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Novel system of communication in crickets originated at the same time as bat echolocation and includes male-male multimodal communication

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Abstract

Understanding the evolutionary origins of communication signals requires careful study of multiple species within a known phylogenetic framework. Most cricket species produce low-frequency calls for mate attraction, whereas they startle to high-frequency sounds similar to bat echolocation. Male crickets in the tribe Lebinthini produce high-frequency calls, to which females reply with vibrational signals. This novel communication system likely evolved by male sensory exploitation of acoustic startle to high-frequency sounds in females. This behavior was previously described for the Lebinthini from Asia. Here we demonstrate that this novel communication system is found in a Neotropical species, *Ponca hebardi*, and is therefore likely shared by the whole tribe Lebinthini, dating the origin of this behavior to coincide with the origin of echolocation in bats. Furthermore, we document male duets involving both acoustic and vibratory signals not previously described in crickets, and we tentatively interpret it as competitive masking between males.

Keywords: Orthoptera, Predation; High-frequency calls; Vibrational signals; Multimodal duets

Introduction

How and why new communication signals evolve are enduring questions in evolutionary biology (Searcy and Nowicki 2005; Bradbury and Vehrencamp 2011). To understand the evolutionary origins of a communication system, studies must test hypotheses with experiments that integrate detailed observations of behavior across multiple species in a phylogenetic framework (Shaw 1995). Evidence from diverse taxa has shown that new mate advertisement signals can arise when novel signals tap into a pre-existing perceptual bias of females (Ryan and Cummings 2013), a process referred to as sensory exploitation. In most cases, males produce signals that are similar to environmental cues that attract females, such as food or shelter (Fleishman 1992; Proctor 1992; Rodd et al. 2002; Christy et al. 2003). Mate attraction signals that resemble predator cues are rare, likely because typical responses to predator cues involve freezing or fleeing and not movement towards the cue. Interestingly, the two taxa in which sensory exploitation of predator cues for mating has been documented are both insects in which males produce high-frequency sounds in the range of bat echolocation calls (moths (Nakano et al. 2013); crickets (ter Hofstede et al. 2015)). A key assumption of these studies is that the signal evolved after the evolution of echolocation in bats. Here we compare new behavioral data with dating from previously published phylogenies to support the hypothesis that the timing of high-frequency calls in the cricket tribe Lebinthini coincided with the timing of the origin of echolocation in bats. Convergence in timing would suggest a rapid change in communication at the same time as the emergence of a new and dangerous predator.

Males of most cricket species in the family Gryllidae produce low-frequency (3-8 kHz) calling songs as intraspecific communication signals for mate attraction (Bennet-Clark 1989). Female crickets find males by following the sound signal (positive phonotaxis). Alternatively, when crickets hear high-frequency sounds in the range typically produced by bats for echolocation, they show stereotyped anti-predator behaviors, including negative phonotaxis in flight (Wyttenbach et al. 1996) and acoustic startle responses (running or jerking the body) when perched on a surface (ter Hofstede et al. 2015). It is unclear whether crickets benefit

from the acoustic startle response on the ground or if it is just a byproduct of the in-flight response to bat calls. A recent study (ter Hofstede et al. 2015) revealed that an alternative communication system evolved in crickets of the Lebinthini tribe (Eneopterinae), involving major changes in every component of the usual cricket system of communication: males produce high-frequency signals (10-28 kHz) (Robillard and Desutter-Grandcolas 2004a), females lack phonotaxis and instead produce vibrational signals in response to male calls, and males locate females via vibrotaxis. The vibrational signal produced by lebinthine females in response to the male's high-frequency call is remarkably similar in latency and structure to the vibrations produced by acoustic startle responses observed in closely related crickets when they hear high-frequency sounds typical of bat calls (ter Hofstede et al. 2015). Therefore, it is hypothesized that the lebinthine communication system evolved through male sensory exploitation of the acoustic startle response to high-frequency sounds in females (ter Hofstede et al. 2015). Lebinthine crickets no longer startle to high-frequency sounds, and females only produce the vibrational signal in response to sound with the temporal pattern of the conspecific male when they are receptive to mating, suggesting that this has evolved into a true communication signal in these species (ter Hofstede et al. 2015).

