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Basic Elements of Behavior of the Cricket *Phaeophilacris bredoides* Kaltenbach (Orthoptera, Gryllidae)

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Abstract—The intraspecific behavior of the non-singing cricket *Phaeophilacris bredoides* Kaltenbach, 1986, which has no tympanal system, stridulatory apparatus, and classical acoustic communication, was studied. Even though this cricket has no song, its intraspecific behavior can be differentiated into reproductive and agonistic (defensive and aggressive), as this was done before for singing crickets. The main elements and the sequence of the phases were described for reproductive behavior. The active role during copulation belongs to the male. Wing-flicks and rocking movements of the male can function as a "song." Wing-flicks apparently generate air movements that function as short-range signals during reproductive and aggressive behavior. Substrate-borne vibrations produced by rocking also seem to be associated with aggressive behavior. Antennal contacts form an important part of interaction between crickets of both sexes. Thus, intraspecific signaling is at least partly mediated by mechanosensory channels. The assumption about the possible direction of evolution in the singing and non-singing groups of crickets was made.

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Most members of the family Gryllidae Laicharting, 1781 possess advanced intraspecific acoustic signaling in the form of a set of species-specific "songs" that play the key role in reproductive (the calling and courtship signals) and agonistic (the aggressive signal) behavior (Zhantiev, 1981). At the same time, it is known that some representatives of this family do not use acoustic signaling in its classical sense. They lack the tympanal hearing organs and the stridulatory apparatus, which is located on the elytra of the singing species. Gorochov (1995) supposed that the stridulatory apparatus in males and the tympanal organs in both sexes of such crickets disappeared in the course of evolution.

It is believed that intraspecific communication in such species may be based on vibrational signals produced either by drumming of the abdomen against the substrate, or by tremulation, or "rocking," of the whole body without the abdomen touching the substrate; in the latter case the signal is transmitted onto the substrate via the legs (Field and Bailey, 1997; Weissman, 2011; Keuper et al., cited after Stritih and Čokl, 2012).

Males of the non-singing cricket *Phaeophilacris spectrum* Saussure, 1878 perform short flapping movements with their wings; such wing-flicks also seem to be used in intraspecific communication. They produce low-frequency (8–12 Hz) oscillations of the air that spread horizontally. Wing-flicks are believed to be the main elements of reproductive and agonistic behavior in *Ph. spectrum*, functionally replacing the songs. Besides, rocking movements were also described in males of *Ph. spectrum* (Heidelbach and Dambach, 1991, 1997).

In our opinion, a detailed study of non-singing cricket species is necessary for better understanding of the origin and evolution of sensory systems and the development of communication mechanisms in the phylogeny and ontogeny of insects. The published data on non-singing crickets are relatively scarce and disconnected (Heidelbach and Dambach, 1991, 1997; Čokl et al., 1995; Stritih and Čokl, 2012). In particular, very little is known about the individual development and ethology of these species, and also about the ontogenetic changes of the different forms of their behavior.

The ontogeny of the non-singing cricket *Ph. bredoides* Kaltenbach, 1986 was described in detail in our previous communication (Lunichkin et al., 2012). The duration of the adult life of this species was shown to be 126 days in males and 125 days in females. The imaginal ontogeny of males and females was subdivided into three periods: pre-reproductive, reproductive, and post-reproductive. The pre-reproductive period lasts 2 (1–4) days in males and 5 (2–7) days in females. The reproductive period lasts 119 (98–135) days in males and 116 (97–133) days in females and includes two alternating phases: copulation and egg-laying. The onset of the egg-laying phase is initiated by successful copulation. The post-reproductive period lasts 3 (2–3) days in males and 4 (2–7) days in females. These data served as the basis for our further research.

The goal of this work was to determine and describe the main elements of intraspecific behavior of *Phaeophilacris bredoides* Kaltenbach, 1986 at different stages of its adult life. This species, like *Ph. spectrum* Saussure, 1878, lacks the tympanal organs and the stridulatory apparatus and, correspondingly, has no specific "songs."

MATERIALS AND METHODS

Our material included adults of the African cave cricket *Phaeophilacris bredoides* from a year-round culture maintained in the Laboratory of Comparative Physiology of Sensory Systems at Sechenov Institute for Evolutionary Physiology and Biochemistry of the Russian Academy of Sciences, St. Petersburg. Altogether, we studied the behavior of 25 crickets (12 males and 13 females) at different stages of their imaginal ontogeny.

