# MATING BEHAVIOR OF 8 STORED-PRODUCT BEETLES (COLEOPTERA: DERMESTIDAE, TENEBRIONIDAE, CUCUJIDAE, AND CURCULIONIDAE)[1]

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ABSTRACT

Mating behavior and mating position were studied for *Anthrenus flavipes* LeConte, furniture carpet beetle; *Trogoderma glabrum* (Herbst); *Tribolium castaneum* (Herbst), red flour beetle; *T. confusum* Jacquelin duVal, confused flour beetle; *Tenebrio obscurus* F., dark mealworm; *Oryzaephilus mercator* (Fauvel), merchant grain beetle; *Cryptolestes pusillus* (Schönherr), flat grain beetle; and *Sitophilus granarius* (L.), granary weevil.

Actions of the male vary with the species and include touching the female abdominal tip with the maxillary palpi prior to mounting, tapping the female with the antennae and maxillary palpi, wiping motions with the legs, touching the female with the mandibles, and aedeagal movements. *C. pusillus* exhibited distinctive postcopulatory behavior.

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The importance of mating behavior is often underestimated in insect biology. Mating behavior functions in speciation, species isolation, and species recognition (Alexander 1962, 1964; Lloyd 1966a, 1966b). A knowledge of mating behavior is important when sex attraction or sterilization techniques are to be used in controlling pest species. Coleoptera, the largest order of insects, has over 250 thousand described species, but the mating behavior of less than 0.1% of these species has been described (Wojcik 1969a).

## MATERIALS AND METHODS

The 8 species studied were *Anthrenus flavipes* LeConte, furniture carpet beetle, and *Trogoderma glabrum* (Herbst) (Dermestidae); *Tribolium castaneum* (Herbst),[2] red flour beetle, *T. confusum* Jacquelin duVal, confused flour beetle, and *Tenebrio obscurus* F.,[3] dark mealworm (Tenebrionidae); *Oryzaephilus mercator* (Fauvel), merchant grain beetle, and *Cryptolestes pusillus* (Schönherr), flat grain beetle (Cucujidae); and *Sitophilus granarius* (L.),[3] granary weevil (Curculionidae). All of the insect colonies except as noted were obtained from Dr. P. T. M. Lum, USDA, Stored-Product Insects Research and Development Laboratory, Savannah, Georgia.

They were reared according to methods described in the USDA rearing manual (1965) except for *T. obscurus* (reared on 95% bran and 5%

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[1]This research was undertaken in conjunction with Cooperative agreement No. 12-14-100-9025 (51), between the University of Florida and the Agricultural Research Service, USDA, and is part of the author's M. S. thesis. University of Florida, Agricultural Experiment Station Journal Series no. 3275.

[2]Obtained locally by Dr. T. J. Walker, University of Florida.

[3]Obtained from Mr. Gailen D. White, Mid-West Grain Investigation Laboratory, Manhattan, Kan.

brewer's yeast) and *S. granarius* (reared on 95% wheat grains and 5% brewer's yeast).

Pupae of each species were removed from the rearing media, sexed, and isolated in vials to obtain virgin adults. The characters given by Halstead (1963) were used to sex the adults and pupae except the following; *A. flavipes* adults (Ayyappa et al. 1957), *Trogoderma glabrum* adults (Hinton 1945), *Tribolium castaneum* and *T. confusum* (Park 1934), and *S. granarius* adults (Richards 1947). Virgin *S. granarius* adults were obtained from isolated wheat grains.

Virgin adults of known age of each species were individually placed in numbered vials (25 mm high X 5 mm diam) except for *Tenebrio obscurus* which were placed in larger vials (30 mm high X 30 mm diam). For observation a male was transferred into a vial containing a female, and the vials were placed in a row. The vials were viewed from the side with a stereo-microscope at 7x to 30x. Usually 10, but no more than 11, vials were observed at one time. During intensive observation of a mating pair, the remaining pairs were not watched continuously. All observations were recorded verbally on magnetic tape. All observations were carried out under fluorescent room lighting (110 ft-c) except for *S. granarius* which were observed under red light (Westinghouse 7½ w red bulb).

The genitalia terminology of Lindroth and Palmén (1956) and Lindroth (1957) is used here. The genitalia of *Tribolium castaneum* and *T. confusum* are described by El-Kifl (1953), and those of *T. confusum* by Stanley and Grundmann (1965), *O. mercator* by Slow (1958), and *C. pusillus* by Reid (1942). The genitalia of the other species studied apparently have not been described. The genitalia of 2 *Anthrenus* spp. are described by Greenwald (1941) and Pradhan (1949); several species of *Trogoderma* by Beal (1954, 1956); and *Tenebrio molitor* L. by Doyen (1966). Not all the preceding authors use Lindroth and Palmen's (1956) terminology but it can be applied using the figures.

The following terms are defined to clarify their usage in this paper.

Attempted mating or attempt to mate—the male assuming the mating position for that species and extruding his genitalia. An attempt was considered terminated when the male's activity ceased. Attempted matings are defined in terms of male activity since the females of the species studied are largely passive during mating.

Successful mating—copulation. If the male withdraws his penis, retracts it into his body, but remains in position and intromits again, it is counted as a new successful mating.

Time in copula—the time span from intromission to withdrawal.

Trial—a pair of beetles placed in an observation vial and observed for at least 15 min. When mating occurred, the trial continued as long as observation was necessary. A trial was counted as an attempted mating if the male attempted to mate once regardless of how many attempts were made in that trial. A trial was counted as a successful mating if the male successfully mated once regardless of how many times the male successfully mated or attempted to mate in that trial.

## Observations

The number of pairs that attempted or successfully mated and the total number of trials are given in Table 1, along with the age in days

TABLE 1. SUMMARY OF MATING OBSERVATIONS OF 8 SPECIES OF STORED-PRODUCT BEETLES.

| Species | Number of trials | | | Days since eclosion: all beetles tested | | Days since eclosion: beetles that attempted or successfully mated | | Time in copula | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | total* | attempted matings** | successful matings** | ♂ | ♀ | ♂ | ♀ | n | mean in min | range in min |
| *Anthrenus flavipes* | 74 | 4 | 7 | 2-39 | 2-39 | 14-31 | 11-28 | 6 | 3.9 | 1-8 |
| *Trogoderma glabrum* | 122 | 17 | 12 | 2-38 | 2-37 | 5-28 | 4-37 | 10 | 2.2 | 0.8-4.5 |
| *Tribolium castaneum* | 34 | 1 | 29 | 7-29 | 7-29 | 7-29 | 7-29 | 14 | 3.0 | 0.3-7.5 |
| *T. confusum* | 28 | 2 | 8 | 1-208 | 1-209 | 3-208 | 6-208 | 3 | — | 1-2 |
| *Tenebrio obscurus* | 54 | 15 | 21 | 1-35 | 1-36 | 4-30 | 1-36 | 19 | 1.7 | 0.3-5.5 |
| *Oryzaephilus mercator* | 26 | 4 | 21 | 13-33 | 13-32 | 13-25 | 13-32 | 22 | 11.2 | 2-30 |
| *Cryptolestes pusillus* | 29 | 3 | 11 | 2-23 | 2-22 | 4-12 | 2-9 | 9 | 33.7 | 11-43 |
| *Sitophilus granarius* | 11 | 2 | 6 | 10-24 | 2-24 | 10-24 | 2-24 | 5 | — | 30+-72 |

* Some individuals and/or pairs were used in more than one trial.

** A trial was counted as an attempted mating if the ♂ attempted to mate once regardless of how many attempts were made in that trial. A trial was counted as a successful mating if the ♂ successfully mated once regardless of how many times the ♂ successfully mated or attempted to mate in that trial.

TABLE 2. SUMMARY OF ATTEMPTED AND SUCCESSFUL MATINGS OF *Anthrenus flavipes*. EACH LINE REPRESENTS ONE TRIAL.

| Female | | | Male | | | | |
|---|---|---|---|---|---|---|---|
| Ident. no. | Activity* | Age in days | Ident. no. | Activity* | Age in days | A or S** | Time in copula in min† |
| 1 | 2-3 | 11 | 1 | 1-2 | 19 | SAAS | 2, × |
| 2 | 2-3 | 12 | 2 | 1-2 | 17 | AAAA | |
| 3 | 1-1 | 14 | 3 | 1-2 | 14 | AAA | |
| 4 | 1-1 | 14 | 4 | 1-1 | 19 | AAS | 4 |
| 2 | 3-3 | 17 | 5 | 2-2 | 21 | AS | × |
| 5 | 1-1 | 19 | 6 | 1-1 | 21 | SS | 5.5, 8 |
| 6 | 1-1 | 23 | 7 | 1-1 | 23 | A | |
| 7 | 1-1 | 23 | 8 | 2-2 | 23 | AAS | × |
| 8 | 3-3 | 23 | 9 | 2-2 | 28 | A | |
| 9 | 1-1 | 28 | 10 | 2-2 | 28 | S | 3 |
| 10 | 2-2 | 31 | 11 | 2-2 | 31 | AAASAA | 1 |

* Activity=trial in which individual attempted or successfully mated, and total no. of trials for that individual; e.g., 2-3, individual mated in the 2nd trial of the 3 in which it was used.

** A=attempted, or S=successfully mated in the sequence given for one trial.

† An × indicates that mating was not timed.

from eclosion of all beetles tested. Mean values and ranges of time in copula are given with the number of successful matings that were timed. Successful or attempted mating after successfully mating once in the same trial was observed in all species; in some species additional successful matings occurred in subsequent trials.

*Anthrenus flavipes*
(furniture carpet beetle)

In 74 trials, 5% of the males attempted to mate without success, and 10% successfully mated (Table 2). The male approaches the female from any direction but does not appear to perceive the female from distances of over 2 mm. Often he first touches the posterodorsal margins of her elytra with his maxillary palpi (Fig. 1).

