, responded to females as

soon as they touched her. In most of the cases this was done with his antennae and in some cases with his tarsi. However, old males didn't respond to females quickly when making contact with their antenna. The older males reacted later to females by touching with their tarsi.

After the male reacted the female, he dashed and mounted her and inserted his penis into her genitalia. Copulation consisted of three phases. The existence of the three phases is very important for accurately measurement of the duration of the copulation process. *A. luxuriosa*, a related genus to *Monochamus*, is unique in that the copulating duration is very long, lasting for 21 s through 10 min 56 s with one peak occurring from 3 to 4 min and another from 7 to 8 min (Akutsu and Kuboki, 1983). On the other hand, the copulating duration of *M. saltuarius* is not as long. Copulation of a little less than one and a half minutes is most frequent in this species (Fig. 1). *M. saltuarius*, however, might be similar to *A. luxuriosa* in that the copulation duration is bimodal, although the bimodal interval of *M. saltuarius* is shorter than *A. luxuriosa*. A bimodal tendency was again seen in Fig. 3 for the first trial of copulation of the three consecutive copulating behaviors. The reason for bimodality could not be identified.

In the present species, namely *M. saltuarius* (Nakayama et al., 1998), as well as in other species such as *A. luxuriosa* (Akutsu and Kuboki, 1983), *M. alternatus* (Togashi, 1998) and *M. scutellatus* (Hughes, 1979), a male does not seem to search for another female after he has finished copulation. The male instead guards the female presumably to

prevent her from being taken by other males. The present observation confirms the presence of guarding behavior.

It has been shown that Cerambycidae adults exhibit multiple copulations while in the mounting posture (Akutsu and Kuboki, 1983; Iwata et al., 1998; Togashi, 1998). The present species, *M. saltuarius*, also exhibited multiple copulations in the same manner. In this study, although the change is not so marked, the copulating duration decreased significantly in multiple consecutive copulations ($p < 0.05$; Fig. 3). However the interval between copulations did not change ($r = 0.5879$, $p < 0.001$; Fig. 2). In this case, the duration of SDP (see Results, Experiment I) seemed to be shortened (Table 3). The average time of SDP is more significant than the other two phases. Because, the IP and DP are needed for copulation process, but the SDP is probably the time engaged in sperm delivery. The quantity of sperm delivered from the male to the female may decrease with decreased SDP time.

Sperm removal behavior associated with “short-time penis insertion” was observed in *P. hilaris* males prior to the real copula (Yokoi, 1990). In *M. saltuarius*, however, such “short-time penis insertion” was not observed. Male appeared to not like “short-time penis insertion” so the mounting continued.

As the mounting continued for a length of time, the female if active enough tried to remove the male from her back. A similar action is known to exist in some cerambycid species, including *A. luxuriosa* (Akutsu and Kuboki, 1983) and *P. hilaris* (Yokoi, 1989). In the present observations, the female of *M. saltuarius* tried to remove the male by carrying out more than one of three aforementioned actions, with the action appearing quite effective for removing the mounted male. Male removing actions of the female took place in 66.7% of the multiple copulation cases. Therefore, it can be concluded that the female does not like male guarding post-copulatory mounting.

Fighting among cerambycid males has been classified into the following. First, fighting takes place with two opposing males only (Sugiyama et al., 1992). Second, another single male meets a post-copulating mounting pair. It has been documented that a fight between the newly arriving male the male mounted on the female, in a guarding position, is more violent than between single

Table 3. Average time for each phase of the first and third copulation of *Monochamus saltuarius* (s)

	IP ^a	SDP ^a	DP ^a	Total ^b
First copulation	17.0	48.7	12.5	80.3
Third copulation	14.7	42.3	15.9	72.3
χ^2 test	$p > 0.05$	$p < 0.01$	$p > 0.05$	$p < 0.05$

^a The number measured from IP to DP is total data ($n = 36$).

^b Total data ($n = 45$).

males (Akutsu and Kuboki, 1983; Togashi, 1998). In the present observation, on touching a paired female in post-copulatory mounting, a single male dashed to her and a violent fight between the males occurred as an attempt on the part of the newly arrived male to take the female from the other male (Fig. 4). Togashi (1998) stated the larger male of *M. alternatus* usually won the fight between males. The present species, *M. saltuarius*, also exhibited the same phenomenon. If the single male touched the paired male first, the single male usually ran away avoiding a violent fight.

Possible presence of a sex pheromone

In the present experiment, we observed the dead female was recognized by the male as a living normal female (Tables 1, 2). An χ^2 test was carried out to determine the difference in the male's reactions to living females and freshly dead female bodies in materials and methods. These results failed to detect any significant differences ($\chi^2 = 0.15$, $p > 0.05$). The male appears to have recognized the living and dead females in the same manner. Therefore, a living female is not an important factor.

In *P. hilaris* a male positive reaction to a dead female was observed for as long as 28 days after death (Fukaya and Honda, 1992). In the case of *M. saltuarius*, the dead male or female smelled badly, beginning to rot in as few as 48 h after death. However, more than half of the males tried to copulate with these corpses (Table 1). The males reacted to the dead individuals as late as 72 h after death, which would indicate the corpse must still retain the factor(s) to induce copulation. Males react promptly to an immediately dead female. The old male tended to be less able to react to the female corpse with his antenna (Table 2). The male reaction to the “dummy” female and/or to the extracted constituent of the female body has been confirmed in *Semanotus japonicus* (Shibata, 1991), *P. hilaris*

(Fukaya and Honda, 1992). In these species, the mating behavior of Cerambycid beetles in general indicate sex pheromones play an important role. In addition, in *M. alternatus*, the congeneric species of *M. saltuarius*, the presence of female volatile sex pheromone(s) attracting males has been experimentally verified (Kim et al., 1992). However, in the case of *M. saltuarius*, the male did not respond to the female unless he touched her. Also, in the petri dish experiment, the male was not observed to walk straight toward the female. In addition, in the attraction experiment, judging the distance at which a female attracts a male, using a T-shaped olfactometer, any significant effect was not detected (Kobayashi, unpublished). From these results, it is highly probable that, as in *P. hilaris* (Fukaya and Honda, 1992), sex pheromone(s) exists on the body surface of the female *M. saltuarius*. Moreover, the substances remain on the dead body for several days, demonstrating that they have stable properties.

Hanks (1999) attributed larval host types (healthy, weakened, stressed and dead plants) to adult reproductive behavioral traits in Cerambycidae. In his criterion, both *M. alternatus* and *M. saltuarius* were classified into insects that oviposit in stressed plants, whose tissue is almost dying. He pointed out that stressed plant attacking cerambycids never produce long range sex pheromones. The present results of ours with *M. saltuarius* coincide well with Hanks' (1999) theory.

A strange behavioral action, mounting of one male against another male has been reported in *M. alternatus* (Fauziah et al., 1987). In the present investigation, a similar phenomenon was observed in *M. saltuarius* males. In this respect, it is noteworthy that the male dashed to the virgin dead male in the same manner as observed toward a normal living female (Table 1). Therefore, the male reaction toward other males is not ascribed to the transfer of cuticular substances from female to male since the male is a virgin, but to a possible fact that the mount-inducing substances exist not only in females, but also in males. On the other hand, males also exhibited aggressive behavior against dead male corpses (Table 1). This aggressive behavior indicates that the dead male may have substances on their cuticle surface that causes living males to react. Further studies need be made to analyze these reactions.

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