The Conditions and Methods of Cultivation

The laboratory culture of *Ph. bredoides* was kept in a chamber with a stable microclimate, at a temperature of 26°C and air humidity of 60%. The light regime was 12 h of light and 12 h of darkness. The chamber was illuminated with LDS-30 fluorescent lamps. The crickets received plant and animal food during their entire life. The succulent part of the diet included cabbage leaves, carrots, and apples, while the dry fraction consisted of oat flakes, nuts (almonds, hazelnuts, and peanuts), dried fruit, dried gammarids, and granulated meat-bone-fish concentrate with microelements and vitamins (Knyazev, 1985; Lunichkin et al., 2012).

On the day of the final molt, the adult crickets were transferred into individual containers marked with the specimen's number and the date of the molt. These crickets were subsequently used in ethological experiments.

The Methods of Studying the Elements of Behavior

The elements of reproductive and agonistic (aggressive and defensive) behavior were studied and the ethograms were compiled using the "open field" method. Males of different age were presented with mature females (for studying reproductive behavior) or mature males (for studying aggressive and defensive behavior). Females of different age were presented with mature males. The male of female was placed at the maximum distance from the tested individual. Unmated crickets were used in all the tests. Altogether, 41 individuals were tested, including 21 females and 20 males.

Two variants of the method were used, in which observations of the insects were carried out in cages of different height and bottom area.

In the first variant, the crickets were placed in pairs in small covered containers (bottom area 88 cm^2, height 5.5 cm), in order to reveal their behavioral responses within a relatively short time (3–5 min) after the beginning of the experiment. Using this technique, we distinguished and described the main forms of behavior of both sexes and the conditions under which they were realized. The behavioral responses of 19 crickets (10 females and 9 males) were studied in this way. Each insect was presented with a test partner at least 5 times.

In the second variant, the crickets were placed in pairs in an open round arena with a total surface area of 907 cm^2, walls 6 cm tall, and the bottom marked with a reference grid. This technique was used to study in detail the phases of reproductive behavior. Altogether, 22 crickets (11 females and 11 males) were used in this variant, and 11 complete courtship sequences that ended in copulation were recorded.

The behavior of crickets in the small containers was documented by three observers. The experiments in the arena were recorded with the Sony DSC-H7 digital camera and the Samsung HMX-H300RP camcorder. Using the recorded videos, we determined the sequence and duration of different phases of reproductive behavior and compiled the ethograms.

RESULTS

Ethological observations allowed us to determine the main elements of behavior of males and females of *Ph. bredoides* and to describe the stages of reproductive behavior leading to successful copulation.

Elements of Behavior of Males during Different Phases of Their Ontogeny

The pre-reproductive period. The elements of the male's agonistic and reproductive behavior were established by the 4 (3–6)-th day of imaginal ontogeny. An immature male, when presented with a mature one, responded either by hiding (reduced mobility with the body pressed to the substrate), or by escape (moving rapidly away). When presented with a mature female, the immature male either avoided it or showed no specific response. The timing of these forms of behavior corresponded to the pre-reproductive period of imaginal ontogeny (Lunichkin et al., 2012).

The behavior typical of the reproductive period was established gradually. The first response to appear in the males was the tracking one. The male stopped 50–80 mm from the female, with its head toward the female and the bodies of the two insects usually arranged at an angle of 30–90°. If the angle was smaller than 70°, the male turned its head so that the female was positioned between the male's antennae. The tracking response was characterized by active "feeling" of the female with the antennae. If the female moved, the male turned to follow it in order to preserve the characteristic position of the antennae. If the female tried to escape, the male either pursued it or remained in its place. The latter variant was observed at early stages of imaginal ontogeny (the 2–5th days), when the tracking response was just forming and the male could lose interest in the female. Mature males could show the tracking and pursuit responses for a long time (over an hour). When two mature males met, each displayed the tracking response with respect to the other, which was then replaced by agonistic behavior.

The reproductive period. The male's aggressive behavior manifested itself in two forms: rocking and fighting. It appeared on the 4 (3–7)-th day after imaginal molt, coinciding with the onset of the reproductive period and the manifestation of the corresponding forms of behavior.

The reproductive period of the male ontogeny was characterized by two main elements of behavior: wing-flicks and rocking.