Copulation occurs with the male firmly mounted, having his venter on her dorsum. When he first mounts, his fore legs grasp her elytra, but as he extrudes his genitalia and starts to copulate, his fore legs are lifted from her. Neither the antennae, held horizontally at right angles to the body axis, nor the palpi touch her. The middle legs grasp the lateral margins of the female's elytra. The hind legs are on the substrate near the apex of her abdomen (a small male may have his hind legs on the tip of her elytra, not on the substrate). At times the ventral surface of one or both middle legs may rub along the forward lateral edges of her elytra in a "wiping motion" (Fig. 2). This wiping motion appears to be unrelated to female restlessness. As the genitalia extrude the aedeagus comes straight out of the male abdomen, bending 90° downward, and the penis is inserted into the female's genital opening. The parameres do not enter the female, but are placed flatly against her 5th sternite. No tapping or

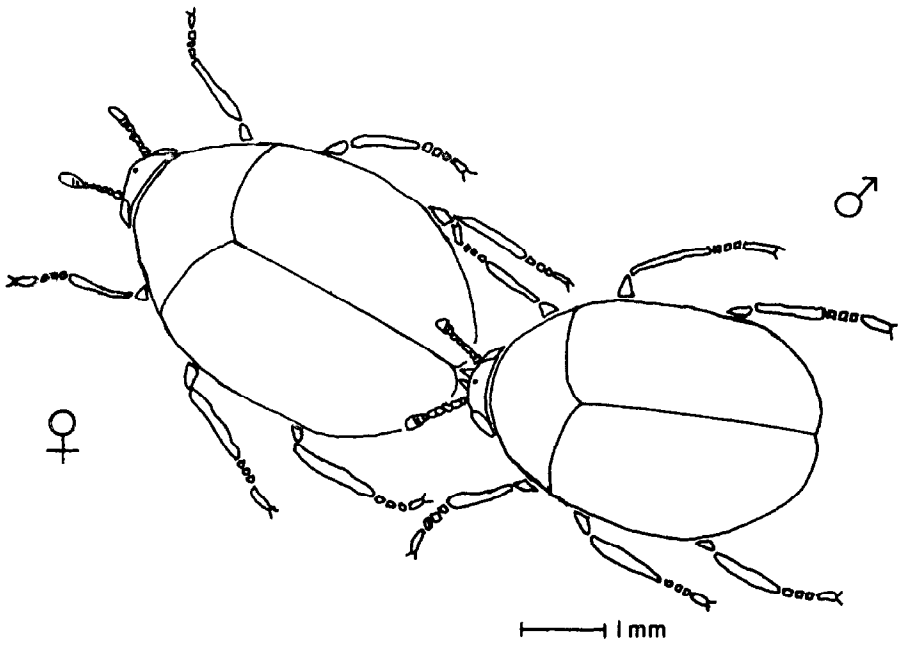


Fig. 1. Precopulatory behavior of *Anthrenus flavipes*; male touching posterodorsal margins of female's elytra prior to mounting.

rubbing of the aedeagus was observed prior to intromission. Greenwald (1941) described the mating position of *A. scrophulariae* L. as male over female with the male grasping the female with his middle and hind legs.

If the female is receptive and does not run from the male, she does not appear to respond to him in any way even if he mounts her facing the wrong way or falls off. The female lowers her 5th sternite prior to copulation. During the entire mating, she stands with all legs on the substrate. Her antennae are held horizontally, or slightly elevated, at right angles to her body axis. Usually her venter is parallel to the substrate, but sometimes she will raise up on her fore legs and lower the tip of her abdomen, so that her venter is at a 15°to 30° angle to the substrate. Copulation ends with the male withdrawing his penis from the female as she raises her 5th sternite.

Copulation usually lasted 1 to 4 min, but one pair remained for 5.5 and 8 min in successive copulations, which is shorter than the 9 min reported by Kunike (1939) for 4 other species of *Anthrenus*. Males usually copulate only once (Table 2), but some will mount repeatedly when they fall off or are dislodged. Some mountings do not lead to copulation.

When copulation is completed or the male falls off, the female walks away from the male if he is not on her dorsum. In 4 trials the male remained mounted on the female's dorsum after successfully mating, attempted to copulate again, and succeeded in 3 cases. Fifteen females and 22 males were used in more than one trial, but only one female and no males attempted or successfully mated in more than one trial.

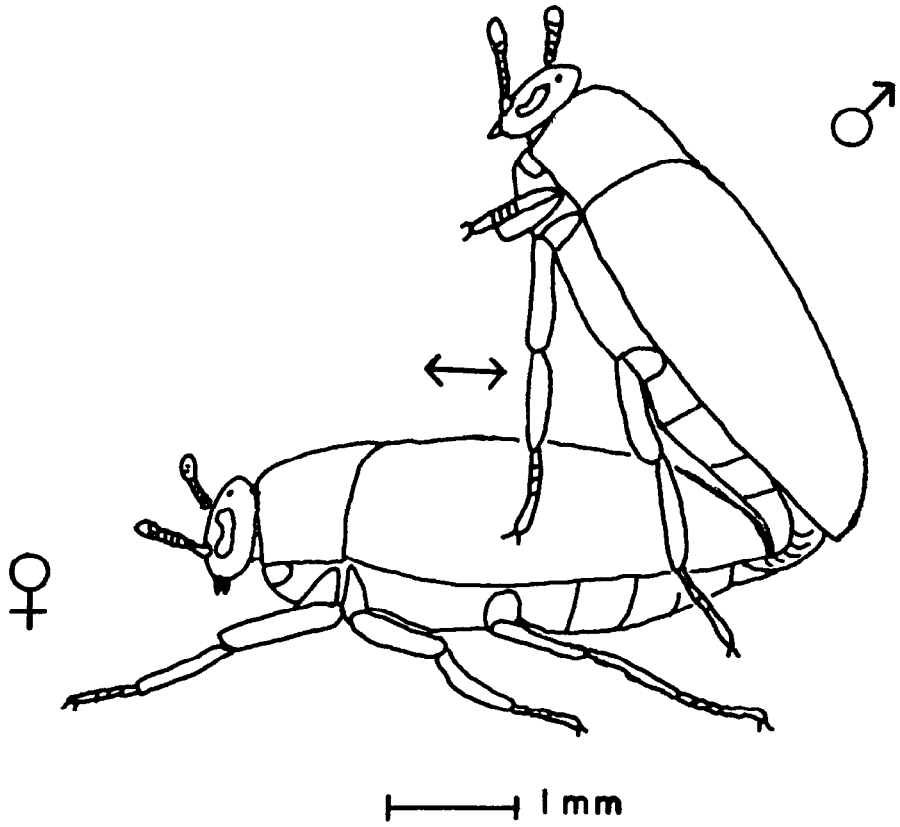


Fig. 2. *Anthrenus flavipes* copulating, arrow shows direction of wiping motion of male's middle legs on forward lateral edges of female's elytra.

*Trogoderma glabrum*

In 122 trials, 14% of the males attempted to mate without success and 10% successfully mated (Table 3). The male seems to perceive the female only if his maxillary palpi or antennae contact the dorsal surface of the female's body. In 3 different trials, after pushing the female's body, apparently attempting to crawl under her, and butting her with his head, the male did not become sexually active. In one of these instances, the male subsequently became sexually active and attempted to mate but only after his maxillary palpi came into contact with the female's elytra. Wodsedalek (1912) and Beal (1954) have reported the necessity of palpal contact as a preliminary to mating in other species of *Trogoderma*.

A chemical emitted from the female, stimulating copulatory activity, has been reported in *T. glabrum* by Burkholder and Dicke (1966). I noted possible evidence of such a pheromone in only 3 trials. The female was on her dorsum in the first and 3rd cases, and right side up in the 2nd case. The male was on his dorsum in the first and 2nd cases, and right side up in the 3rd case. In each instance, the female extended her abdomen with the intersegmental membrane visible between each segment, without the geni-

talia being extruded. While extended, the abdomen was undulated up and down for 2 to 5 sec. During the undulation, the elytra were sometimes raised with the wings flapping. (This behavior of the female cannot be distinguished from that of other females and of males in attempting to

TABLE 3. SUMMARY OF ATTEMPTED AND SUCCESSFUL MATINGS OF *Trogoderma glabrum*. EACH LINE REPRESENTS ONE TRIAL.

| Female | | | Male | | | | | |
|---|---|---|---|---|---|---|---|---|
| Ident. no. | Activity* | Age in days | Ident. no. | Activity* | Age in days | A or S** | Time in copula in min† | Reproduction noted‡ |
| 1 | 2-3 | 4 | 1 | 2-3 | 7 | AA | | |
| 2 | 1-4 | 6 | 2 | 1-1 | 10 | SA | 1.5 | + |
| 3 | 2-3 | 7 | 3 | 2-3 | 5 | AS | 2 | + |
| 4 | 2-3 | 8 | 4 | 2-3 | 5 | S | × | + |
| 5 | 3-4 | 8 | 5 | 3-4 | 9 | AS | 3 | + |
| 6 | 1-5 | 8 | 6 | 1-6 | 10 | AA | | |
| 7 | 1-5 | 9 | 7 | 1-5 | 8 | A | | |
| 8 | 1-1 | 9 | 8 | 1-1 | 11 | S | × | + |
| 9 | 3-5 | 10 | 9 | 3-5 | 7 | A | | |
| 10 | 4-5 | 10 | 10 | 4-5 | 13 | A | | |
| 9 | 4-5 | 11 | 9 | 4-5 | 8 | AAS | 2 | + |
| 11 | 1-1 | 11 | 11 | 1-1 | 9 | AAA | | |
| 12 | 1-1 | 11 | 12 | 1-1 | 11 | A | | |
| 13 | 1-1 | 11 | 13 | 1-1 | 11 | A | | |
| 14 | 3-3 | 11 | 14 | 3-3 | 14 | AA | | |
| 15 | 4-5 | 13 | 15 | 4-5 | 10 | S | 2 | + |
| 16 | 4-5 | 13 | 16 | 4-4 | 12 | AA | | |
| 17 | 1-1 | 14 | 17 | 1-1 | 17 | AAAAA AAS | × | — |
| 18 | 1-1 | 15 | 18 | 1-2 | 17 | AAAA | | |
| 19 | 1-1 | 19 | 19 | 1-1 | 19 | A | | |
| 20 | 1-2 | 20 | 20 | 1-2 | 18 | A | | |
| 21 | 4-4 | 31 | 21 | 4-4 | 29 | A | | |
| 22 | 4-4 | 31 | 22 | 4-4 | 29 | AAAAA ASASAA | 1, 0.8 | — |
| 23 | 4-4 | 31 | 23 | 4-4 | 30 | AA | | |
| 10 | 5-5 | 33 | 10 | 5-5 | 36 | AAAAA | | |
| 9 | 5-5 | 34 | 9 | 5-5 | 31 | AAAAS | 3 | N.A. |
| 15 | 5-5 | 36 | 15 | 5-5 | 33 | AA | | |
| 6 | 5-5 | 36 | 6 | 6-6 | 38 | AAS | 2.2 | N.A. |
| 24 | 2-2 | 36 | 24 | 2-2 | 38 | AAAAS | 4.5 | — |
| 7 | 5-5 | 37 | 7 | 5-5 | 36 | S | × | N.A. |

* Activity=trial in which individual attempted or successfully mated, and total no. of trials for that individual; e.g., 2-3, individual mated in the 2nd trial of the 3 in which it was used.

