

Biology of the Myrmecophilous Cricket, *Myrmecophila manni* (Orthoptera: Gryllidae)¹

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ABSTRACT: Crickets were collected from colonies of 5 species of ants in southeastern Washington, but the western thatching ant, *Formica obscuripes* Forel, seems to be the primary host for these inquilines. These crickets are generally treated in a hostile manner by worker ants and avoid attack only through their constant alertness and rapid escape behavior. However, the crickets mimic the antennal signals of worker ants which permits them to engage in trophallaxis with the ants. They also frequently strigilate on the bodies of ants, presumably to acquire nourishment or colony odor. The mating behavior of these crickets is similar to that described for other, free-living crickets in that the female is on top of the male while in copula. However, in *Myrmecophila manni*, a male signals the female of his readiness to mate and runs under her when she is in the proper mating position. The eggs, 1.1 mm long, are laid into holes in the substrate. This probably shields them from attack by the ants. Hatching in the field occurs in mid-July, and is synchronized at all colonies. The crickets probably disperse from nest to nest using the foraging trails of the ants that frequently overlap.

Most ant species share their nest with myrmecophiles of one type or another. The ant nest provides an energy rich system that remains relatively stable from year to year. Most myrmecophiles have evolved adaptations that allow entrance and integration into the ant nest. These adaptations usually involve behavioral, morphological, and/or chemical mimicry. This mimicry appears to take advantage of the very attribute that makes ants so successful, their sociality. Social Hymenoptera are innately predisposed to rearing their young, to mutual grooming and trophallaxis, and to protection of the queen and nest. This is accomplished through simple, though not well understood, tactile and chemical forms of communication.

Myrmecophila Latreille is comprised of a number of species of small, apterous crickets that inhabit the nests of many ant species. Few detailed observations have been made on the biology of these myrmecophiles. However, Wheeler (1900) found that *Myrmecophila* strigilate their host and suggested that they derive nourishment from materials scooped from the integument. Schimmer (1909) showed that *Myrmecophila* also engage in trophallaxis with their host. Accounts of *Myrmecophila* behavior indicated that the ant hosts were hostile to their cricket guests, and that the crickets mimicked the mutual grooming and trophallaxis behavior of the ants in order to get close (Wheeler, 1900; Schimmer, 1909). It was further suggested that the commensal association was only possible because the cricket was much quicker and could escape any aggressive ant (Wheeler, 1900).

The present study reports the biology of a single species, *Myrmecophila manni* Schimmer. This small cricket (2.3-4.0 mm) occurs in semiarid and arid regions

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from northern Idaho and southeastern Washington southward into Mexico (Hebard, 1920; Graves et al., 1976; Clark and Blom, 1982). *M. manni* has been collected with at least 13 different ant species, however, little is known of its biology and ecology. Field and laboratory studies were conducted on intra- and interspecific interactions of this insect, with special attention placed on characteristics that permit its cohabitation with ants.

Materials and Methods

FIELD: Forty ant colonies were sampled within a 40 km radius of Pullman, Washington during June and July 1983 to study the distribution and abundance of *M. manni* in southeastern Washington. Fifteen of these nests were *Formica obscuripes* Forel, and it soon became obvious that these ants were the primary host of *M. manni* in this area. Therefore, most of the studies and collections were directed to this species. Thirteen trips to these *F. obscuripes* nests were made the following summer to determine the number of crickets occupying each nest. Flat boards were placed on top of the nests, pushed into place in the thatch, and later checked at random times during 24 hr daily cycles for crickets. The boards retained moisture under them and crickets as well as ants tended to aggregate there.

Two *F. obscuripes* nests harboring large numbers (>50) of *M. manni* were observed for ca. 100 hours during the spring, summer, and fall of 1983 and 1984. The nests were not disturbed during observation periods, and thus cricket behavior in the field was limited to observations of activities outside the nest. Flat boards were placed at several locations on and near the nest, and along the foraging trails. Counts of crickets under the boards were used to determine travel of the crickets along foraging trails and near the nest. Activity periods of ants and crickets were determined over 24 hr cycles with special attention given to understanding how the behavior of crickets and ants might influence each other. Night observations were made with a head lamp equipped with a red Plexiglas® covering. Most insects are insensitive to red light, and this light caused no visible disturbance to the crickets nor to the ants.

Since crickets were active on foraging trails, the foraging activity of the ants was sampled from 1 June to 30 July 1984 by counting the total number of ants traveling in either direction past a 10 cm cleared area of a specific trail. Eight, one minute counts were taken during 4 time periods from 0500–2300 hr, and the counts were averaged. Also three foraging trails were measured with a tape measure to determine distances traveled by *F. obscuripes* workers.