The lebinthine communication system was previously described for three species of different genera from Asia and islands from the Pacific region (Fig. 1). The second major branch of the Lebinthini, however, is found in the Neotropics (Fig. 1) (Vicente et al. 2017), but communication has not been studied in these species. If species in the neotropical clade demonstrate the same acoustic-vibrational duet as seen in the Asian-Pacific species, it would support the hypothesis that this novel communication system evolved in the ancestor of the entire tribe. The tribe Lebinthini is estimated to have diverged ~55 million years ago (Ma) (95% highest posterior density: 44.43–69.53 Ma (Vicente et al. 2017)), which coincides with the time estimated for the origin of an echolocating ancestor in bats ~58 Ma (Shi and Rabosky 2015; Thiagavel et al. 2018). Here, we test whether the species *Ponca hebardi* Robillard, 2005 from the Neotropical Lebinthini lineage (Fig. 1) demonstrates the alternative acoustic-vibrational communication system found in species from the Asian-Pacific clade of

the Lebinthini. We recorded the calling song of this species for the first time and used the recorded calls for playback experiments to test the behavioral responses of both sexes.

Methods

Study animals

Ponca hebardi is a nocturnal eneopterine cricket species (Fig. 1) previously known by only two type specimens collected in 1954 on Barro Colorado Island, Panama (Robillard and Desutter-Grandcolas 2005). We collected juveniles in the same locality in March 2017 and maintained them in the laboratory. Crickets were separated by sex before final moult and were tested in playback experiments two to four weeks after final moult. All male call recordings and playback tests were conducted in a room lined with sound-attenuating foam at controlled temperature and humidity conditions (temperature: 23.5 ± 1 °C, humidity: 60 ± 15 %). Specimens were deposited in the Muséum national d'Histoire naturelle, Paris (MNHN-EO-ENSIF4124-4127) and recorded .wav files were deposited in the sound library of MNHN under accession numbers MNHN-SO-2019-87 to MNHN-SO-2019-90 (<https://sonotheque.mnhn.fr/>).

Male recordings and acoustic analysis

Call recordings were obtained from four males with a modified condenser microphone (CM16, Avisoft Bioacoustics, Berlin, Germany) with a frequency range of 3-150 kHz $\pm$ 6 dB (R. Specht, pers. comm.). Each male was put individually in a suspended textile net cage overnight with the lights off and the microphone suspended 30 cm above the cage. Sound-triggered recordings were made using Avisoft Recorder software version 2.97 (Specht 2008) and an 8-Pro MOTU sound card at a sampling rate of 96 k-samples per second (16 bit). To generate audio files with accurate power spectra, we applied a user-defined finite impulse response (FIR) filter in Avisoft-SASLab Pro version 4.40 that corrected for the microphone frequency response. Temporal and spectral song features were measured using the automatic parameter measurements feature in Avisoft-SASLab Pro (FFT length 256,

rectangle window, 50% overlap). We measured syllable duration, syllable period (time from start of one syllable to start of next) and dominant frequency (frequency with maximum energy, kHz).

Playback experiments

The responses of female and male *P. hebardi* to male calls were tested within a dark arena (1.54 m x 0.65 m). Playback experiments were conducted using an UltraSoundGate Player 216H with Avisoft recorder USGH software and Avisoft Ultrasonic Dynamic Speaker Vifa. We selected five calls from one male recording with acoustic parameters similar to the mean values of the four recorded males. These calls were broadcasted at an amplitude of 65 dB at the cricket, matching the natural amplitude of the call at 80 cm, measured with an SVAN971/SvanteK sonometer. Playback experiments were monitored using a SONY Handycam HDR-HC3 video camera using the night-shot vision function.

Six unmated females were tested for behavioral responses to male calls. In a first set of experiments, phonotactic response was assessed with free moving individuals in an arena. The floor of the arena was covered by white filter paper that was changed after each experiment to remove any odor cues left by previously tested individuals. We placed each cricket in the middle of the arena, broadcasted male calls for 10 minutes and observed whether the female walked towards the speaker (positive phonotaxis). In a second set of experiments, females were placed on a foam base covered by a layer of filter paper and covered by a nylon mesh cage. For two of the six females, a custom accelerometer was placed underneath the filter paper to record vibrational signals. Using a microphone pointed at the speaker and the accelerometer below the female, we simultaneously recorded the male call playback and the female vibrational responses on two channels using Avisoft Triggering Hard-disk Recorder. From these recordings, we measured the dominant frequency (kHz), duration (ms), and time delay after the male call (ms) of the female vibrational signals using Avisoft-SASLab Pro.

In a third set of experiments, two unmated males were tested for behavioral responses to male calls. Males were placed in the middle of the arena and covered by a nylon mesh cage. A microphone was pointed at the cricket to record both the calls of the focal cricket and the playbacks from the speaker behind the male. Due to the microphone orientation, the focal male's calls and the broadcasted calls differed in amplitude on the oscillogram. From these recordings, we measured the dominant frequency (kHz), duration (ms) and time delay after the playback (ms) of the male calls using Avisoft-SASLab Pro. Videos monitoring playback experiments were analyzed frame by frame to document the timing of the vibration behavior of the focal male.