** A=attempted, or S=successfully mated in the sequence given for one trial.

† An × indicates that mating was not timed.

‡ +=additional adults, larvae, and/or eggs observed; —=none observed; and N.A.=data not available.

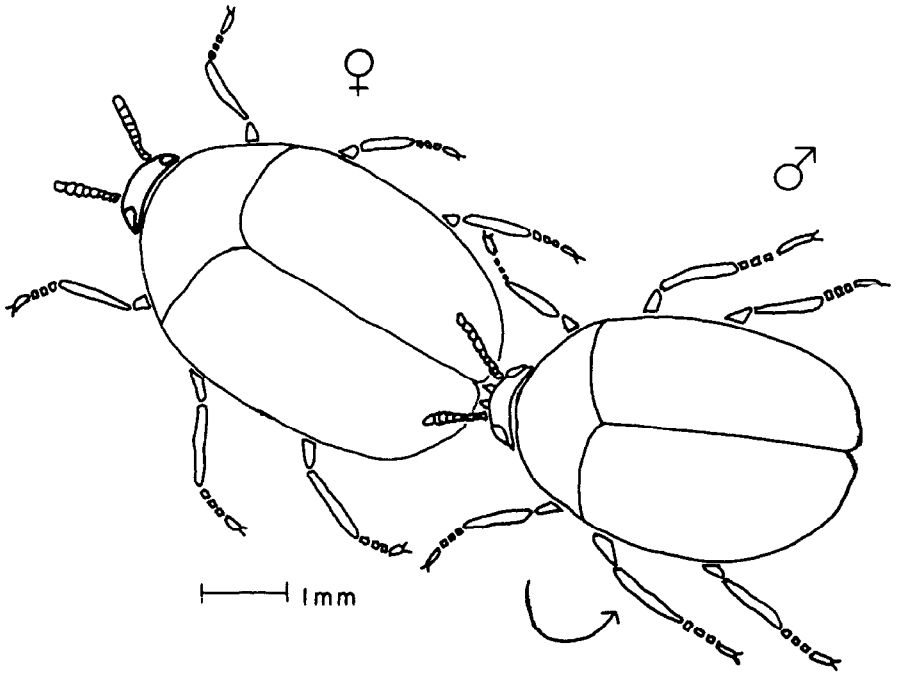


Fig. 3. Precopulatory behavior of *Trogoderma glabrum*, male touching end of female's abdomen prior to copulation. Arrow indicates direction male turns.

turn over when placed on their dorsum.) Each time this activity occurred the male responded by waving his antennae excitedly, becoming very agitated, and extruding his genitalia. Similar activity was observed by Burkholder and Dicke (1966). In the 3rd case, where the male was upright, he crossed the vial quickly and attempted to mate.

In all other instances the male became sexually active only when he came in contact with the female and touched her dorsal surface with his antennae or maxillary palpi. Regardless of where he first touches the female, the male moves to the apex of her abdomen, tapping her body with his maxillary palpi as he moves caudad. Upon reaching the abdominal apex, he ceases moving, and touches the end of her elytra and abdomen with his maxillary palpi. Then, while extruding his aedeagus, he turns around either clockwise, if he is on her right, or counter clockwise, if he is on her left, and attempts to copulate (Fig. 3). Two males attempted copulation from both the right and left sides successively. When in copula the male and female stand with all legs on the substrate. The male is at a 60° to 90° angle to the female's body, and only the tips of their abdomens touch (Fig. 4). Once the male inserts his penis, the only movement other than rhythmic abdominal contractions is an occasional twitch of an antenna.

Prior to intromission the male lowers the last sternite, raises the last tergite, and extends the aedeagus. Upon emerging from the abdomen, the aedeagus immediately bends 90° in the horizontal plane so that it extends directly away from the female and parallel to and above her longitudinal

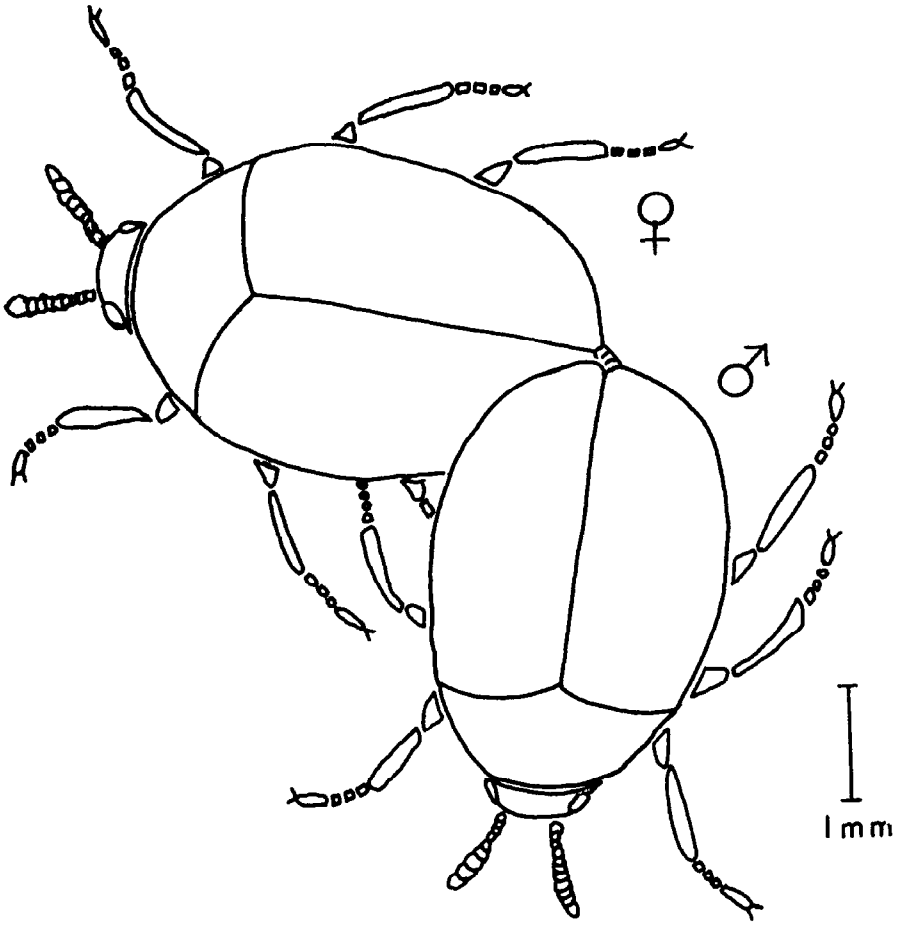


Fig. 4. *Trogoderma glabrum* copulating.

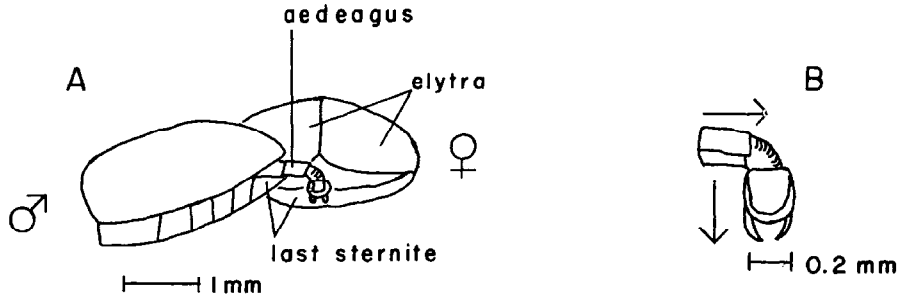


Fig. 5. *Trogoderma glabrum.* A. copulating pair, end view of female, lateral view of male. B. Extruded aedeagus with arrows showing bending.

body axis. The aedeagus then bends 180° cephalad to her body and intromission follows. The large lobe-like parameres do not enter the female but extend under her last sternite (Fig. 5). Apparently she does not lower her last sternite but only raises her last tergite.

If the male does not immediately intromit upon touching the end of the female's abdomen, he rubs his aedeagus about the end of her abdomen and may thereby find the genital opening. The parameres sometimes appear to tap the female's last sternite.

Often, when the male turns around, he swings too far or turns away from the female, missing her entirely. When this happens, he returns to his original position. Upon relocating the female, he again touches her abdominal apex and turns into the copulatory position. Copulations were observed only when the male stood 60° to 90° to the female.

Copulations lasted less than 1 min to 4.5 min (Table 3). In only 2 cases did a male attempt to copulate a 2nd time in a single trial (succeeding in one case) (Table 3). Twenty-nine females and 26 males were used in more than one trial, but only 5 females and 5 males attempted or successfully mated in more than one trial.

Similar mating behavior and position of other species of *Trogoderma* have been reported by Wodsedalek (1912) and Beal (1954). Beal (1954) reported 4 *Trogoderma* spp. as copulating at a 130° angle while I observed *T. glabrum* to copulate only at a 60° to 90° angle. The mean time in copula (2.2 min) agrees with the time in copula (2.5 min) reported by Beal (1954). However some of the copulations lasted considerably longer than any reported by Beal.