The wing-flicks formed the key element of reproductive and agonistic behavior of *Ph. bredoides* males. This element consisted of two components. The first component included the flapping movement of the wings in an arc of 90–180° to the head, with the simultaneous forward movement of the body. The second component consisted of several short, rapid back-and-forth movements of the wings positioned at 70–90° to the longitudinal body axis. After the end of the second component the wings often remained raised at 55–90° to the body axis. The wing movements during the first component seem to generate a powerful thrust of air spreading forward, in the direction of the other cricket. The back-and-forth movements produced several short thrusts directed forward and backward, forming an intricate air current.

The first wing-flicks appeared in the males on the 4 (3–6)-th day of imaginal ontogeny in the form of individual flapping movements with long intervals (up to 20–30 min) between them. Later, such movements occurred in series while the pauses between them were reduced to 9 s (2–28; n = 132).

This form of behavior was observed only in the presence of a conspecific individual of either sex. Mature males sometimes performed wing-flicks as soon as 60–90 s after presentation of another cricket. No wing-flicks were recorded in males isolated from other crickets. On encounter with a mature receptive female, this behavior led to successful copulation though it was not its necessary condition. In case of contact with a mature male, either defensive behavior (hiding and/or escape) or a fight was observed. Unreceptive females also showed defensive behavior in response to the male's wing-flicks.

Wing-flicks were either directed toward the conspecific individual or had no specific orientation. The undirected response was observed in strongly exited males, for example, in the winner of the fight. In this case, the thrusts of air were not directed toward another cricket.

Rocking, or tremulation, consisted in rhythmical back-and-forth body movements with increasing amplitude, the antennae pointing backwards. At the initial moment the male moved back, "crouching" on its hind legs; in the process of rocking it tilted forward with its whole body or even made several steps forward. The duration of rocking movements was 4–5 s (n = 11). This form of behavior was observed either on encounter with a mature male, or in the case of a female not responding to courtship for a long time. Such females were possibly in the pre- or post-reproductive period or at the oviposition stage within the reproductive period. Rocking was followed by wing-flicks in most cases. Rocking movements appeared in males on the 6 (3–8)-th day of their imaginal ontogeny.

Elements of Behavior of Females during Different Phases of Their Ontogeny

Rocking was typical of males, but it was sporadically observed in females as well, its biological significance in the latter case being still unknown. Of the known elements of communicative behavior, females showed orientation toward the conspecific individual and feeling it with the antennae. Unreceptive females showed the avoidance response to signals of mature males. Mature females in this case displayed elements of reproductive behavior.

The post-reproductive period. This period was characterized by the absence of reproductive behavior in both sexes and a general decrease in activity. It lasted 3 (2–3) days in males and 4 (2–7) days in females, and ended with the death of the insect (Lunichkin et al., 2012).

The Forms of Behavior of Males and Females

Aggressive behavior. Wing-flicks and rocking were the typical elements of agonistic relations. When two males met, one of them might provoke the defense or escape response in the other. In this case the dominant male often pursued the runaway and attacked it with rapid lunges. A similar picture was observed when a mature male met an immature female or a female at the oviposition stage. If one of the males did not escape after agonistic encounter, two males remained facing one another at a distance of 10–15 mm and exchanged single wing flaps and series of short wing-flicks, being at the same time engaged in antennal contact. Then either one of the males escaped, or the confrontation developed into the next stage of active conflict and fight.

In females aggressive behavior was weakly expressed in the form of sporadic attacks on immature or diseased males, sometimes leading to cannibalism.

Reproductive behavior. On encounter of a male and a receptive female, their reproductive behavior started after an *indifferent phase* 30–60 s long, during which the male did not show any detectable response with respect to the female (Fig. 1, *1*). Reproductive behavior included several phases: initial male orientation, wing-flick signaling, mutual orientation, the precopulatory phase, preparation for coupling of the terminalia, and copulation with spermatophore transfer.

The phase of the male's initial orientation toward the female. The male positioned itself with its head toward the female at a distance of 50–80 mm (Fig. 1, *2*), so that the female was between the male's antennae. The male started feeling the female with its antennae. This phase lasted 129 s (16–386; $n = 10$). At this stage the male might perform rocking movements, which did not interfere with further development of courtship behavior and successful copulation. The males not ready to copulation displayed orientation behavior but did not proceed to active courtship. In all appearance, these two phases constituted the general response to the presence of a conspecific individual.

