

Calling Behavior in Female Cockroaches (Dictyoptera: Blattaria)¹

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ABSTRACT: Females of several species of cockroaches exhibit specific "calling stances". Typically, the abdomen is lowered toward the substrate. In some species the genitalia are expanded and relaxed periodically. Both virgin and previously mated females (after parturition or egg deposition) assume "calling poses". In the field, females with protracted copulations (e.g., *Xestoblatta*) call during defined time intervals early in the night; females which copulate for shorter periods (e.g., *Nyctibora*) call later. Calling has been observed in three of the five cockroach families, and may be involved with the release of pheromones.

Most of the approximately 4000 described species of cockroaches have a tropical distribution. Because of the paucity of studies on non-synanthropic species, and because of their nocturnal activity, little information is available about these cockroaches outside of the taxonomic literature.

Roth and Willis (1952), Barth (1968), Bell (1982), Breed (1983), and Schal et al. (1984) review the occurrence of volatile and contact sex pheromones, the most common mate-location mechanism in the Blattaria. Volatile pheromones may be emitted by females or by males. The role of male pheromones is thought to involve both mate-location and mate-selection (Breed, 1983); their operational distance is rather short. Female volatile sex pheromones are known in three of the five families of cockroaches and may attract males over several meters (Tobin, 1981; Seelinger, 1985a, b).

Roth and Willis (1952) and Barth (1970) delineated the courtship sequence of *Periplaneta americana* (Blattidae: Blattinae), and Wharton et al. (1954a, b), Rust (1976), and Tobin et al. (1981) quantified the relationship between female equivalents of the sex pheromone and the male's responses. The midgut has been suggested as the most likely site of sex pheromone production in this species (Bodenstein, 1970; Takahashi et al., 1976). Two components of the sex pheromone of *P. americana* have been isolated and characterized from extracts of female feces (Persoons et al., 1979; Talman et al., 1978; Sass, 1983), and one component, periplanone B, has been synthesized (Adams et al., 1979; Still, 1979). In the lab and in the field *P. americana* males are attracted to the synthetic compound in a wind current from distances of up to 28 m (Tobin, 1981; Seelinger, 1985a, b), and in still air over a distance of up to 10 m (Tobin et al., 1981; Bell et al., 1984). Both the production of sex pheromone by females and the responses of males are known to be influenced by temperature (Appel and Rust, 1983).

This report describes specific "calling" postures of female tropical cockroaches. Previous to these findings, Willis (1970) described "calling behavior" in *Lati-*

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blattella (Blattellidae: Plectopterinae) from Honduras, in which females lowered the tips of their abdomens, assuming positions similar to those of "courting males", and males were attracted to calling females. Tobin (pers. comm.) also observed this behavior in virgin females of four *Periplaneta* species. Hales and Breed (1983) reported a similar behavior in *Supella longipalpa* (Plectopterinae).

Materials and Methods

The insects were observed and collected at Finca La Selva, an Organization for Tropical Studies field station in the Caribbean lowlands of Costa Rica (see Holdridge et al., 1971 for description of site). Most observations were conducted during March to July 1979, February to May 1980, and March to June 1981.

Diel calling and mating patterns of *Xestoblatta* (Blattellidae: Blattellinae) were observed in the field. The frequencies of occurrence of these behaviors were determined at hourly intervals and standardized for the amount of time spent searching. Insects were also reared in soil-lined plastic cages in an outdoor insectary. Food and water were provided ad lib.

Other species were also observed in the field, but data on patterns of calling and male responses were collected at the University of Kansas in a laboratory maintained at approximately 25°C with a 12:12 hr light: dark regime.

