THE MATING BEHAVIOR OF *PARCOBLATTA FULVESCENS* (SAUSSURE AND ZEHNTNER) (BLATTARIA, BLABEROIDEA, BLATTELLIDAE, BLATTELLINAE)[1]

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This communication is the sixth in a series of largely descriptive papers dealing with the mating behavior of cockroaches (see Barth, 1961, 1964, 1968a & b, 1970; Roth and Barth, 1967). The aim of this series is twofold: first to provide background information for experimental studies, and second to provide the detailed comparative information necessary for a study of the evolution of mating behavior within the Blattaria. A more general introduction to the series may be found in Barth (1964). The mating behavior of the Fulvous wood cockroach, *Parcoblatta fulvescens* (Saussure and Zehntner), forms the subject of this communication.

Materials and Methods

Stock cultures of *P. fulvescens* were maintained as described by Barth (1964) for *Byrsotria fumigata.* The observations on mating behavior were made in the evening (the normal activity period for these animals) under red illumination in specially designed observation chambers constructed of wood (13″ × 9″ × 5″ deep) with a removable partition dividing the chamber into two equal parts (for details, see Barth, 1964). In each observation 2 to 3 males and 2 to 3 females were employed. The ethological terms employed in the description have been previously defined by Barth (1964).

Results and Discussion

Parcoblatta fulvescens is a small (11 to 17 mm in length) cockroach generally found in wooded areas under leaf litter and other debris and is widely distributed in eastern, southern, and central areas of the United States. It shows marked sexual dimorphism. The females are robust and wingless with reduced tegmina that extend over the first abdominal segment. They are orange-brown

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dorsally with a darker abdomen. The males are more slender and winged, and their tegmina extend beyond the abdominal tip. They are light brown in dorsal coloration.

There seem to be no previous accounts of the mating behavior of this species in the literature although a brief account of the courtship behavior of *Parcoblatta virginica* (Brunner) is given by Roth and Willis (1958). According to their description, males of *P. virginica* raise their wings after contacting the female with their antennae. The female, attracted by the secretion of the male tergal gland, mounts and feeds until she reaches the first abdominal tergite of the male at which time genital connection is achieved; this is followed by assumption of the opposed position.

Description of Normal Mating Behavior

The following description is based on observations of 5 sequences resulting in successful copulation and numerous unsuccessful copulation attempts.

1. Behavior of males triggered by olfactory reception of female sex pheromone

Upon olfactory reception of the volatile female sex pheromone, males exhibit sexual arousal by assuming an alert posture and increasing the rate of antennal waving. Oriented locomotion to the pheromone source ensues. Without reference to contact with females the behavior of sexually aroused males is characterized by rapid locomotion, frequent flying, and wing raising.

The manner in which the male flies is variable. Some flights cover more distance than others. For example, a male may fly across the mating chamber or upward to an inverted landing on the underside of the lucite covers atop the chamber. Other flights are more circumscribed, the male flying several inches upward and then returning to the substratum. During some of these flights, the male pivots to face in the opposite direction and then lands; this often results in the male landing on his back.

In addition to rapid running and flying, sexually excited males show a great deal of wing raising of a quite variable nature. When the wings are raised, the angle formed by the wings and the abdomen varies between 20 and 80 degrees. The wings may be raised and lowered quite rapidly in what is essentially a pumping motion. This cycle of wing raising and lowering may be repeated a number of times in quick succession. On the other hand, the wings may remain in the elevated position for a brief period. And

in some cases a male will run about with his wings continuously raised. All of these variations in wing raising are frequently performed while the male is engaged in forward locomotion. The occurrence of wing raising while the male locomotes forward has also been observed in *Periplaneta americana* (Barth, 1970; Simon and Barth, in prep.).

As the wings are raised, they are frequently spread laterally. Wing fluttering usually accompanies lateral spreading. The wings are fluttered at the high point of the wing raise and during the flutter the tegmina are spread laterally from the sagittal plane to an angle of 10 to 50 degrees (but usually about 45 degrees) and their lateral edges are directed forward. The wings are slightly less spread laterally and are not elevated as much vertically. For instance, if the tegmina are raised to 80 degrees during a flutter, the wings are only raised to about 60 degrees. One observation may be cited which underlines the amount of variation possible with regard to wing raising. In this case a male ran around very excitedly with his wings continuously elevated to about 20 degrees and then periodically raised them completely, very rapidly, with fluttering at the point of maximum elevation.

During the wing raising displays, the abdomen is flexed so that the dorsal surface is convex and the tip contacts the substratum.