The mound building behavior of *F. obscuripes* was examined in relation to temperature control of the nest during June and July 1984. Temperature regulation may be an important reason for cricket habitation of the nest. Internal nest temperatures were recorded using a Yellow Springs Instrument Tele-thermometer® with a six inch temperature sensitive probe. Readings of nest temperatures were taken at a six inch depth into the mound. Ambient temperature was recorded immediately following each internal nest recording for comparison.

LABORATORY: Two hundred fifty *M. manni* were collected from 10 nests within a 40 km radius of Pullman, Washington from March 1983 to August 1984 and brought back to the laboratory for observation. Crickets were transported to the laboratory using moist containers to prevent desiccation and death during transfer. These containers were 6.5 cm deep × 15 cm diam clear plastic, with a plastic lid,

and a thin bottom layer of plaster of Paris and charcoal. In the laboratory crickets were held in similar containers kept moist with distilled water to maintain high relative humidity (90–100%). All laboratory crickets and ants were maintained on a 16:8 L/D photoperiod at ca. 20°C.

Twenty-five containers with four to seven crickets each were set up to study intraspecific behavior and to determine if crickets were dependent on their ant hosts. Crickets were fed unfiltered honey, placed on paper toweling, every third day. Old honey was removed at that time. Crickets were individually marked on the thorax or abdomen with Liquid Paper® for identification purposes.

Fifteen containers harboring crickets and ants were set up to study interspecific behavior with seven ant host species. These insects were also fed unfiltered honey. Ant species used included: *F. obscuripes*, *F. fusca* Linne, *F. haemorrhoidalis* Emery, *Camponotus vicinus* Mayr, *Camponotus modoc* Wheeler, *Tapinoma sessile* (Say), and a *Myrmica* sp. Crickets harbored with *F. obscuripes*, *Myrmica*, and *Tapinoma* were field collected with the associated ant species. Crickets harbored with other ants were originally collected from *F. obscuripes* nests.

Seventy-seven observations of 1 hr duration were made at random times over the 24 hr cycle between May 1983 and November 1984. All time periods were included in the 24 hr cycles so that if the behavior of the crickets varied, these changes would be detected.

Results and Discussion

HOST: Crickets were found in nests of five species of ants in southeastern Washington. A total of 40 nests was sampled, and crickets were found in 14. The ants included *Formica fusca* (crickets present in 1 of 7 nests sampled), *F. obscuripes* (8/13), *F. haemorrhoidalis* (2/5), *Tapinoma sessile* (2/9), and *Myrmica* sp. (1/6). The colonies of *F. obscuripes* harbored 15 or more crickets per colony, and one colony had over 300. Three or fewer crickets were found per colony with all other ant species. These collections would seem to indicate that *F. obscuripes* is the major host species for *M. manni* in this area.

INTERACTIONS WITH HOST ANTS: The ants were aggressive towards the crickets, no matter how long they were housed together. However, an ant usually had to be within 4 mm before it perceived and attacked a cricket. Since the crickets were always alert, and tended to avoid approaching ants by circling around behind them, attacks were not as common as might be expected. However, when a cricket was attacked, one of two escape modes were used. The typical escape consisted of the cricket running quickly in a zig-zag pattern. The crickets were much faster than the ants, and most reacted swiftly to avoid an aggressive ant. The second escape mode was by jumping to avoid the ant. One cricket jumped 40 cm. In spite of the constant aggressiveness by the ants, only three crickets were seen being caught and killed.

Despite the nearly constant aggressiveness of the ants, the crickets tended to stay close to their hosts. Thus, a cricket was usually nearby when an ant started to groom itself or to engage in trophallaxis with a conspecific, and would invariably approach the ant(s), usually from behind. The cricket used its antennae to contact the ant, and if the ant did not react aggressively, the cricket usually moved in closer to strigilate or to engage the ant in trophallaxis. Once the ant was thus engaged, it appeared paralyzed. Then the cricket sometimes became very bold,

and crawled on top of the ant as it strigilated. If another ant approached at any time during this sequence, the cricket abandoned this activity and departed.

The crickets have apparently broken the code to elicit feeding by ants via trophallaxis. They are seemingly able to duplicate the antennal drumming sequence ordinarily given by an ant to a conspecific to elicit feeding, since they were observed being fed many times (> 50) in the laboratory containers.

To accomplish trophallaxis and strigilation with aggressive ants requires that the crickets be constantly alert. Additionally, they appear to be able to sense the alertness state of the ants, suggesting that the crickets may also be able to perceive the pheromones used by the ants. However, this aspect was not investigated further.

FEEDING BEHAVIOR: Honey: Feeding on honey by the ants and the crickets was common in the laboratory containers, and honey was probably the main source of food for both insects. As the crickets fed their heads assumed a prognathous position with the mandibles and maxillae pulling the honey-soaked paper into the buccal cavity. They changed their position with respect to the honey often. The metathoracic legs were always outstretched during feeding. This posture may be an adaptation for escape, enabling the cricket to quickly back away from the food source. This feeding posture is probably related to the crickets' association with ants.