### *Tribolium castaneum*
(red flour beetle)

In 34 trials, 3% of the males attempted to mate without success and 86% successfully mated (Table 4). The male approaches the female from any direction but does not appear to perceive her from distances over 2 mm. Usually he mounts immediately after coming into contact with the female. Sometimes he touches the tips of her elytra with his maxillary palpi before mounting. In mounting, he climbs on her posterior dorsum and, walking forward, taps the top of her prothorax lightly with his maxillary palpi. Then, sliding backwards, he lowers his last sternite, and extrudes his aedeagus. Copulation is achieved with the male firmly mounted having his venter on her dorsum. A few of his sternites touch the end of her elytra. His head is bent down with his maxillary palpi lightly touching the dorsal surface of her prothorax. His antennae are held horizontally at right angles to the body axis. The maxillary palpi may twitch slightly. The fore legs grasp the side of her prothorax, with the middle legs being placed at the humeral angle and the hind legs holding near the end of her elytra. None of his legs touch the substrate although those of a large male are long enough. At times the ventral surface of one or both fore or middle tarsi may be rubbed in a wiping motion along the lateral edges of her prothorax, or elytra, respectively. The fore and middle legs were never observed to rub at the same time (Fig. 6).

While protruding his genitalia, the male drops his last sternite and extrudes his aedeagus. The aedeagus rotates 180° about its longitudinal axis as it is extruded, simultaneously moving down and forward. El-Kifl (1953) states that the tip of the aedeagus points caudad and dorsally when at rest, and points cephalad and ventrally when fully extruded. If the female does not admit the aedeagus immediately, the male pushes and

TABLE 4. SUMMARY OF ATTEMPTED AND SUCCESSFUL MATINGS OF *Tribolium castaneum*. EACH LINE REPRESENTS ONE TRIAL.

| Female | | | Male | | | | | |
|---|---|---|---|---|---|---|---|---|
| Ident. no. | Activity* | Age in days | Ident. no. | Activity* | Age in days | A or S** | Time in copula in min† | Reproduction noted‡ |
| 1 | 1-1 | 7 | 1 | 1-1 | 7 | S | × | + |
| 2 | 1-1 | 7 | 2 | 1-1 | 7 | S | × | — |
| 3 | 1-1 | 9 | 3 | 1-1 | 11 | S | × | + |
| 4 | 1-1 | 12 | 4 | 1-1 | 12 | S | × | — |
| 5 | 1-1 | 13 | 5 | 1-1 | 7 | S | × | + |
| 6 | 1-2 | 13 | 6 | 1-2 | 13 | S | × | + |
| 7 | 1-2 | 13 | 7 | 1-2 | 13 | SS | 2, 3 | + |
| 8 | 1-1 | 13 | 8 | 1-1 | 29 | S | × | + |
| 9 | 1-1 | 15 | 9 | 1-1 | 13 | S | × | + |
| 10 | 1-1 | 15 | 10 | 1-1 | 15 | S | × | — |
| 11 | 1-1 | 15 | 11 | 1-1 | 15 | S | × | — |
| 12 | 1-1 | 15 | 12 | 1-1 | 15 | AAS | × | + |
| 13 | 1-1 | 15 | 13 | 1-1 | 15 | SASA | 0.5, 1 | — |
| 6 | 2-2 | 17 | 6 | 2-2 | 17 | SA | 1 | N.A. |
| 7 | 2-2 | 17 | 7 | 2-2 | 17 | S | 1 | N.A. |
| 14 | 1-1 | 18 | 14 | 1-1 | 15 | AS | × | + |
| 15 | 2-2 | 19 | 15 | 2-2 | 17 | S | 3.5 | + |
| 16 | 1-1 | 22 | 16 | 1-1 | 22 | S | 4.5 | + |
| 17 | 1-1 | 22 | 17 | 1-1 | 22 | S | 5 | + |
| 18 | 1-1 | 22 | 18 | 1-1 | 22 | SA | 5 | + |
| 19 | 1-1 | 23 | 19 | 1-1 | 13 | S | × | — |
| 20 | 1-1 | 24 | 20 | 1-1 | 22 | S | 7 | + |
| 21 | 1-1 | 24 | 21 | 1-1 | 24 | AS | × | + |
| 22 | 1-1 | 24 | 22 | 1-1 | 24 | SA | 7.5 | + |
| 23 | 1-1 | 24 | 23 | 1-1 | 24 | SAS | 0.3, 1 | + |
| 24 | 1-1 | 27 | 24 | 1-1 | 27 | ASAA | × | — |
| 25 | 1-1 | 27 | 25 | 1-1 | 27 | SAA | × | + |
| 26 | 1-1 | 29 | 26 | 1-1 | 25 | A | | |
| 27 | 1-1 | 29 | 27 | 1-1 | 25 | AS | × | + |
| 28 | 1-1 | 29 | 28 | 1-1 | 25 | S | × | + |
| 29 | 1-1 | 29 | 29 | 1-1 | 29 | S | × | + |

* Activity=trial in which individual attempted or successfully mated, and total no. of trials for that individual; e.g., 1-2, individual mated in the first trial of the 2 in which it was used.

** A=attempted, or S=successfully mated in the sequence given for one trial.

† An × indicates that mating was not timed.

‡ +=additional adults and/or larvae observed, —=none observed, and N.A.=data not available.

prys at her with the aedeagus, but no tapping was observed. Only the small, narrow, dark-colored penis, not the fused parameres, enters the female. For the male to intromit, the female must lower her last sternite. In copula she usually stands with all legs on the substrate, without bend-

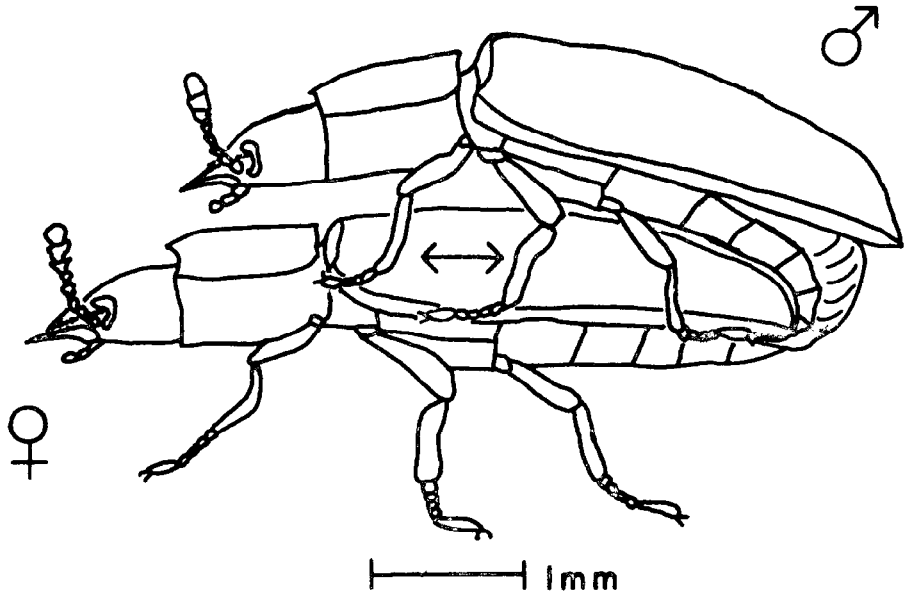


Fig. 6. *Tribolium castaneum* copulating. Arrow indicates direction of wiping motion of male's fore and middle legs on the lateral edges of the female's elytra.

ing her body, holding her antennae horizontally, straight forward. While in copula she may walk or feed.

The male sometimes mounts from the female's anterior and, when fully on her turns around to the correct position and attempts to copulate. Copulations lasted from less than 1 to 7.5 min (Table 4). After successfully mating, 8 males attempted to mate again in the same trial and 3 succeeded. After intromission the male stays in copula even if the pair falls on their sides or turns completely over onto his dorsum. After the male withdraws, the female walks around, often falling over and dislodging him. Three females and 3 males were used in more than one trial, with 2 females and 2 males successfully mating in more than one trial.

### *Tribolium confusum*
(confused flour beetle)

In 28 trials, 7% of the males attempted to mate without success and 29% successfully mated (Table 5). The male may approach the female from any direction but does not appear to perceive her from distances of over 2 mm. After coming into contact with her the male usually mounts immediately from her posterior (without tapping her with his antennae) and attempts to copulate. Other times he will slowly climb on her body, tapping her with his antennae. Frequently he touches the posterodorsal margins of her elytra with his maxillary palpi before mounting. He sometimes mounts from the female's anterior and, when fully on her, turns around to the correct position and attempts to copulate. Copulation is achieved with the male firmly mounted, having his venter on her dorsum,

TABLE 5. SUMMARY OF ATTEMPTED AND SUCCESSFUL MATINGS OF *Tribolium confusum*. EACH LINE REPRESENTS ONE TRIAL.

| Female | | | Male | | | | | |
|---|---|---|---|---|---|---|---|---|
| Ident. no. | Activity* | Age in Days | Ident. no. | Activity* | Age in days | A or S** | Time in copula in min† | Reproduction noted‡ |
| 1 | 1-1 | 6 | 1 | 3-3 | 13 | S | × | — |
| 2 | 1-1 | 8 | 2 | 1-1 | 3 | S | × | — |
| 3 | 2-2 | 10 | 3 | 1-1 | 7 | S | × | — |
| 4 | 1-1 | 13 | 4 | 1-1 | 8 | AS | × | + |
| 5 | 2-2 | 13 | 5 | 1-1 | 8 | S | × | — |
| 6 | 2-2 | 13 | 6 | 4-4 | 13 | AAAAS | × | + |
| 7 | 1-2 | 78 | 7 | 1-2 | 77 | A | | |
| 8 | 1-1 | 86 | 8 | 1-1 | 81 | A | | |
| 9 | 2-2 | 206 | 9 | 1-1 | 206 | S | 1 | — |
| 10 | 1-1 | 208 | 10 | 1-1 | 208 | SSSS | 1 to 2 | + |

* Activity=trial in which individual attempted or successfully mated, and total no. of trials for that individual; e.g., 3-3, individual mated in 3rd trial of the 3 in which it was used.
** A=attempted, or S=successfully mated in the sequence given for one trial.
† An × indicates that mating was not timed.
‡ +=adults and/or larvae observed, and —=none observed.

with his last few sternites touching the end of her elytra. His body axis is convexly curved. The male taps with his antennae on the forward and lateral margins of her prothorax (the exact point of contact depends on the size of the male). He may touch the tips of his mandibles to the forward margin of her prothorax, while slowly tapping the tips of his maxillary palpi on her prothorax. The positions of his legs are variable. Usually the fore legs grasp the female between the prothorax and mesothorax, with the middle and hind legs grasping the lateral edges of her elytra. The ventral surface of the fore tarsi may be rubbed in a wiping motion along the lateral margins, near the humeral angle of her elytra. The speed of this wiping motion did not seem to be correlated with female restlessness. None of his legs touch the substrate although those of a large male are long enough (Fig. 7).