2. Male displays in the vicinity of the female

The majority of male-female contacts are very brief. Unreceptive females most frequently decamp rapidly immediately after coming into contact with a male. When a sexually aroused male makes contact with a female, he immediately raises his wings, turns away from the female, and backs. The wing raising display, turning, and backing are all released by the initial momentary antennal contact; no further contact with the female is required. The elevation of the wings in the male's display varies from display to display and is anywhere from 15 to 80 degrees. The amount of turning varies between 90 and 180 degrees. The male's abdomen is arched so that its dorsal surface is convex and the tip touches the substratum. The male's backing movement may be oriented toward the female from any direction.

Two cases were observed, one of which led to a successful copulation, in which the female contacted the male from behind (without contacting his antennae) resulting in the male wing raising and backing but without any turning. It seems that in these in-

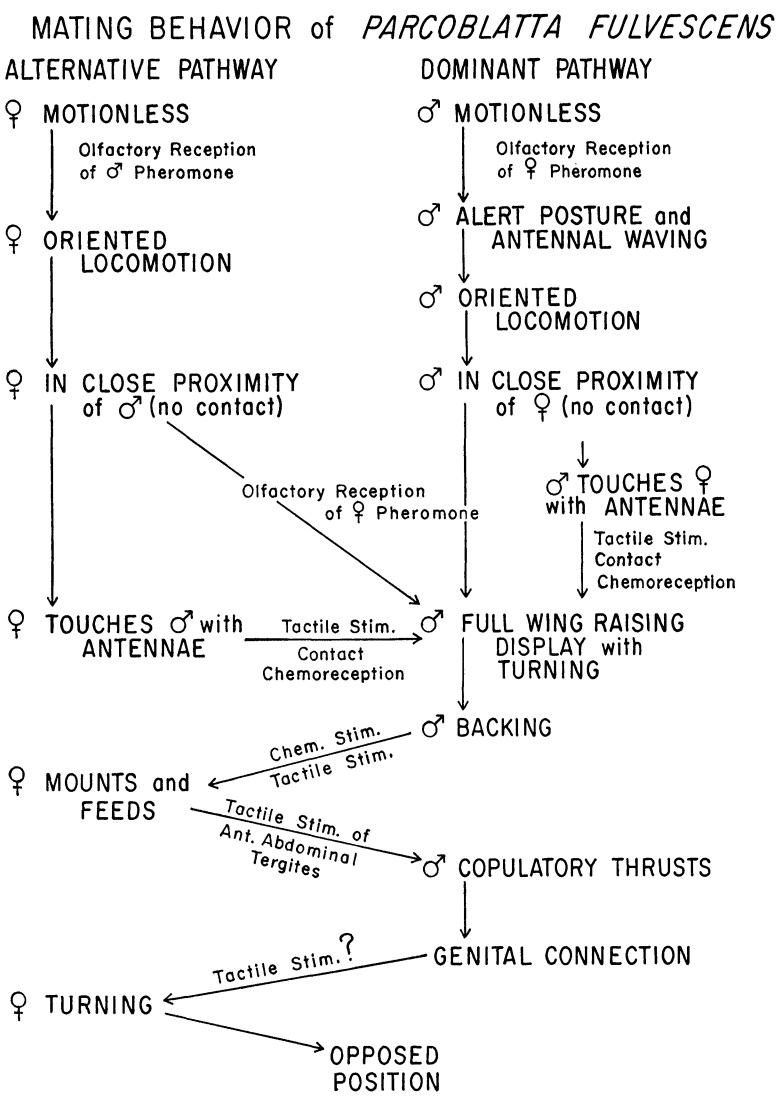

Figure 1. A summary of the mating behavior of *Parcoblatta fulvescens* indicating the possible releasers for each step in the sequence. For explanation of alternative pathways, see text.

stances olfactory reception of the female sex pheromone combined with tactile stimulation of the male's hindparts was sufficient to release the wing raising display and that tactile stimulation of the male's hindparts inhibited turning.

There were twelve observations in which a male on coming close to a female, but without contacting her, wing raised, turned, and backed. This represents approximately 20 percent of all observations for which the events preceding display were recorded. In these cases the wing raising display, turning, and backing were all apparently released merely by olfactory reception of an intense concentration of volatile female sex pheromone in the absence of any contact chemoreception or tactile stimulation. One of these twelve displays led to a successful copulation.

If the female does not respond to the male's display after a brief period, the male frequently will flutter his raised wings or pump and flutter them. This possibly serves to disseminate the male sex pheromone to a female who is not responding to the male's display. Occasionally, after leaving the site of an unsuccessful copulation attempt, a male will locomote around with his wings still partially raised (10 to 30 degrees) for 30 seconds to one minute.