Strigilation: Crickets strigilated live and dead ants 70 and 10 times, respectively (Figs. 1, 2). This occurred with every species of ant tested. Dead worker ants were strigilated intermittently for up to two days while dead queen ants were strigilated for up to 30. *Myrmecophila* may strigilate their host ants to derive nourishment from the oily secretions on the body (Wheeler, 1900). Strigilation usually did not occur until the ant was self-grooming or grooming a conspecific. Crickets initiated strigilation at the gaster or metathoracic legs of the host ant 90 percent of the time ($n = 72$). *M. manni* approached its host slowly, with its metathoracic legs outstretched to allow a quick retreat if necessary. The crickets often made several moves toward and away from the ants before returning to strigilate. Initial contact was always made with the antennae. Ants use their antennae extensively in contacting nestmates for recognition purposes. This behavior was mimicked by the cricket to gain access to the ant for strigilation. The ant usually accepted the mimicked recognition signals displayed by the cricket and assumed a passive posture. Sometimes, however, the ant remained aggressive toward the cricket. On these occasions, the cricket retreated, and re-initiated the sequence when the ant resumed grooming. Once antennal contact with either the ant's body or antennae was made and accepted, the cricket began strigilation. The cricket's antennae moved constantly over the ant's body throughout this process. Crickets usually did not strigilate any one area for more than five seconds but moved about, often going from gaster to legs to thorax, and back again. Occasionally as the ant was strigilated it moved its body to allow the cricket easier access to certain areas, such as the base of the legs. However, the strigilated ant also seemed to be in a state of semi-paralysis.

During 15 observed strigilations nearby crickets joined in the strigilation of the same ant. The crickets always maintained at least a 45° angle from each other when strigilating the same ant and displacement occurred regularly as the crickets changed positions. In five cases the head of a live host was also strigilated. Wheeler



Figs. 1, 2. 1. *M. manni* strigilating an *F. obscuripes* worker. 2. *M. manni* strigilating a dead *F. obscuripes* worker.

(1900) stated that *Myrmecophila* never strigilated the head region because of the obvious danger of the ant's mandibles.

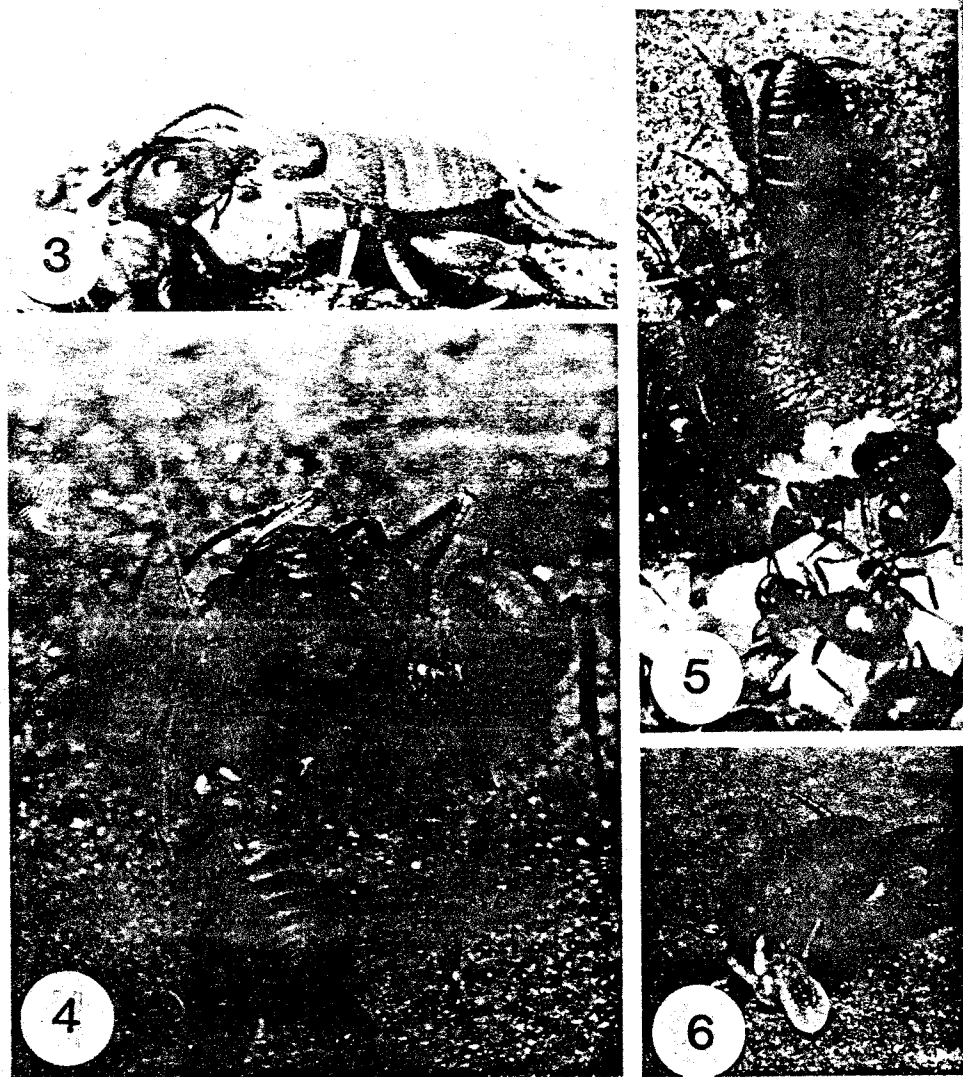
Trophallaxis: Trophallaxis occurred ($n = 22$ timed events) between ants and crickets with every ant species tested (Figs. 3, 4). Even workers of *Tapinoma*, which were smaller than the cricket, fed the cricket by trophallaxis. On each of two occasions, a cricket positioned itself between two ants already in trophallaxis and imbibed some of the fluid. Usually, however, the cricket made direct movements toward an ant and elicited trophallaxis by antennating the ant, and by manipulating the ant's mouth parts with its maxillary and labial palpi. The antennae of the cricket always made the initial contact with the ant and appeared to be the primary structure used in eliciting trophallaxis. Antennal contact usually required less than three seconds before acceptance or rejection was apparent. In 12 instances intense and persistent antennal contact occurred between cricket and ant before the ant became receptive. The ant then opened its mandibles, and the labial and maxillary palpi of the cricket repeatedly contacted the mouth parts of the ant. This action apparently mimics the tarsal signals in trophallaxis used by conspecific ants (Wilson, 1971). When in trophallaxis, the cricket maintained a tense posture with its metathoracic legs outstretched. Trophallaxis usually lasted ca. five seconds before the ant became aggressive, and vigorous antennal contact by the cricket was required to maintain trophallaxis beyond this time. However, in three cases an ant remained in a position for trophallaxis for over a minute; the cricket left and returned several times within that period.