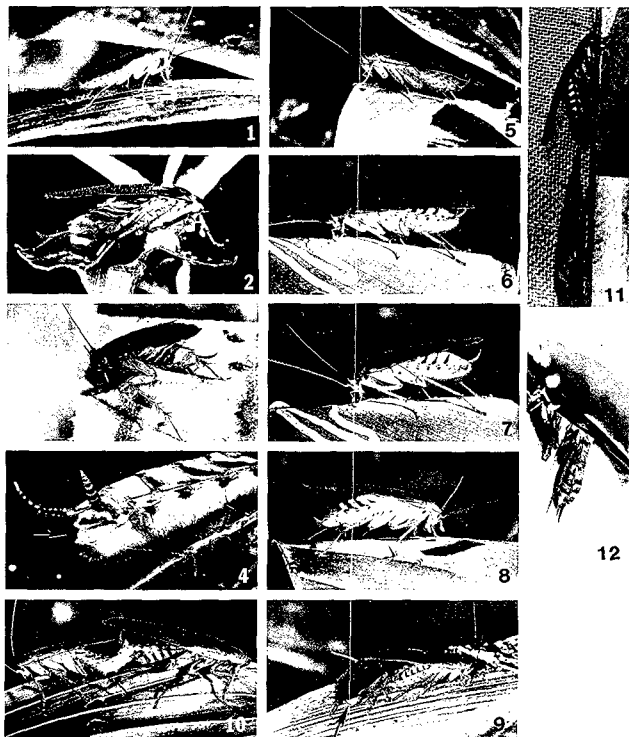
Results and Discussion

DESCRIPTION OF CALLING: Females of *Xestoblatta cantralli*, *X. hamata* (Blattellidae: Blattellinae), *Nyctibora notivaga*, *N. lutzii*, *Megaloblatta blaberoides* (Blattellidae: Nyctiborinae), *Capucina patula* (Blaberidae: Zetoborinae), and *Epilampra maya* (Blaberidae: Epilamprinae) exhibit specific calling stances. Typically, calling females appear to raise their wings in a manner similar to courting males (Figs. 1-12). However, as noted by Willis (1970) and in conflict with Hales and Breed's (1983) interpretation, this display results from lowering of her prothorax and distal abdominal segments so that the abdomen is flexed away from the folded wings. Her legs, particularly the hind legs, are straightened, lifting the body away from the substrate.

Unlike males, females of three species of *Latiblattella* that engage in calling behavior do not have modified abdominal terga, but males are attracted to and palpate the female's dorsum (Willis, 1970). *Epilampra* and *Capucina* females also apparently lack specialized tergal glands. In *Xestoblatta* and *Nyctibora* females, however, intersegmental and genital membranes are exposed continuously or periodically during calling (Figs. 2-4, 7-9, 11, 12). *X. cantralli* females expose a conspicuous yellow membrane which is normally hidden by terga 8 and 9. Unlike other females, *X. cantralli* also roll the distal abdominal segments laterally (Fig. 3), thus alternately directing the exposed dorsal membrane to the left and right. Simultaneously, the genital pouch is expanded by lowering the seventh sternite, exposing the vestibulum and the intersternal folds (terminology of McKittrick, 1964).

Nyctibora and *Capucina* females also periodically expand the genital aperture in a manner previously described for *Supella longipalpa* (Hales and Breed, 1983). The function of this behavior and the significance of its temporal pattern are unknown.