The male drops his last sternite to extrude his aedeagus, which rotates 180° about its longitudinal axis, as it moves down and forward. El-Kifl (1953) states that the tip of the aedeagus points caudad and dorsally when at rest, pointing cephalad and ventrally when fully extruded. If the female does not admit the aedeagus immediately, the male pries and pushes at her with his aedeagus. He may repeatedly extend and withdraw his aedeagus, thus tapping her. Only the small, narrow, dark-colored penis enters the female; the fused parameres do not. The female must drop her last sternite prior to intromission. While in copula, she slightly extrudes her ovipositor so that the styli are visible. The styli are poined downward towards the substrate (probably being forced in this position by the parameres). She usually stands with all legs on the substrate with her body in a straight position. Her antennae are held horizontally straight forward. While in copula she may walk around and feed.

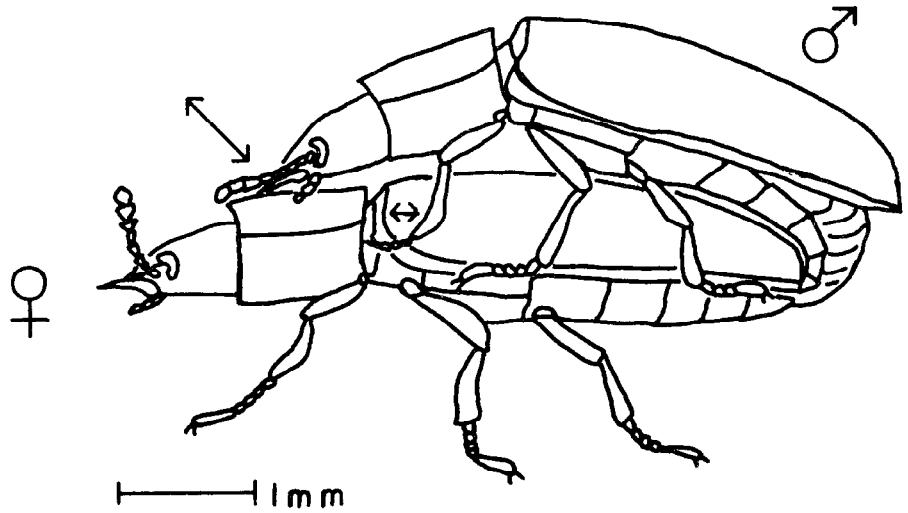


Fig. 7. *Tribolium confusum* copulating. Arrows show direction of movement of male's antennae and fore legs on female, and placement of male's mandibles and maxillary palpi on female's prothorax.

Copulation lasted from 1 to 2 min. After intromission the male usually stays in copula even if the pair falls on their sides or completely over onto the male's dorsum. Upon withdrawal, the male either remains in position and attempts copulation again, or walks off the female. One male mated 4 times in a single trial. However, of the 6 females and 5 males used in more than one trial, none attempted or successfully mated in more than one trial.

The observed mating behavior and position agrees with the mating behavior and position reported by Park (1934) and by Stanley and Grundmann (1965). The latter did not associate the wiping motion of the male's legs with copulatory behavior. The rhythmic tapping of the aedeagus reported by Stanley and Grundmann (1965) was observed, and prying and pushing of the aedeagus was also observed.

*Tenebrio obscurus*
(dark mealworm)

In 54 trials, 28% of the males attempted to mate without success and 39% successfully mated (Table 6). The male approaches the female from any direction, but does not appear to perceive her from more than 10 mm. The male stops 5 to 10 mm away from her and slowly waves his antennae from side to side. As he moves closer and mounts her, he very rapidly waves his antennae from side to side. His head and prothorax also move slightly from side to side. In mounting, he climbs onto her posterior dorsum and moves forward rapidly tapping her elytra, prothorax, and finally her head with his antennae. When on her dorsum, he holds on to her elytra with his middle and hind legs and rubs the ventral surface of his front tarsi along the lateral margins of her prothorax. He rubs the tips of his maxillary palpi on the dorsal surface of her prothorax and rapidly

TABLE 6. SUMMARY OF ATTEMPTED AND SUCCESSFUL MATINGS OF *Tenebrio obscurus*. EACH LINE REPRESENTS ONE TRIAL.

| Female | | | Male | | | | |
|---|---|---|---|---|---|---|---|
| Ident. no. | Activity* | Age in days | Ident. no. | Activity* | Age in days | A or S** | Time in Copula in min† |
| 1 | 1-4 | 1 | 1 | 1-1 | 12 | A | |
| 1 | 2-4 | 1 | 2 | 1-2 | 14 | S | 1.6 |
| 2 | 1-1 | 1 | 3 | 1-1 | 26 | A | |
| 3 | 1-1 | 4 | 4 | 1-1 | 4 | S | × |
| 1 | 4-4 | 6 | 5 | 1-1 | 7 | A | |
| 4 | 1-2 | 6 | 6 | 1-2 | 10 | A | |
| 5 | 1-1 | 10 | 7 | 1-1 | 11 | S | 1 |
| 6 | 2-3 | 11 | 8 | 1-1 | 7 | AA | |
| 7 | 1-1 | 11 | 6 | 2-2 | 10 | S | 1 |
| 6 | 3-3 | 11 | 9 | 1-1 | 11 | A | |
| 8 | 1-2 | 11 | 10 | 1-1 | 11 | S | × |
| 9 | 1-1 | 12 | 11 | 1-1 | 13 | ASSSASS | × |
| 10 | 1-3 | 13 | 12 | 1-2 | 12 | S | 1.5 |
| 11 | 1-2 | 14 | 13 | 1-2 | 13 | SSS | × |
| 12 | 1-1 | 14 | 14 | 1-1 | 14 | S | 1 |
| 13 | 1-2 | 14 | 15 | 1-1 | 15 | S | × |
| 14 | 1-1 | 18 | 16 | 1-1 | 23 | A | |
| 15 | 1-1 | 20 | 17 | 1-1 | 21 | S | 2 |
| 16 | 1-1 | 20 | 18 | 1-1 | 22 | ASASS | 0.3, 1, 2 |
| 17 | 1-1 | 21 | 10 | 1-1 | 24 | AS | 1 |
| 10 | 2-3 | 22 | 2 | 2-2 | 14 | A | |
| 18 | 1-1 | 22 | 20 | 1-1 | 24 | S | 2.5 |
| 19 | 1-1 | 24 | 21 | 1-1 | 25 | A | |
| 20 | 1-1 | 24 | 22 | 1-1 | 26 | S | 3 |
| 10 | 3-3 | 27 | 12 | 2-2 | 26 | S | × |
| 21 | 1-1 | 28 | 23 | 1-1 | 25 | AS | 3 |
| 22 | 1-1 | 28 | 24 | 1-1 | 26 | AAA | |
| 23 | 1-1 | 29 | 25 | 1-1 | 26 | AAA | |
| 24 | 1-1 | 29 | 26 | 1-1 | 29 | AAAA<br>AAS | 0.5 |
| 25 | 1-1 | 29 | 27 | 1-1 | 30 | AAA | |
| 26 | 1-1 | 30 | 28 | 1-1 | 25 | AAAA | |
| 27 | 1-1 | 30 | 29 | 1-1 | 29 | AS | 2 |
| 28 | 1-1 | 31 | 30 | 1-1 | 28 | AAAS<br>AAS | 0.8, 5.5 |
| 29 | 1-1 | 33 | 31 | 1-1 | 30 | SS | 0.3, 0.3 |
| 13 | 2-2 | 36 | 32 | 1-1 | 29 | A | |
| 11 | 2-2 | 36 | 13 | 2-2 | 25 | A | |

* Activity=trial in which individual attempted or successfully mated, and total no. of trials for that individual; e.g., 1-4, individual mated in the first trial of the 4 in which it was used.

** A=attempted, or S=successfully mated in the sequence given for one trial.

† An × indicates that mating was not timed.

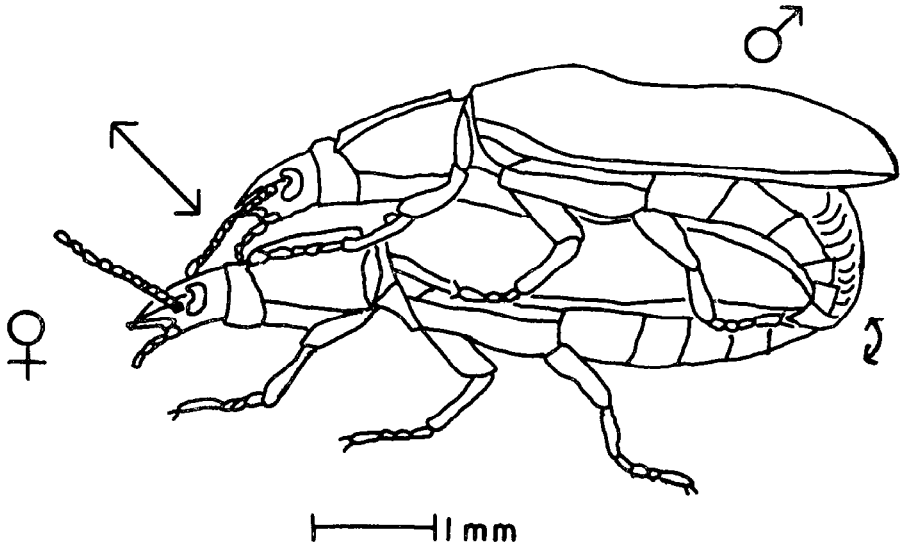


Fig. 8. *Tenebrio obscurus* copulating. Arrows show direction of movement of male's antennae, forelegs, and aedeagus.

taps her head with his antennae. Once he has inserted the penis, the rapid rubbing of the fore legs and tapping of the antennae ceases. The fore legs hold on to the bases of her elytra, while the antennae are held forward over her prothorax. His maxillary palpi lightly touch the rear margin of her prothorax. His body is convexly curved over hers (Fig. 8). When in copula the pair is inactive with little movement of antennae, mouthparts, or legs. The male's antennae may slowly move from side to side without touching her, and his mouthparts or legs may occasionally twitch.