Trophallaxis of ant larvae: Observations of the *Tapinoma* container showed crickets attempting to get close to the ant brood on 13 occasions. The cricket always approached the brood slowly and as it got closer it contacted the worker ants with its antennae (Fig. 5). The ants reacted aggressively, and each time the cricket was chased away by the workers. On one occasion a cricket gained access into the brood area through an unguarded area. It quickly touched a larva with its maxillary and labial palpi, picked it up in its mandibles, and carried it for about 5 cm before engaging in mutual gnathal contact (Fig. 6). However, the cricket's feeding was very rapid and within five seconds a worker ant chased it from the larva. Examination revealed that the head region and mouth parts of the larva had been slightly lacerated.

Strigilation of ant eggs: Crickets often strigilated the chorion of ant eggs. They rolled the eggs as they scraped the chorion with their mandibles. However, in a container housing a *Camponotus* queen, eight of her eggs, and two crickets, the eggs disappeared and were assumed eaten by the queen. It is possible the crickets ate the eggs but this was not observed.

LONGEVITY: The crickets lived for about three months in the laboratory without ants and averaged four months with ants (Henderson, 1985). Although this information suggests that the crickets are not dependent on the ants to provide them with nourishment, the increased longevity when harbored with ants suggests that the ants provide something. Perhaps added nutrition is provided to the crickets when engaging their host in strigilation and trophallaxis.