The phase of wing-flick signaling ("courtship," or preparation of the female for further contacts) started with the characteristic wing-flicks directed toward the female (Fig. 1, *3*). If the female did not respond with antennal contact, the male moved around the female, made wagging movements, and shifted "from one leg to another," with its head invariably oriented toward the female. The phase of active wing-flick signaling lasted 104 s (15–263; $n = 10$). This element of behavior was sometimes absent both in males with normally developed wings and in wingless ones; it does not seem to be necessary for successful copulation.

In response to this "courtship," the female started to turn to face the male, if it had not already been in the proper position. This moment marked the beginning of the *phase of mutual orientation.* The insects positioned themselves head to head (Fig. 1, *4*), with the longitudinal axes of their bodies in alignment. The distance between them decreased to 10–20 mm, and mutual feeling with the antennae took place. During this phase the male sometimes performed wing-flick signaling.

In the next, *precopulatory phase* the male started regular synchronous sideward movements of the cerci (Fig. 1, *5*). These movements, indicating readiness for copulation, continued to the very end of reproductive behavior. Sometimes the precopulatory phase was observed before that of mutual orientation. This phase, like the preceding one, might include wing-flick signaling, but no rocking movements were observed at this stage. In response to "courtship," the female assumed the posture needed for successful copulation, with the body raised on the fore legs and the abdomen bent under (Fig. 1, *6*).

The phase of preparation for coupling of the terminalia (copulation) started with the male turning to bring the tip of its abdomen close to the female's head (Fig. 1, *7*). In the process, the male corrected its position relative to the female by feeling it with the