The female stands still after the male contacts her, and she lowers her last sternite as the male taps with his antennae on her prothorax and head. Prior to intromission she raises her last tergite, and slightly extrudes her ovipositor. While in copula the female has all legs on the substrate, and her motionless antennae are held forward.

In extruding the genitalia the male lowers his last sternite and bends the aedeagus down and forward. Only the fine needle-like penis enters the female. If she does not admit it when he first attempts to copulate, he moves the tip of the aedeagus from side to side across the end of her abdomen until she lowers the last sternite and permits copulation.

Time in copula ranged from 0.3 to 5.5 min. Males often showed no further response to the female immediately after copulating but 5 males did copulate more than once in one trial (Table 6). Of the 10 females and 4 males used in more than one trial, 5 females and 4 males attempted or successfully mated in more than one trial. Copulations occurred only with the male mounted on the female's dorsum, both facing in the same direction. Occasionally a male mounted the female's dorsum from the anterior and probed at her head with the penis. After probing this way for 1 to 3 min the male either walked off the female or turned and attempted to

copulate in the correct position. Females occasionally showed behavior similar to the mounting behavior of the males. In these cases the female mounted the male's dorsum, slightly moved her fore legs on the male's elytra, and then walked off.

The mating behavior and position reported for *T. molitor* by Tschinkel et al. (1967) are similar to the mating behavior and position I observed for *T. obscurus*.

*Oryzaephilus mercator*
(merchant grain beetle)

In 26 trials, 15% of the males attempted to mate without success and 81% successfully mated (Table 7). Males do not seem to perceive the

TABLE 7. SUMMARY OF ATTEMPTED AND SUCCESSFUL MATINGS OF *Oryzaephilus mercator*. EACH LINE REPRESENTS ONE TRIAL.

| Female | | | Male | | | | | |
|---|---|---|---|---|---|---|---|---|
| Ident. no. | Activity* | Age in days | Ident. no. | Activity* | Age in days | A or S** | Time in copula in min† | Reproduction noted‡ |
| 1 | 1-1 | 13 | 1 | 1-1 | 13 | A | | |
| 2 | 1-1 | 13 | 2 | 1-1 | 15 | S | 10 | — |
| 3 | 1-2 | 13 | 3 | 1-2 | 15 | S | 13 | + |
| 4 | 1-2 | 13 | 4 | 1-2 | 15 | SS | 18.5, 3 | + |
| 5 | 1-1 | 15 | 5 | 1-1 | 18 | A | | |
| 6 | 1-1 | 15 | 6 | 1-1 | 18 | SS | 29, 9 | — |
| 7 | 1-2 | 15 | 7 | 1-2 | 20 | SA | 30 | + |
| 8 | 1-1 | 15 | 8 | 1-1 | 21 | A | | |
| 9 | 1-1 | 15 | 9 | 1-1 | 21 | SSA | 20.5, 2 | + |
| 3 | 2-2 | 18 | 3 | 2-2 | 20 | S | 5 | N.A. |
| 4 | 2-2 | 18 | 4 | 2-2 | 20 | S | 6 | N.A. |
| 10 | 1-1 | 18 | 10 | 1-1 | 32 | S | × | — |
| 11 | 1-1 | 18 | 11 | 1-1 | 35 | AS | × | — |
| 7 | 2-2 | 20 | 7 | 2-2 | 25 | S | 6 | N.A. |
| 12 | 1-1 | 25 | 12 | 1-1 | 27 | S | 2.5 | + |
| 13 | 1-1 | 25 | 13 | 1-1 | 27 | SS | 23, 2 | + |
| 14 | 1-1 | 25 | 14 | 1-1 | 27 | SAA | 11 | + |
| 15 | 1-1 | 25 | 15 | 1-1 | 27 | SSAAAA | 15, 2 | + |
| 16 | 1-1 | 26 | 16 | 1-1 | 27 | SS | 5, 9 | + |
| 17 | 1-1 | 26 | 17 | 1-1 | 27 | SA | 29 | + |
| 18 | 1-1 | 26 | 18 | 1-1 | 27 | SAA | 15 | + |
| 19 | 1-1 | 30 | 19 | 1-1 | 31 | AS | × | — |
| 20 | 1-1 | 30 | 20 | 1-1 | 35 | A | | |
| 21 | 1-1 | 32 | 21 | 1-1 | 24 | AS | × | — |
| 22 | 1-1 | 32 | 22 | 1-1 | 26 | AS | × | — |

* Activity=trial in which individual attempted or successfully mated, and total no. of trials for that individual; e.g., 1-2, individual mated in the first trial of the 2 in which it was used.

** A=attempted, or S=successfully mated in the sequence given for one trial.

† An × indicates that mating was not timed.

‡ +=additional adults, larvae, and/or eggs observed, —=none observed, and N.A.=data not available.

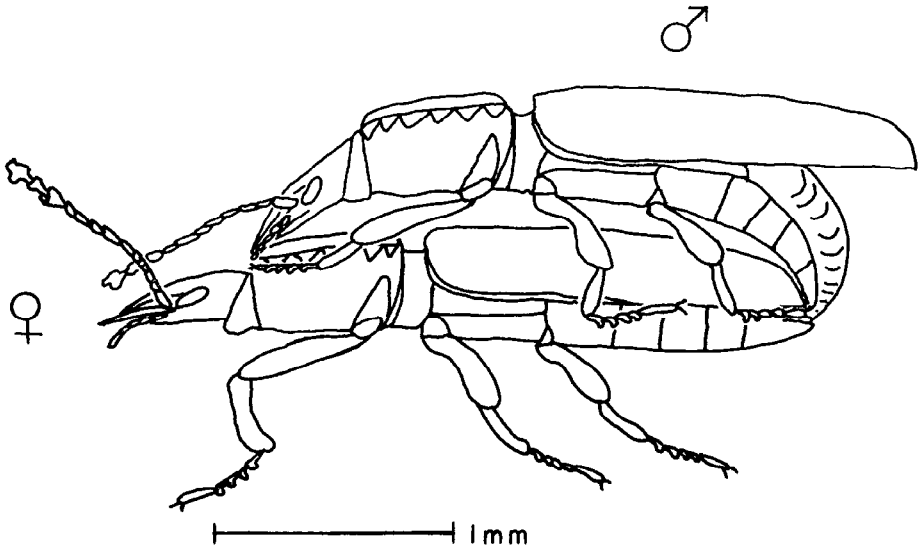


Fig. 9. *Oryzaephilus mercator* copulating. Note placement of male's antennae and mandibles.

females unless their antennae or maxillary palpi contact the female. Regardless of where he first touches the female's body, the male always moves to her rear before mounting. Often he touches the tip of her abdomen with his maxillary palpi before mounting. As he mounts and moves forward he taps her dorsal surface with his maxillary palpi. Meanwhile the female stands still and holds her antennae horizontally at 90° to her body axis. His antennae are held forward crossing over and sometimes touching her antennae (Fig. 9). The male lowers his last sternite and extrudes his genitalia. The female lowers her last sternite and admits the penis. While in copula his legs grasp her body, the position varying with the size of the male. If she is inactive during copulation, he slowly nibbles the middle ridge of her prothorax with his mandibles and lightly touches her prothorax with his maxillary palpi, but his antennae do not touch her antennae although they are held over hers. If she is active during copulation, he chews more actively on the middle ridge, and sometimes on the raised forward margins of her prothorax (with no apparent injury). His maxillary palpi actively tap on her prothorax and his antennae cross and touch her antennae. In copula his body is arched with the last few sternites touching her elytra. In about half of the copulations observed the female's body was also arched downward.

Prior to intromission the aedeagus bends 90° down and then forward. I was not able to observe if the penis was inserted into the female. It is dorsoventrally flattened and has a long internal sac (Slow 1958). The parameres do not enter the female but are held against her last sternite.

Once in copula the male remains in position even if the pair rolls over on their sides or completely over onto his dorsum. The male may remain in position after withdrawal and attempt to copulate again. Six of 10 males succeeded in a 2nd consecutive copulation in a single trial, although

TABLE 8. SUMMARY OF ATTEMPTED AND SUCCESSFUL MATINGS OF *Cryptolestes pusillus*. EACH LINE REPRESENTS A TRIAL.

| Female | | | Male | | | | |
|---|---|---|---|---|---|---|---|
| Ident. no. | Activity* | Age in days | Ident. no. | Activity* | Age in days | A or S** | Time in copula in min† |
| 1 | 1-1 | 2 | 1 | 1-1 | 5 | AS | 30 |
| 2 | 1-1 | 2 | 2 | 1-1 | 6 | AAS | 31 |
| 3 | 1-1 | 4 | 3 | 1-1 | 4 | A | |
| 4 | 1-1 | 4 | 4 | 1-1 | 4 | AAAA AAAA | |
| 5 | 1-1 | 4 | 5 | 1-1 | 5 | AAAA AS | 38 |
| 6 | 1-1 | 4 | 6 | 1-1 | 7 | SAAA | 35 |
| 7 | 1-1 | 4 | 7 | 1-1 | 7 | AAAA AA | |
| 8 | 1-1 | 5 | 8 | 1-1 | 11 | S | × |
| 9 | 1-3 | 6 | 9 | 1-2 | 11 | S | × |
| 10 | 1-1 | 7 | 10 | 1-1 | 7 | ASAAA | 11 |
| 11 | 1-1 | 9 | 11 | 1-1 | 7 | AS | 39 |
| 12 | 1-1 | 9 | 12 | 1-1 | 9 | AAAAS | 39 |
| 13 | 1-1 | 9 | 13 | 1-1 | 11 | AAAA AAAS | 43 |
| 14 | 1-1 | 9 | 14 | 1-1 | 12 | S | 37 |

* Activity=trial in which individual attempted or successfully mated, and total no. of trials for that individual; e.g., 1-3, individual mated in the first trial of the 3 in which it was used.

** A=attempted, or S=successfully mated in the sequence given for one trial.

† An × indicates that mating was not timed.

it was usually much shorter than the first. Time in copula varied from 2 to 30 min. Three females and 3 males used in 2 trials successfully mated in both trials.