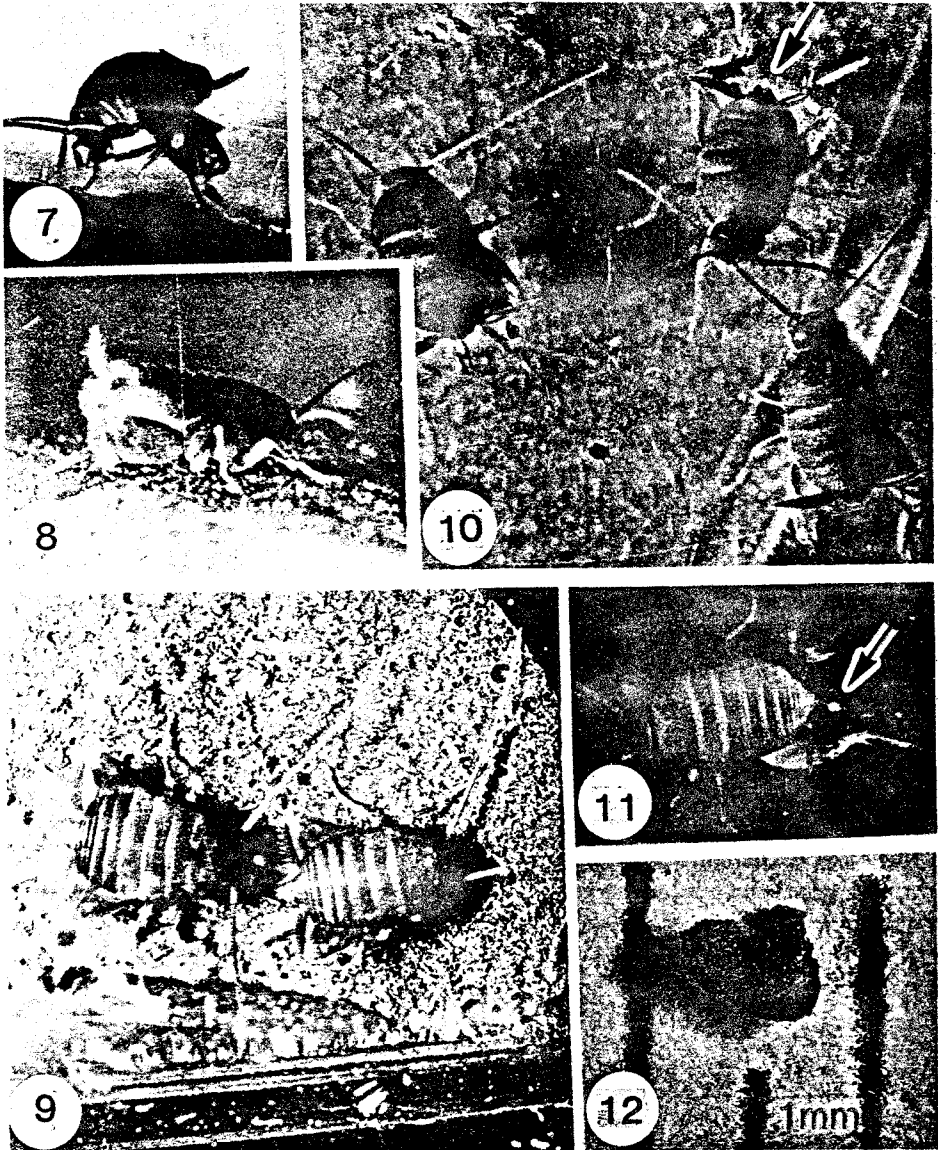
GROOMING: Self-grooming activity by a cricket occurred an average of five times every observation period and was the most consistently observed activity. Grooming involved cleaning of the antennae, legs, and cerci. These regions contain the sensory structures that are most important in recognition of approaching ants,



Figs. 3-6. 3, 4. *M. manni* in trophallaxis with an *F. obscuripes* worker. 5. *M. manni* near the *Tapinoma* brood. 6. *M. manni* in trophallaxis with a *Tapinoma* larva.

and thus, they must be kept free of debris. During leg cleaning, the cricket alternately brought a metathoracic leg under the body and groomed the tibial spines and spurs with its mouth parts. This required the cricket to arch its back upward to allow the head to reach under and make contact with the leg (Fig. 7). Cercal scraping invariably followed and was probably the reason for leg cleaning. Immediately after the leg was cleaned it was brought over top of the cercus and then along the length of the cercus once or twice. A cricket that was marked with White-out® for identification purposes repeatedly tried to remove it with its metathoracic legs and eventually cleaned the cercus. Crickets that were missing a metathoracic leg used the mesothoracic leg to clean the cerci ($n = 3$).

REPRODUCTIVE BIOLOGY: *Mating*: Mating in *M. manni* is similar to that re-



Figs. 7-12. 7. *M. manni* cleaning spines and spurs of metathoracic leg. 8. Male *M. manni* in mating stance. 9. Male *M. manni* displaying behind female prior to copulation. 10. Males fighting over courtship rights to female *M. manni*. Note spermatophore ball (arrow) on male in upper right. Female is to the left. 11. Male *M. manni* with stalked spermatophore (arrow) attached to the subgenital plate. 12. *M. manni* egg.

ported for related crickets (Alexander, 1961). The female is on top of the male during copulation. However, in other crickets the female positions herself on top of the male, whereas *M. manni* males run underneath the female to attain the copulatory position. Over 500 observations of *M. manni* in various stages of mating were recorded in the laboratory. The mating behavior was stereotypic, and the following description is a collation of three observations that recorded

the complete mating sequence. First, the male apparently set up a "mating arena" by marking an area. The cricket pressed its anus to the substrate and then dragged itself in an ever decreasing spiral using only the prothoracic and mesothoracic legs. The diameter of the marked area was approximately 2 cm. The male then assumed a mating stance (Fig. 8). The posterior end of the body was held high in relation to the substrate, while the head was appressed to the ground. The male remained in this posture through the entire process. The male then left the mating arena in search of a female. When contact with a female was made (Fig. 13a), the male oriented himself behind her and a chase ensued until the female was pursued and pushed, through intermittent contacts, to the marked area. Once there, she stopped and remained still (see Fig. 9). At this point the mating stance of the male increased in its visual and vibrational display. Again, the male oriented himself directly behind the female (Fig. 13b) and moved forward in quick, jerky movements, while vibrating the antennae. The vibratory movement began at about a 40° arc that became progressively smaller and faster, repeating every four seconds. At the same time the male backstepped in short spurts, and the cerci vibrated in synchrony with the short, fast backstepping. The female, motionless up to this point, lifted her body as high off the ground as possible and arched her back upward (Fig. 13c). The male then quickly moved under the female and copulation occurred (Fig. 13d). Copulation lasted ca. three seconds, while the complete mating sequence took five minutes. The female then left the marked area, and the male returned to a mating stance, apparently searching for another female.