Field results provided only indirect evidence that calling females are more

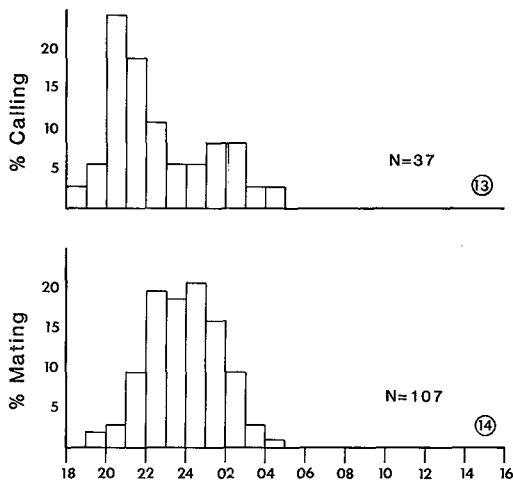


Figs. 1-12. Calling postures of some cockroach species. 1. *Xestoblatta cantralli* in normal position perching on a leaf. 2-4. *X. cantralli* in a calling posture. Note rolling motion in 3. Arrow indicates exposed genital membranes. 5. Normal perching posture of *X. hamata*. 6-9. Stages in calling behavior of *X. hamata* females. Arrow in 9 indicates expanded genitalia of courted female. 10. Mating *X. hamata*. 11, 12. Calling *Nyctibora noctivaga* female in the laboratory.

attractive to males than are non-calling females. In several instances unusually high male densities were observed near calling *Xestoblatta* females. However, we were unable to attract males to calling females in screened cages, nor to calling females tethered on leaves.

In cages in the laboratory, non-calling females were not attractive to males, whereas calling females elicited locomotion and courtship.

FACTORS AFFECTING CALLING: In all species in the present study, as well as in



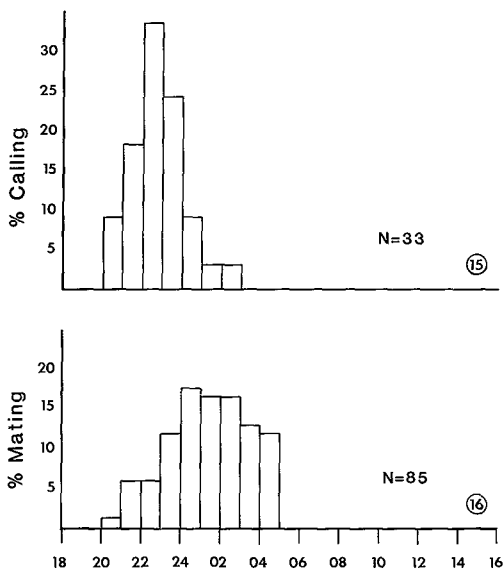
Figs. 13, 14. Diel calling and mating patterns of *X. cantralli* in the field.

those observed by Willis (1970) and Hales and Breed (1983), both virgin and previously mated females assumed calling poses, but calling was rare in newly eclosed females, recently mated females, and females forming oothecae. The delay between eclosion and calling was not recorded, but in the species observed, calling did not occur in the first three days after the imaginal molt.

Calling was not observed in recently mated females and is not resumed until after parturition or after oothecae are deposited. Possibly, the mechanism which renders females unreceptive after mating also inhibits calling behavior. Roth (1962) concluded that mechanical distension of the genital pouch by the spermatophore and by oviposited eggs is responsible for nervous feedback to the brain. Clearly, additional studies of the nervous and endocrine controls of calling in female cockroaches are warranted.

Previously mated females may call after one or more oviposition cycles. Again, it is not known whether sperm depletion in the spermatheca or other factors mediate the resumption of calling.

A conspicuous change in the female's calling behavior occurs upon contact with a male. *X. cantralli* females stiffen their legs, thus further elevating the body from the substrate, and lower the tip of the abdomen. In *X. hamata*, *N. noctivaga*, and *Capucina*, contact with males stimulates the females to expand the genital pouch (Fig. 9). In several encounters, female *X. hamata* mounted courting males with expanded genitalia. Willis (1970) also noted that physical contact with males



Figs. 15, 16. Diel calling and mating patterns of *X. hamata* in the field.

stimulated females to call more vigorously, suggesting that the behavior may be a signal that the female is ready to mate.

Like *Latiblattella* (Willis, 1970) and *S. longipalpa* (Hales and Breed, 1983), but unlike courtship of most cockroach species, *Xestoblatta* males remain in the "wings-raised" position for up to 15 minutes without physical contact with the female. In *Blattella germanica* the male lowers its wings and turns approximately 180° if its tergum is not touched within seconds after the initial courtship turn (Roth and Willis, 1952; Bell and Schal, 1980).