### *Cryptolestes pusillus*
### (flat grain beetle)

In 29 trials, 10% of the males attempted to mate without success and 38% successfully mated (Table 8). The male does not seem to perceive the female until his antennae touch her. If he approaches her from the front, they both stop moving when their antennae touch. Usually his antennae cross over hers. He then moves to her side. If he approaches her from the rear, he touches the tips of her elytra and abdomen with his maxillary palpi, and then moves to her side. After moving to or approaching from her side, the male places his antennae horizontally along the side of her body, pushing her body with his mouthparts (Fig. 10). He does this for 0.3 to 1.0 min, and then moves to the tip of her abdomen and touches the end of her elytra and abdomen with his maxillary palpi, placing his antennae horizontally forward, one along each side of her body. Intermittently he raises up on his legs, spasmodically twitching his body for a few seconds, then lowers himself to his normal position and resumes

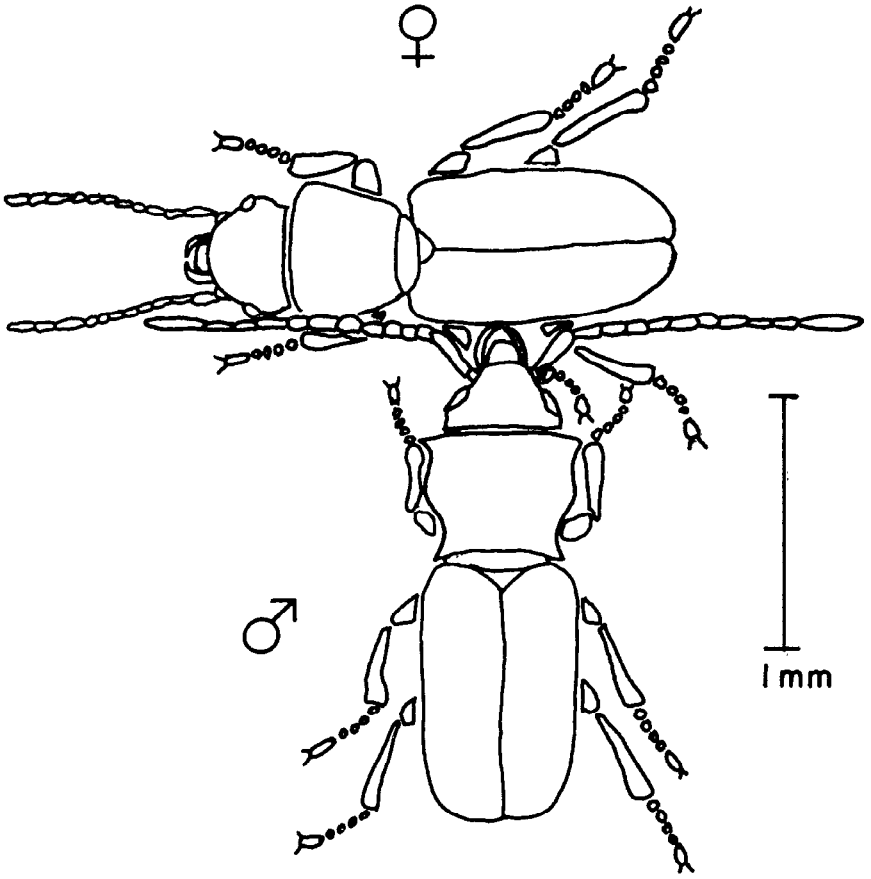


Fig. 10. Precopulatory behavior of *Cryptolestes pusillus*. Male pushing against side of female preparatory to copulation.

touching the end of her abdomen. After 0.3 to 1.5 min, the male extrudes his genitalia slightly and turns 180°. He slightly raises his elytra (held together, not spread) while slightly lowering his abdomen. With the last tergite raised and the last sternite lowered, he backs into the female and pushes hard against her abdomen (Fig. 11), occasionally pushing hard enough to raise the end of her abdomen up in the air. I was unable to observe which parts of the male's genitalia enter the female. The female lowers the last sternite (I was not able to observe if the last tergite is raised). During the entire courtship she does not move, except for an occasional twitch of an antenna.

When in copula, the ends of the abdomens are tightly pressed together. The male's elytra overlap the female's elytra, and his last sternite overlaps hers. All of their legs are on the substrate, and the antennae are held horizontally 90° to the side. Usually the only movement observed during copulation is an occasional twitch of an antenna. In 2 cases, however, the pair rhythmically moved up and down while in copula. Time in copula ranged from 11 to 43 min (Table 8).

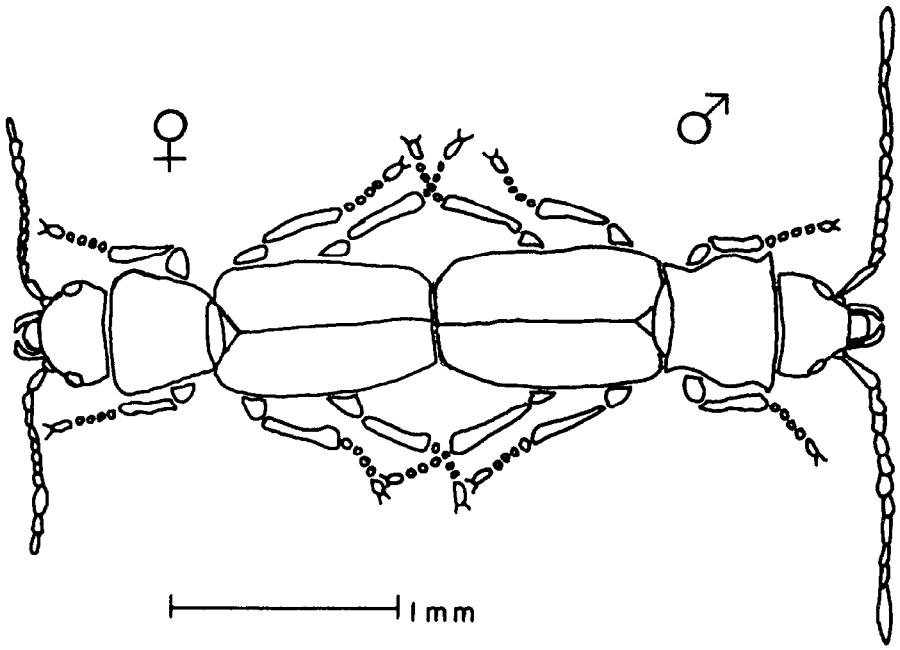


Fig. 11. *Cryptolestes pusillus* copulating.

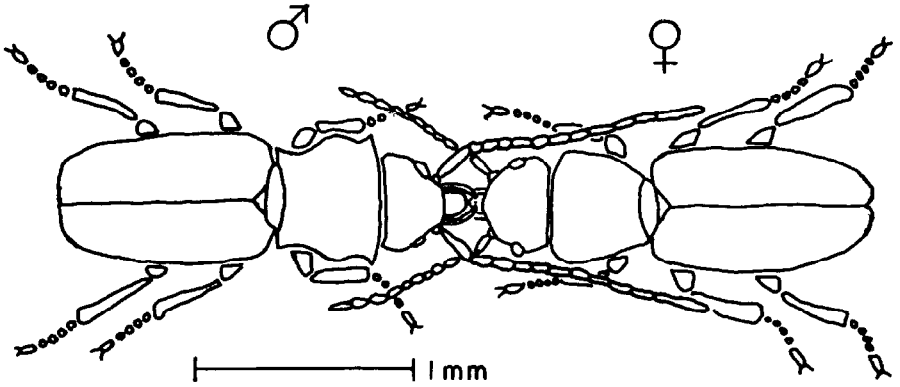


Fig. 12. Postcopulatory behavior of *Cryptolestes pusillus.* Male's antennae cross over female's antennae prior to male touching female with his mandibles.

In withdrawal, the male pulls himself away from the female and retracts his slightly protruded genitalia. He then walks in front of her head and crosses her antennae with his on top. Then he moves forward and touches her head, particularly the mandibles, the clypeal area, the eyes, and immediate area, with his mandibles and maxillary palpi (Fig. 12). For the first time the female moves, and she repeats these actions on the male. The pair may continue this activity for 1 to 2 min.

After this postcopulatory behavior the pair usually separates and the male shows no further reaction to the female. In 2 cases the male did at-

TABLE 9. SUMMARY OF ATTEMPTED AND SUCCESSFUL MATING OF *Sitophilus granarius*. EACH LINE REPRESENTS ONE TRIAL.

| Female | | | Male | | | | |
|---|---|---|---|---|---|---|---|
| Ident. no. | Activity* | Age in days** | Ident. no. | Activity* | Age in days** | A or S† | Time in copula in min‡ |
| 1 | 1-1 | 2 | 1 | 1-1 | 10 | AS | 55.5 |
| 2 | 1-2 | 3 | 2 | 1-2 | 11 | AS | 36+ |
| 2 | 2-2 | 9 | 2 | 2-2 | 17 | AS | 72 |
| 3 | 1-2 | 11 | 3 | 1-2 | 18 | ASA | × |
| 4 | 1-2 | 11 | 4 | 1-2 | 18 | AS | 30+ |
| 4 | 2-2 | 17 | 4 | 2-2 | 24 | A | |
| 5 | 1-2 | 18 | 5 | 1-2 | 18 | A | |
| 5 | 2-2 | 24 | 5 | 2-2 | 24 | AS | 43 |

* Activity=trial in which individual attempted or successfully mated, and total no. of trials for that individual; e.g., 1-2, individual mated in the first trial of the 2 in which it was used.

** Age is no. of days since emergency from wheat grains.

† A=attempted, or S=successfully mated in the sequence given for one trial.

‡ An × indicates that mating not timed.

tempt to copulate again in the same trial. In one case the attempt was immediately after completing the postcopulatory behavior. None of the 3 females, nor the one male used in more than one trial, attempted or successfully mated in more than one trial.