3. Terminal events in the copulation sequence

A receptive female responds to the male's display with active mounting and feeding, moving in a forward direction over the male's exposed abdominal tergites. If the male's backing is poorly oriented, the female adjusts her position accordingly. When the female is about two-thirds forward over the male's abdomen, the male begins probing extensions with his abdomen which is now concave on the dorsal surface, the abdominal tip contacting the female's undersurface. The female advances with her feeding activities to the region of the first tergite at which point genital connection is achieved. The female then performs a turning movement which results in the animals facing away from each other in the 180 degree opposed position which is maintained for the duration of copulation. In this position the male's wings slightly overlie the abdominal tip of the female, covering her cerci.

4. Behavior of copulating pairs

Five accurately timed copulations lasted 54.5, 55, 58, 59, and 67 minutes. The duration of a sixth copulation was less than 53 minutes. Copulating pairs were generally quiescent, showing little antennal activity for most of the copulation period unless disturbed

by other animals. The female is entirely responsible for the pair's locomotion which can be quite rapid.

In three copulations, an area of moisture was noticed on the paper towel liner beneath the male's head. It appeared that this was due to the male extruding water or some other fluid from his mouth. In one instance, a sudden surge of this moisture on the paper coincided with a movement of the male's head. These wet spots appeared within the first few minutes of copulation and were visible for about 4 minutes.

The females of copulating pairs assume an arched posture in which the body is held rather high above the substratum and flexed sharply ventrally. The posterior part of a copulating female's abdomen curves downward to where it joins the male's abdominal tip which is very close to the substratum. This arched posture may be pronounced enough to cause the male's wings (which overlie the female's abdomen) to be raised somewhat. This posture may be observed throughout the copulation, but it varies in extent; periods of very marked arching alternate with periods during which the arching is much less noticeable.

In two copulating pairs, rhythmical movements were observed for which the female appeared responsible. This entailed a pivoting of the female's body about a transverse axis such that her abdominal tip moved upward, pulling the male's abdominal tip upward with it. In both pairs these movements were observed toward the end of copulation and occurred in a series which ceased and then was later resumed.

The Role of Various Releasers in the Courtship Sequence

A diagram illustrating the various avenues courtship behavior may take is presented in Figure 1. Possible releasers of various events in the courtship sequence are indicated.

1. Release of the male's behavior

Olfactory reception of the volatile female sex pheromone, the primary releaser of the male's courtship behavior, is sufficient to release all of the male's courtship behavior up to and including backing. In addition to the mating chamber observations, tests using filter papers removed from the female side of the chamber were conducted prior to the observation period. The males responded with vigorous antennal waving, oriented locomotion, flying and wing raising with fluttering. The rapid locomotion became random after a short while. Tactile stimulation from other males was not in-

volved in eliciting these responses. The males of this species are small and no more than three were ever employed; in the mating chamber, contact between males was infrequent in this situation. Probably because of the low density of males, neither homosexual or pseudofemale behavior was observed in the mating chambers although one instance of a male mounting a displaying male was observed in the more crowded breeding culture. That males have a considerable ability to orient to a pheromone source was shown in several instances during the observation periods when a male precisely followed the "trail" of a female that had previously decamped.

Turning and backing were not released during the filter paper tests nor in the behavior observations except when a male was very close to a female. Turning and backing in the majority of these cases were released by contact chemoreception and/or tactile stimuli when the male's antennae contacted a female. However, in a significant number of cases the release of these activities was triggered solely by the apparently intense concentration of sex pheromone immediately surrounding the female.

Tactile stimuli are necessary for the release of copulatory thrusts and phallomere extension. Copulatory thrusts begin when the mounting female's mouthparts have progressed about two-thirds of the way forward over the male's abdominal tergites. Whether phallomere extension occurs at this point or not until the female reaches the region of the first tergite is uncertain.

Predominance of the female sex pheromone in the release of male courtship behavior has also been reported for the distantly related species, *Periplaneta americana* (Blattinae) (Barth, 1970; Simon and Barth, in prep.). As mentioned above, both species show wing raising in the absence of tactile stimuli and during forward locomotion. However, turning and backing (in addition to the full wing raising display) only rarely occur in the absence of tactile stimulation in *P. americana* (Barth, 1970) but are not infrequently observed in *P. fulvescens*. In this respect, the female sex pheromone plays a more prominent role in courtship behavior in *P. fulvescens* than in *P. americana*. Backing in *P. americana* (as well as in four other species of *Periplaneta* and also *Blatta orientalis*) often occurs without any tactile stimuli in addition to those which release wing raising with turning (Simon and Barth, in prep.). This is also true of *P. fulvescens* in those cases in which tactile stimuli release the wing raising display. *P. americana* males differ from

P. fulvescens in the exhibition of phallomere extension without the stimuli derived from female mounting and feeding; contact of the abdominal tip with the female suffices to release this response.