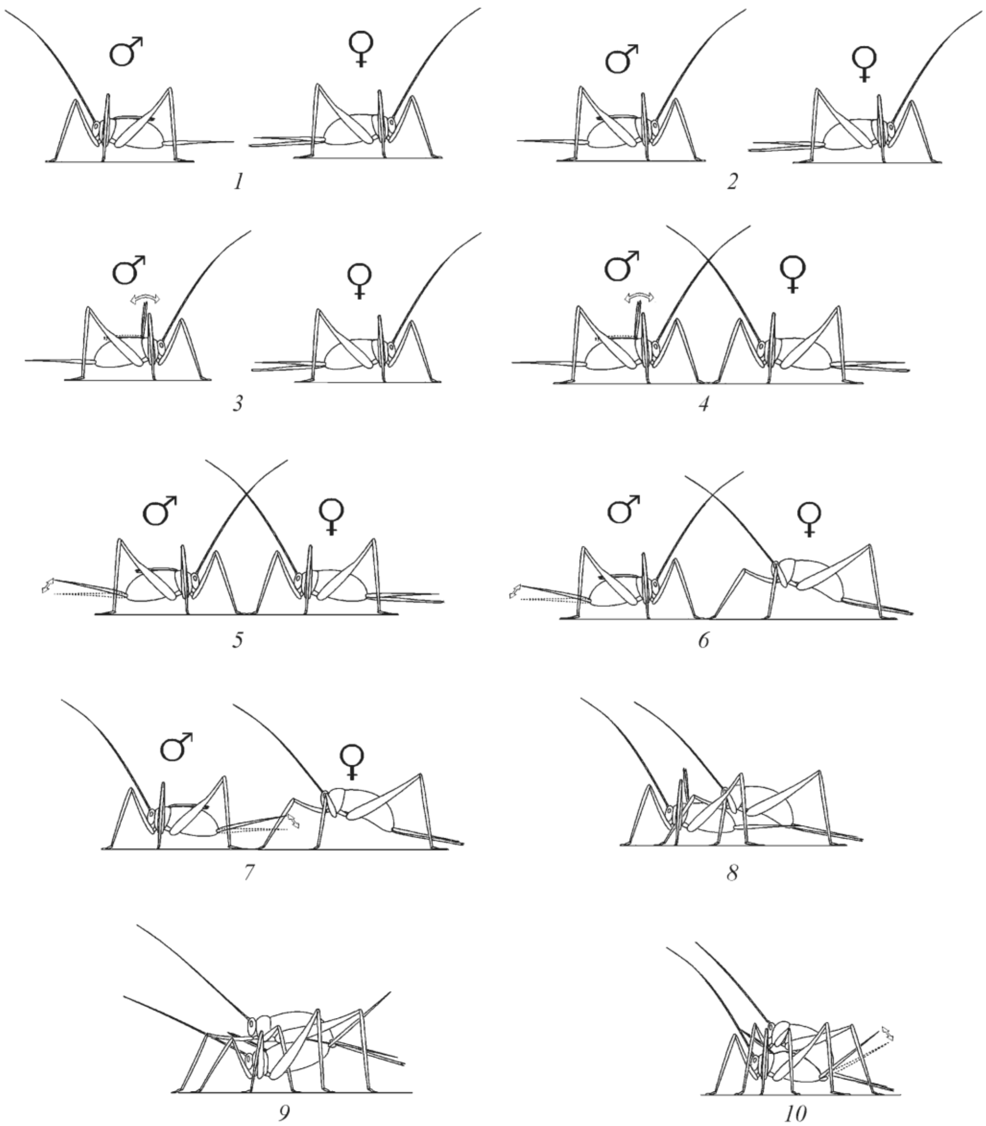

Fig. 1. Ethogram of reproductive behavior of the cricket *Phaeophilacris bredoides* Kalt.: (*1*) indifferent phase, the male showing no response to the female; (*2*) phase of initial orientation of the male; (*3*) phase of wing-flick signaling by the male; (*4*) phase of mutual orientation; (*5*) precopulatory phase, the male making lateral movements with its cerci; (*6*) precopulatory phase, the female assuming the proper posture; (*7*) the male turning; (*8*) the male assuming the proper posture for copulation; (*9*) coupling of the terminalia; (*10*) copulation with spermatophore transfer. Short back-and-forth movements of the raised wings and lateral movements of the cerci are indicated with arrows; the resting position of the wings is shown in dotted line.

antennae. After this turn, the male's antennae were directed backward, touching the female. The gap between the beginning of the cercal movements and the beginning of the turn was 134 s (38–325; $n = 10$). The complete turn took about 10–20 s ($n = 10$). After the turn, the male assumed the position necessary for copulation (Fig. 1, *8*). For this purpose, the male moved backwards trying to get itself exactly under the female, and waggled its body forcing the female to mount its back. At the same time, the male raised its wings at 90–120° to the body. The female's abdomen was positioned between the male's cerci, and its tip was exactly above the tip of the male's abdomen. This stage lasted from 18 to 116 s ($n = 15$).

This phase could be interrupted in three cases: if the male failed to make the proper turn, if it failed to assume the position needed for coupling of the terminalia, or if it did not raise its wings for some reason; in the latter case the female started biting the male's wings and the male escaped. In all the variants, the male returned to the initial "head-to-head" position and repeated all the elements from that moment. In such cases, the time required for successful completion of the coupling preparation phase might be extended to 20 min.

The copulation phase started with coupling of the mates' terminalia. The male performed abrupt upward movements with the tip of its abdomen until coupling occurred (Fig. 1, *9*). Several seconds later, the spermatophore was released by the male and the process of its transfer started (Fig. 1, *10*). During coupling and spermatophore transfer the male stimulated the female's abdomen by lateral movements of its cerci. At the end of successful copulation the female detached itself from the male in an upward movement. This phase lasted on average 65 min (30–145; $n = 40$).

During the whole sequence of reproductive behavior the female was relatively passive while the male was the active mate. Wing-flicks, rocking, feeling with the antennae, the characteristic position of the male's antennae, and active movements of its cerci seem to keep the mature receptive female from moving away and prompt it to assume the proper position for successful copulation.

DISCUSSION

We have observed in *Ph. bredoides* all the main forms of communicative behavior that occur in the singing crickets, for example, species of the genera *Gryllus* and *Gryllodes*: reproductive and agonistic (defensive and aggressive) behavior. Earlier it had been shown that the imaginal ontogeny of *Ph. bredoides* could be subdivided into the same periods that occurred in the ontogeny of the singing species (Lunichkin et al., 2012). The ethological characteristics of these periods in *Ph. bredoides* and the singing species were the same: agonistic (defensive) behavior prevailed during the pre- and post-reproductive periods, while reproductive and aggressive behavior was typical of the reproductive period.