Actual coupling during copulation was difficult to see. However, during one mating sequence, the crickets fell over onto their sides while remaining in copula, and coupling was observed.

The three complete sequences used to describe the mating sequence were all performed by the same male and took place in the same marked area. Only potential mates crossed the boundaries of the marked area, other males often skirted the edge of the boundary. However, the area could not be considered a territory since it was not seen defended. When the male was not actively searching for a female the mating arena boundary seemed to disappear and male and female crickets moved through this area.

During the mating sequence, the female lifted her body in response to the male's constant visual and vibrational cues. If she did not respond in this manner, it was impossible for the male to move underneath and for copulation to occur. In ca. 40 male-female contacts it was the female that first contacted the male, usually using the antennae, but sometimes contacting the male with head butts. When numerous contacts occurred within a short duration (a few seconds apart) the mating sequence increased in length and overall activity. It appears, therefore, that the female took an active role in mating, although female behavior was more subtle than the overt displays of males.

Spermatophores: Spermatophores of *M. manni* were observed regularly. They consisted most often of a ball of liquid left behind on the dorsal cleft of the subgenital plate (Fig. 10). Spermatophores were usually evident when males were in a mating stance. If mating was interrupted (e.g., another cricket displaced the male or there was not a receptive female present), males removed spermatophores by pressing the end of the abdomen to the substrate and scraping until the spermatophore was dislodged. This behavior is common among crickets (Alexander,

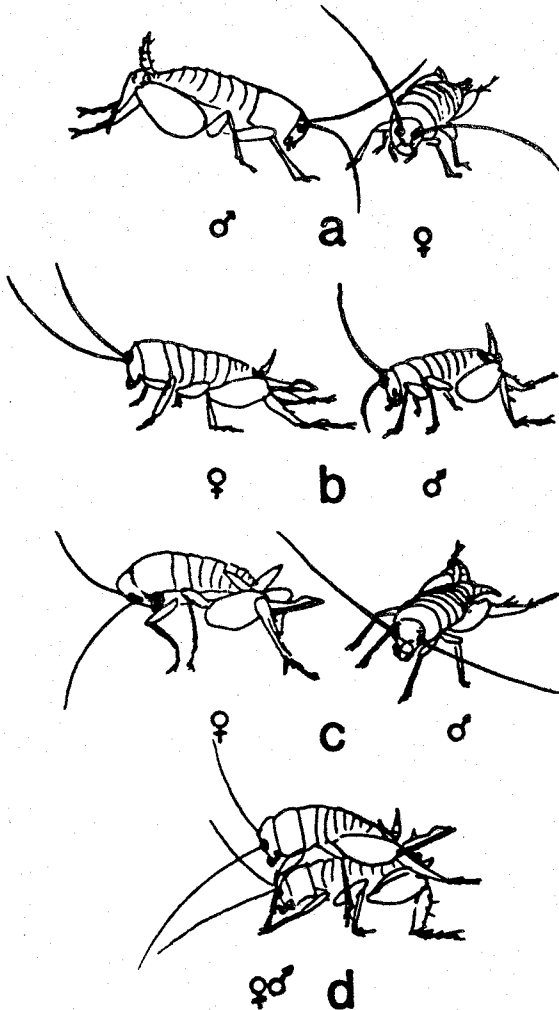


Fig. 13. (a-d) Mating behavior of *M. manni*. First the male searches for a female (a). Upon finding a female the male gets behind her (b) and pushes her to a marked mating arena. Once in the arena, the female is prompted into the copulatory position (c). The male then runs under the female and mating is completed (d).

1961). In two instances, however, the spermatophore was elongated while the crickets tried to scrape it off, thus creating a stalked base upon which the main portion of the spermatophore was perched (Fig. 11). In one instance, the spermatophore scraped off was in a free-standing position with the bulbous end extending upward. Within 24 hr the spermatophore was collapsed and shriveled. Usually, however, there was no stalk, and the spermatophore was scraped off and apparently eaten. In one case, a male backed up over the area where it had just left a spermatophore and strigilated the substrate for several minutes. Spermatophores consist mainly of protein (Khalifa, 1949) and the cricket probably ingested it. Spermatophore eating is common among orthopterans (Alexander, 1961).

Egg-laying behavior: Three females were observed prior to egg laying. Aggres-

sion toward males, about three days before oviposition, was the first detectable sign that a female was about to oviposit.