The mating position reported by Rilett (1949) for *C. ferrugineus* is similar to that observed for *C. pusillus*, but differences are apparent between the 2 species in precopulatory behavior. *C. ferrugineus* did not move to the side of the female but stayed at her rear. *C. ferrugineus* did not exhibit any postcopulatory behavior. The observed times in copula for *C. pusillus* were much less than the maximum time in copula reported for *C. ferrugineus*. Rilett reported successive matings of *C. ferrugineus* while *C. pusillus* did not successfully mate more than once (only 2 males attempted to mate again after successfully mating in one trial).

### *Sitophilus granarius*
### (granary weevil)

In 11 trials, 18% of the males attempted to mate without success and 55% successfully mated (Table 9). The male approaches the female from any direction and does not appear to perceive her until he touches her. On contacting the female, he mounts her immediately. The male grasps her with 3 pairs of legs. The fore and middle legs wrap around her body from the side. The hind legs are positioned as follows: coxae placed against her elytra, femora held against his abdomen, and tibiae and tarsi held against the sides and bottom of her abdomen. He is positioned far back on her with his abdomen bent downward along the top of her elytra (Fig. 13). The tip of his beak touches the top of her prothorax. If she starts to move about, he rubs his beak across the top of her prothorax thus quieting her. His antennae may lightly tap the sides of her prothorax; usually they are held in the air and may twitch slightly.

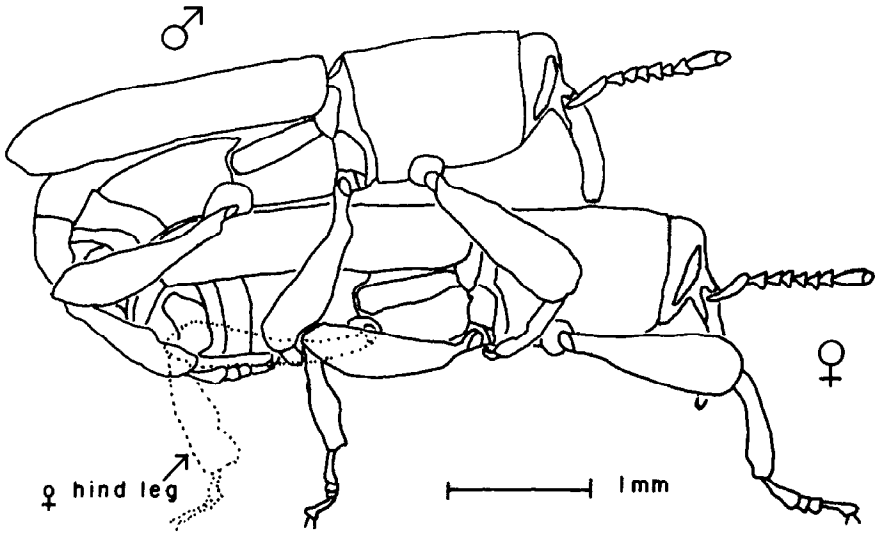


Fig. 13. *Sitophilus granarius* copulating. Female's rear leg stippled to show placement of male's rear leg. Note placement of male's beak on female's prothorax.

In extruding his aedeagus, the male raises his pygidium and extrudes the last (hidden) tergite downward and forward, rubbing it about on the female's pygidium. When she raises her pygidium and lowers her last sternite, he inserts the aedeagus which has been covered by the last tergite. The last tergite is pointed posteriorly until extruded and then moves down and forward, resting upon her lowered last sternite. None of the female's genitalia are extruded (Fig. 14).

In no other curculionids have the males been reported to rub the top of the female's prothorax with the beak, but Malkin (1949) reported this action for a brentid, *Brenthis anchorago* L.

Copulation lasted from 30+ to 72 min. The next longest time in copula, reported for a curculionid, is up to 30 min for *Anthonomus grandis* Boheman (Cross and Mitchell 1966). In only one trial did the male remain mounted on the female's dorsum after successfully mating and attempt to copulate again. Four females and 4 males were used in more than one trial with one female and one male successfully mating in more than one trial.

## Discussion

Males use many tactile stimuli (see Table 10 for particular species) as part of the precopulatory behavior. The male often touches the apex of the female's abdomen and elytra with his maxillary palpi prior to mounting. Some males tap the female with their antennae while mounting prior to intromission. The males of some of the species which copulate in the male over female position, move the fore or middle legs in a wiping movement on the female. The possible quieting function of this activity has not been recognized by many authors. The maxillary palpi are sometimes used to tap the female after mounting. The mandibles were used in

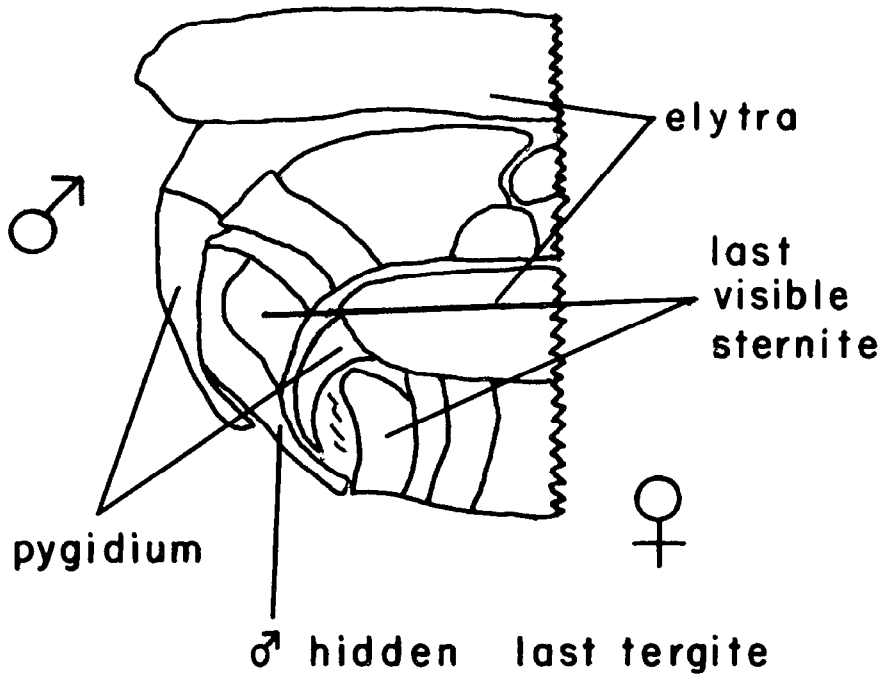


Fig. 14. Lateral view of *Sitophilus granarius* copulating. All legs removed to show placement of male's hidden last tergite.

precopulatory behavior in only 4 species. *O. mercator* chewed on the edges of the female's prothorax with his mandibles, *T. confusum* and *S. granarius* placed their mandibles on the top of the female's prothorax, and *C. pusillus* pushed against the female with his mandibles. In some cases, after extruding the aedeagus, the male taps, pushes, pries, or rubs the aedeagus on the end of the female's abdomen prior to intromission. This was usually done when the female did not immediately expose her genitalia and permit copulation.

After intromission, the male is quiet or shows little movement unless the female becomes active. If she becomes active, he usually repeats all of the actions he had performed after mounting except aedeagal movements. Receptive females in all cases were passive and did not show any special behavior during courtship and mounting, except for lowering the last sternite, raising the last tergite, or both permitting copulation. *C. pusillus* was the only species observed to exhibit distinctive postcopulatory behavior.

Neither audible nor ultrasonic stridulatory sounds were produced during any of the observations (Wojcik 1969b). *C. pusillus* is the only species studied with a presumed stridulatory apparatus (Reid 1942).

Some differences in behavior are apparent between species where there is sufficient information available to allow comparisons. The *Tribolium confusum* male taps the female with his antennae prior to intromission, touches the female's prothorax with his mandibles before and after intromission, and taps the female with his antennae after intromission; *T. castaneum* does not. Prior to and after intromission, *T. confusum* wipes

TABLE 10. SUMMARY OF OBSERVED MATING BEHAVIOR

| Behavior | Species | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | *Anthrenus flavipes* | *Trogoderma glabrum* | *Tribolium castaneum* | *Tribolium confusum* | *Tenebrio obscurus* | *Oryzaephilus mercator* | *Cryptolestes pusillus* | *Sitophilus granarius* |
| *Before mounting* | | | | | | | | |
| ♂ touches ♀ abdominal tip with maxillary palpi | A | A | A | A | N | A | A | N |
| *Mounted before intromission* | | | | | | | | |
| ♂ taps ♀ with antennae | A | N | N | A | A | A | A | A |
| ♂ wipes ♀ with legs | A | N | A | A | A | N | N | N |
| ♂ touches ♀ with mandibles | N | N | N | A | N | A | A | A |
| ♂ touches ♀ with maxillary palpi | A | N | A | A | A | A | N | ? |
| aedeagel movements | N | A | A | A | A | N | N | ? |
| ♀ lowers last sternite | A | N | A | A | A | A | A | A |
| ♀ raises last tergite | N | A | N | N | A | N | ? | A |
| *After intromission* | | | | | | | | |
| ♂ taps ♀ with antennae | N | N | N | A | N | A | N | A |
| ♂ wipes ♀ with legs | A | N | A | A | N | N | N | N |
| ♂ touches ♀ with mandibles | N | N | N | A | N | A | N | A |
| ♂ touches ♀ with maxillary palpi | N | N | A | A | A | A | N | ? |
| *Postcopulatory behavior* | N | N | N | N | N | N | A | N |

Symbols used: A, always or almost always occurs, N, never or almost never occurs, ?, not observed.

the female's elytra only with his fore legs, while *T. castaneum* uses either the fore or middle legs. The mating behavior of *C. pusillus* is different in some respects from *C. ferrugineus*. *C. ferrugineus* does not move to the side of the female as does *C. pusillus*. The male of *C. pusillus* does not nudge or push the end of the female's abdomen with his head as does the male of *C. ferrugineus*. Finally *C. ferrugineus* does not have any postcopulatory behavior such as occurs with *C. pusillus*.

The morphological differences between the 2 species of *Tribolium* and the 2 species of *Cryptolestes* are not great, and mating behavior differences probably serve as isolating mechanisms.

ACKNOWLEDGEMENTS

I wish to express my thanks to Dr. T. J. Walker and Dr. D. H. Habeck, University of Florida, for their aid and encouragement, and to the USDA, Stored-Product Insects Research and Development Laboratory, Savannah, Georgia, for supplying the funds which made this research possible.

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