The release of flying by males in sexual situations has previously been observed in *Epilampra azteca* and *Epilampra columbiana.* In *E. columbiana,* females as well as males fly, and for courtship activity to occur it appears necessary for both the male and female to have flown just previously. The most frequent stimulus releasing courtship in a male which has just flown is a female landing next to him (Barth, unpublished data).

2. Release of the female's behavior

The mounting and feeding behavior of females is released by the male sex pheromone in many cockroach species (Barth, 1968c). Such a male sex pheromone, "seducin," was extracted by Roth and Dateo (1966) from males of *Nauphoeta cinerea.* There is some evidence for the existence of a volatile male sex pheromone in *P. fulvescens.* The frequent wing fluttering by isolated males and particularly the wing fluttering that follows unsuccessful copulation attempts suggests the function of dissemination of a male sex pheromone. This function has been suggested for wing fluttering in *P. americana* (Barth, 1970; Simon and Barth, in prep.) and for various vibration and trembling movements in various species of coackroaches (Roth and Hartman, 1967; Barth, 1968c). The function of flying in courtship situations remains a mystery, but male sex pheromone dissemination is a possibility.

During the observation periods, there were occasions in which females approached males in a manner which appeared to be nonrandom and suggestive of an awareness of the male's presence. The following procedure was followed to test for oriented locomotion in females in response to a source of volatile male sex pheromone. Prior to an observation period, a filter paper from a beaker containing a single male was placed into the female side of the mating chamber on the side opposite to the location of the two females. Before the filter paper was introduced, the females were relatively quiescent showing some locomotion and slight antennal waving. After introduction of the paper, one female showed increased antennal activity and the other female started to locomote in the general direction of the paper, palpating the substratum as she moved. When she had progressed to within two inches of the paper, she turned directly toward it and came into antennal contact with the paper. She then stroked the paper lightly with her antennae,

drummed it rapidly with her maxillary palps, and walked across it. This first female initially made contact with the paper about 1.5 to 2 minutes after its introduction and had remained upon it for about a minute when the other female arrived. The second female touched the paper with her antennae and showed the same behavior toward it as the first female. Then there was some aggressive behavior between the two females. The second female drove the first one away and then proceeded to move around the paper, palpating it and waving her antennae gently. More work is clearly needed to confirm the hypothesis of volatility of the male sex pheromone in this species.

Aggressive Behavior

Two examples of male-female aggression were observed. In one, a female approached a male from in front of him. The male, in what appeared to be an aggressive gesture, jerked his head toward the female and she decamped. In the second case, a male and female made antennal contact, facing each other. The female lunged toward the male and then ran off. The male gave chase for a short distance.

In addition to the aggressive female-female encounter described above, an observation was made in which two females were facing each other and antennal fencing. One female lunged toward the other and chased it away.

Female aggression directed toward a copulating pair was observed in two cases. In the first case, a female (with protruding egg case) twice in rapid succession approached and jumped on top of the copulating pair — primarily on the dorsum of the copulating female — and then glanced off rather rapidly. Later this female twice butted into the side of the copulating female but did not jump on it; the copulating female moved the pair several inches away. In the second case, a female antennally contacted a copulating pair and then, about a second later, charged toward the center of the pair and bumped them.

The fact that aggression was never observed between males may very likely be due to the fact that only 2 or 3 were ever employed during observations, greatly decreasing the chances of interaction.

Summary

In *Parcoblatta fulvescens*, the volatile female sex pheromone plays a very prominent role in the release of the male's courtship behavior. Olfactory reception of the female sex pheromone releases in males

an alert posture, increased antennal waving, and oriented locomotion toward the female. Flying and wing raising are also released by the female sex pheromone, no contact with females being required. Wing raising is quite variable in nature and is frequently accompanied by lateral spreading with fluttering. Wing raising is frequently performed by males engaged in forward locomotion. The majority of male-female contacts are quite brief, unreceptive females rapidly decamping. When a male contacts a female, he raises his wings, turns away from the female, and backs. About 20 percent of the time, an intense concentration of female sex pheromone is apparently solely responsible for the release of wing raising, turning, and backing when the male has come close to a female but without contacting her. A receptive female mounts and feeds in a forward direction over the male's exposed abdominal tergites. Tactile stimuli release the male's copulatory thrusts when the female is two-thirds forward over the male's abdomen. When the female reaches the vicinity of the first abdominal tergite, genital connection is achieved. The female then turns, resulting in the assumption of the opposed copulatory position. Evidence for the existence of a volatile male sex pheromone is presented. The function of pheromone dissemination is suggested for the male's wing fluttering and flying.

Also included in this communication are some observations on aggressive behavior and the behavior of copulating pairs.

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