Ovipositor cleaning also occurred near the time of oviposition. This entailed bringing the ovipositor under the body and arching the back so the head could reach the tips of the valvulae. The tips contain numerous sensory receptors and were extensively groomed. Observations of ovipositor cleaning revealed that the valves can be moved independently of each other. Oviposition cleaning lasted ca. one minute and was observed up to three times per observation period.

One female showed extreme physogastry three days prior to egg laying. She appeared very lethargic and remained motionless for hours at a time. On the second day the palpi of the mouth parts hung down and dragged on the ground. After oviposition this female resumed normal appearance and behavior.

When a female was ready to oviposit she searched the substrate with her mouth parts appressed to the ground while the ovipositor probed many openings. This behavior seemed to peak when water was added to the containers. Alexander (1961) found that in most field crickets insertion of the ovipositor into the substrate is apparently initiated upon contact of the maxillary and labial palpi with a damp surface. In addition, he suggested that the ovipositor bears sensors which must encounter dampness before eggs can be released.

It was difficult to determine when egg laying was taking place since the eggs were quite fluid, and the female did not exhibit visible signs of the actual occurrence. However, in the laboratory container, freshly-laid eggs were continually found for over two months.

Eggs were laid vertically into the substrate at a depth of 1 to 2 mm. Forty-three eggs were found in four containers from June to August 1984. Eggs were 1.1 mm long and a fine reticulation of the chorion was visible under the light microscope (Fig. 12). In the laboratory cultures, the crickets frequently laid their eggs in holes in the plaster left by air bubbles. Eggs laid in imperfect holes were deformed, usually being constricted at one end to conform to the hole. Cricket eggs were very similar in size and shape to the eggs of *F. obscuripes*.

Reproduction in the field: *Myrmecophila* oviposit within the nests of their host, and the eggs require ca. six weeks to develop (Schimmer, 1909). The nest probably provides the same benefits for cricket eggs as it does for ant eggs. The nest is maintained at relatively high and stable temperatures throughout the summer.

F. obscuripes builds thatch mounds up to four feet high from coarse grass clippings and small twigs. Nest location and mass of the thatch are prime factors in collection and retention of solar radiation (Weber, 1935). *F. obscuripes* workers also help to control nest temperatures by opening and closing mound entrances. As the day progressively became warmer the ants opened up to six entrances allowing for ventilation of internal chambers. At night, the ants covered entrances with thatch, thereby decreasing heat loss.

The nest provides temperature regulating benefits to *M. manni*. The average temperature within one *F. obscuripes* mound differed significantly from ambient temperatures for most of the day (Fig. 14). Stable nest temperatures are undoubtedly instrumental in the rapid development and hatching of cricket eggs. Also, worker ants provide protection from predation to the ant brood and queen, and inadvertently provide this protection to the crickets and cricket eggs.

On 17 July 1983 first instars of *M. manni* were found in large numbers (>25)

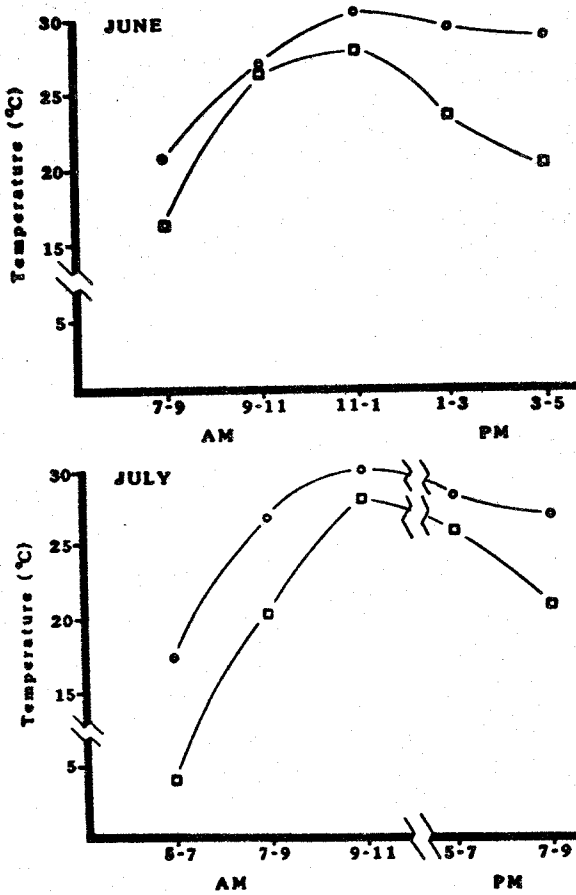


Fig. 14. Graphs show the difference between ambient temperatures (□) and internal nest temperatures (○) of an *F. obscuripes* nest for the months of June and July. Each value is for 7 readings which were averaged. The averaged temperature within one *F. obscuripes* mound differed significantly from ambient temperatures for most of the day (*t*-test, $P < 0.05$).

under boards placed directly over nests of two *F. obscuripes* colonies. The nests were separated by a distance of ca. 2.2 km. All first instars were 1.4 mm in length and were very active, entering the ant mound whenever the nest boards were overturned. Again, on 27 July 1984 first instars of *M. manni* were found in two widely separated (3 km) *F. obscuripes* nests. The immatures exited and entered the mound entrances repeatedly, and were apparently unnoticed by the ants.