A considerable role in the intraspecific communication of *Ph. bredoides* belongs to the tactile (contact mechanosensory) component, namely the feeling with the antennae. Antennal contacts seem to serve for determining the spatial position of the other cricket, mutual orientation of the bodies, and keeping the female close to the male during courtship. Mutual feeling with the antennae is a necessary component of both reproductive and agonistic behavior that continues during the entire act of communication.

During reproductive behavior the female is positioned "in line" of the male's antennae. This allows the male to monitor the female's movements and adjust its position accordingly. An important role during copulation seems to belong to stimulation of the female's abdomen with the male's cerci. This stimulation probably keeps the female in the required position and prevents it from interrupting copulation before the transfer of the spermatophore.

Our experiments showed that wing-flicks and rocking movements were performed only in the presence of a conspecific individual of either sex.

It was supposed that intraspecific signaling in a closely related species *Ph. spectrum* was realized by wing flaps. Heidelbach and Dambach (1991, 1997) concluded that the key role in perceiving the male's signals by the female belonged to the air vortices in the cercal area, generated by the flapping wing movements. In the course of multiple flaps composing the wing-flicks the signal is enhanced due to summation of the air currents, changes in their dynamic structure, and increasing turbulence. The cited authors noted that the parameters of wing-flicks were more stable in *Ph. spectrum* than in *Ph. bredoides*, though they performed no comparative analysis.

It may be supposed that wing movements performed by the male of *Ph. bredoides* also form air thrusts spreading toward the other cricket. These short-range thrusts are perceived by specialized trichobothria on the insect body, which form the densest clusters on the cerci (Ivanov, 2000). The principal and the most sensitive organ detecting the wing-flick signals seems to be the cercal apparatus (Knyazev, 1972, 1978).

Thus, similar to the classical acoustic communication, wing-flick signaling may also use the distant mechanosensory channel. However, unlike the acoustic calling signal, this mechanism of communication acts at short range and cannot be used over considerable distances. This may not be the only function of wing-flicks.

Wing-flicks are characteristic elements of reproductive and agonistic behavior, i.e., they represent a polyfunctional form of signaling. In this respect wing-flicks resemble the acoustic calling signals of other crickets which, besides their main function of attracting females, serve as territorial signals and affect the distribution of males in the population (Zhantiev, 1981).

During reproductive behavior, wing-flicks seem to act as the "mating signal" aimed at keeping the female close to the male. In response to such signals the female adjusts its position with respect to the male and assumes the proper posture allowing the male to accomplish copulation. During the entire preceding period and during copulation proper, the female does not try to escape but remains passive and practically motionless. The active movements ensuring copulation are performed exclusively by the male. At the same time, it was shown that successful copulation could take place even in the absence of air thrusts formed by wing flapping (for example, when the male's wings were glued together or damaged).

During agonistic behavior, wing-flicks seem to trigger the escape response or counter-aggression.

Rocking mostly occurred in mature males as an element of agonistic behavior in response to the approaching mature male or unreceptive female. In some cases, this element was recorded during the phase immediately preceding courtship. Rocking probably signals the high degree of excitation. This form of behavior was also described in the singing crickets, both in adults and nymphs. No behavioral response to rocking per se was observed.

Oscillations of the body of the "rocking" cricket are naturally transmitted to the substrate through its legs. The substrate vibrations may be perceived by the subgenual organs and campaniform sensilla on the legs of the recipient. This type of communication is widespread among insects (Autrum, 1941; Autrum and Schneider, 1948; Dambach, 1972; Dohlen, 1981). Rocking movements were previously described in *Ph. spectrum* (Heidelbach and Dambach, 1991) but their role in intraspecific communication was not considered; this problem awaits further research.

Thus, intraspecific communication during reproductive and agonistic behavior in *Ph. bredoides* is based on specific signaling that uses a multimodal mechanosensory channel. This channel includes distant mechanosensory communication mediated by air thrusts and substrate-borne vibrations, and also tactile communication based on direct physical contacts.

In all appearance, the main structures perceiving distant communication signals are the cercal apparatus (wing-flick signaling) and the subgenual organs and campaniform sensilla on the legs (substrate-borne vibrations). Thus, the absence of tympanal organs in *Ph. bredoides* appears to be compensated for by the enhanced function of other mechanosensory systems: the cercal one, perceiving low-frequency air oscillations (including low-frequency acoustic signals), the subgenual organ, and the cluster of campaniform sensilla on the legs.

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