DIEL PERIODICITY OF CALLING: *Xestoblatta* females were observed in the field. Soon after sunset (approximately 1800 hr) *X. cantralli* females fly from their diurnal resting sites in the leaf-litter onto foliage approximately 40 cm above the ground (Schal, 1982; Schal and Bell, 1985). Calling was observed soon thereafter (Fig. 13). Mating pairs were most commonly found at 2200 hr and pairs remained *in copula* for about 3 hr (Fig. 14).

X. hamata females become active later than *X. cantralli* females (Schal and Bell, 1985). They also fly onto nocturnal perches about 30 cm above the ground (Schal, 1982; Schal and Bell, 1984), but calling is delayed until approximately

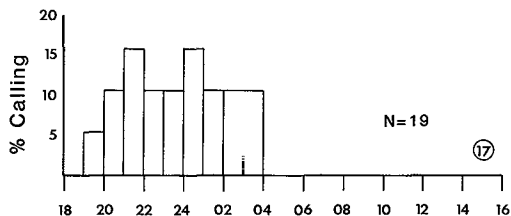


Fig. 17. Diel calling pattern of *N. noctivaga* as determined in the laboratory. Lights off at 1800 hr, on at 0600 hr.

2200 hr (Fig. 16) and pairs remain coupled for more than 4 hr (Schal and Bell, 1982).

In laboratory studies, *N. noctivaga* females called throughout the scotophase (Fig. 17) as did *S. longipalpa* females (Hales and Breed, 1983). Unlike *Xestoblatta* and *Capucina*, which call from horizontal surfaces (leaves, fallen tree trunks), *Nyctibora* and *Megaloblatta* females were found more often facing upward on trunks of standing trees and on vertical surfaces in the laboratory (Figs. 11, 12). It is interesting to note that in *X. cantralli* and *X. hamata*, which copulate for 3 to 4 hr, calling in the field peaks before 2400 hr, presumably to allow sufficient time for copulation. *N. noctivaga* spends about 30 min in copula and calling is more evenly distributed throughout the night.

In one case a *Capucina* female was observed on a dead standing tree trunk with her head and thorax in a small cavity and the lowered abdomen with exposed genitalia extended outward.

PHYLOGENY OF CALLING BEHAVIOR: Willis (1970) proposed that additional study of calling in female cockroaches be focused on the subfamily Plectopterinae (Blattellidae) because *Latiblattella* and *Ellipsoidion* (Roth, 1968) assumed calling stances. Hales and Breed (1983) demonstrated calling in *Supella* (Plectopterinae), but the occurrence of calling in *Nyctibora* and *Megaloblatta* (Nyctiborinae) and *Xestoblatta* (Blattellinae) indicate that the behavior is probably common throughout the Blattellidae. Moreover, its occurrence in the blaberids *Epilampra* and *Capucina*, and *Eublabeus posticus* (Tobin, pers. comm.), and in the blattids *Periplaneta americana*, *P. australasiae*, *P. fuliginosa*, *P. brunnea* and *Blatta orientalis* (Tobin, pers. comm.), indicate that the behavior may be even more universal than previously suggested by Willis. Robinson and Robinson (1979) documented a similar behavior in a tropical mantid (Dictyoptera: Mantodea).

It is not known whether calling behavior in the Blattaria has a monophyletic or polyphyletic origin. The evolution of calling with volatile sex pheromones is subject to strong ecological pressures. It is imperative that widely dispersed individuals at low abundance be able to communicate over long distances. Since these ecological criteria are common in representatives of all families of Blattaria (see Schal et al., 1984), similar pressures on species to retain or evolve long range pheromone communication presumably operate in many forest species. That

ecological rather than phylogenetic traits are most important in shaping behavior of cockroaches was also concluded by Schal and Bell (1985) and Schal et al. (1984).

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