Synchrony of reproduction, in widely separated nests, suggests that egg-laying is probably controlled by climatic factors in *M. manni*. Photoperiod most likely exerts control over synchronous egg laying, whereas temperature probably plays an important role in development.

DISPERSION TO OTHER ANT COLONIES: *F. obscuripes* workers foraged along well established trails that were maintained throughout the summer. Trails radiated from the main nest and usually led to bushes or trees where the ants tended aphids and preyed upon other insects. Sixty-three crickets, including both sexes and all nymphal instars, were observed traveling on these trails. Three trails extended

over 20 m, and thirteen crickets were found this far from the nest. However, cricket travel only occurred from dusk until about 2300 hr, after which all cricket activity outside of the nest ceased. The ant foraging activities were fairly constant from 0500–2300 hr, and few ants foraged from 2300–0500 hr (Henderson, 1985). These trails are probably a major dispersal route for crickets to enter new areas and to join other colonies. They frequently overlap with trails from other colonies, so the crickets would be able to follow trails all the way.

Crickets were observed on various trails emanating from *F. obscuripes* colonies on nearly every evening. The crickets appeared to move randomly while on the trails, other than avoiding attacks by the ants. Thus, although the crickets were constantly present on the trails in the evenings, no obvious behavior was observed which might help to explain their presence.

Ants commonly move the entire colony, including nest material, when conditions become unfavorable (Donisthorpe, 1927). One *F. obscuripes* colony was observed in the process of relocation in April 1984. The ants followed a single trail that led directly to the new nest site about one meter away. They carried other ant workers and thatch from the old nest to the new nest site over a period of ca. two weeks. During this time crickets were consistently found under flat boards on the old nest. However, when relocation was complete, and ants were no longer present in the old nest, the crickets also abandoned it and were subsequently found under flat boards on the new nest. This indicates that crickets relocate with the colony by using the trails.

Also, colony formation, intercolony communication, and mating behavior exhibited by *F. obscuripes* probably help facilitate *M. manni* dispersion. *F. obscuripes* frequently build secondary nests along the foraging trails to bring the ants closer to a food source (Weber, 1935). In early June 1984 a secondary nest of *F. obscuripes* was found 20 m from the main nest. Shallow tunnels were excavated by worker ants under a flat board and a supply of food consisting mostly of immature insects was always present. About 30 worker ants were found under the board at any one time and, during a one month period, 13 crickets were also found in association with this nest.

The mating behavior of *F. obscuripes* differs from that of most ants in that there is no true nuptial flight (Weber, 1935). Talbot (1972) found that *F. obscuripes* reproductives mate in ground swarms. Females swarm to a ground location near the nest and mate with males on the ground. Inseminated *F. obscuripes* probably found colonies by invading already established nests (Weber, 1935), and it is probable that secondary nests of *F. obscuripes* may accept a queen at this time also. Thus, if the secondary colonies become permanent in this manner, they could already be occupied by crickets from the parent colony.

The following major points of *M. manni* biology were brought out during this study:

- (1) Crickets were not dependent on ants for survival in the laboratory.
- (2) Ants were hostile to their cricket guests regardless of the length of time housed together or whether ants and crickets were field collected from the same nest. Speed and quickness were essential for the cricket in avoiding capture by a host ant.
- (3) Crickets took advantage of their host by strigilating ant eggs, live and dead ants, and by making adult, and perhaps larval, ants regurgitate food. They ap-

parently accomplish this trophallaxis by mimicking recognition signals used by ant conspecifics.

(4) Self-grooming was a very important part of the cricket's life. Cleaning of the cerci and antennae were important since they contain many of the sensory structures used in intra- and interspecific interactions.

(5) The mating behavior of *M. manni* was unique in that the male ran under the female for copulation. Spermatophores were regularly evident on the dorsal cleft of the subgenital plate during mating rituals in which the male went through a stereotyped visual and vibrational display.

(6) The eggs of *M. manni* are about 1 mm long and are laid at a depth of 1 to 2 mm into the substrate in the laboratory.

(7) Cricket reproduction in the field was synchronous and probably keyed to external climatic factors. The nest probably provides the temperature and humidity required by the cricket brood.

(8) Adult and immature crickets were found on the foraging trails of *F. obscuripes*. Crickets probably use these trails to follow ants in the establishment of new colonies.

(9) Dispersal by the cricket appears closely tied to the mating, colony formation, and intercolony communication behavior of its main host, *F. obscuripes*.

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