Results

The call of *P. hebardi* consisted of a single syllable with a mean duration of 51.2 ± 8.6 ms (mean $\pm$ SD), syllable period of 4.6 ± 2.2 s and a dominant frequency of 17.6 ± 0.3 kHz (N = 4 crickets, n = 160 calls). The dominant frequency corresponded to the third harmonic peak (Fig. 2A-B). Calls were emitted in bouts of 8.9 ± 4.2 syllables, lasting 35.7 ± 16.7 s, with a bout period of 52.6 ± 0.1 s.

Playback experiments were conducted with six *P. hebardi* females, all of which were observed visually and video recorded, and two of which were recorded with an accelerometer. Playback experiments revealed that female *P. hebardi* (N = 6 crickets) produced vibrational signals at a specific time interval after male calls and showed no phonotactic activity (SI-Video_part1). The female vibrational signal (N = 2 crickets, n = 200 signals) occurred 327.8 ± 14.6 ms after the male's call and had a duration of 169.8 ± 5.8 ms, with a dominant frequency of 97.0 ± 3.9 Hz.

The playback experiments demonstrated that male *P. hebardi* (N = 2 crickets, n = 177 $\pm$ 4 playbacks per cricket) also responded to calls of other males, both by alternating their own call between playbacks and by producing vibrational signals similar to those documented in females (SI-Video_part2). The mean delay between a male call and the male vibrational signal was 351 ± 509 ms (N = 1 cricket, n = 59 vibrational signals), but was

relatively variable, ranging from 30 to 2,490 ms. Male vibrational signals were the first replies to call playbacks and were usually followed by a call after 2.1 ± 0.6 s (Fig. 2).

Discussion

Our data show that the Neotropical lebinthine species *P. hebardi* exhibits the same type of communication behavior as the lebinthine species of the Asian-Pacific clade. The call of *P. hebardi* consists of a single syllable with a high dominant frequency corresponding to the third harmonic peak (Fig. 2A-B). The frequency structure is similar to other Lebinthini species, and the call particularly resembles that of the species *Cardiodactylus muria* (ter Hofstede et al. 2015). Playback experiments revealed that female *P. hebardi* produce vibrational signals at a specific time interval after male calls and show no phonotactic activity (SI-Video_part1). The female vibrational signal occurs after the males's call with a similar delay and dominant frequency as previously studied Lebinthini species (Table 1). Therefore, this novel communication system consisting of high-frequency male acoustic signals and female vibrational replies likely evolved in the ancestor of the Lebinthini tribe, representing a key innovation leading to the evolutionary diversification of these crickets (Robillard and Desutter-Grandcolas 2004b; ter Hofstede et al. 2015).

A fascinating and unexpected result of the playback experiments demonstrated that male *P. hebardi* also respond to calls of other males, both by alternating their own call between playbacks and by producing vibrational signals similar to those documented in females. These male vibrational signals have not been looked for in previously studied species. The mean delay between a male call and the male vibrational signal was similar to the delay measured for female signals, but was much more variable compared to the delay between male call and female vibrational signals. Interestingly, most of the male vibrational signals (49 of 59, 83 %) had shorter delays than the mean female delay, with five very long delays generating the higher mean and much larger standard deviation for male than female delays.

Considering that *P. hebardi* male vibrational signals are similar to female responses and occur in response to male calls, we suggest that the male vibrational signal evolved to mask female replies to a rival male's calls, thereby preventing rival males from detecting and locating females. This disruptive male strategy of mimicking the female signal in response to another male's signal has been documented in other vibrationally duetting insects (Tauber 2001; Bailey et al. 2006; Mazzoni et al. 2009a, b; Legendre et al. 2012; Polajnar et al. 2014). The delay between male call and male vibration signal was usually shorter than the delay measured in females, perhaps ensuring that the male signal reaches the rival male before the female reply. However, males occasionally produced vibrational signals at very long intervals after another male call, suggesting that spontaneous vibrational signaling might also be part of this species' signaling repertoire. In addition, *P. hebardi* males produce their own acoustic signal between acoustic signals of the rival male, allowing them to maintain a duet with the female. This behavior has the potential to increase a male's mating success if the male can produce a masking signal that increases the time required by the rival male to reach the female (Bailey et al. 2006; Legendre et al. 2012; Cocroft et al. 2014) without decreasing his own call production (Bailey et al. 2006; Legendre et al. 2012).

In crickets, male-male interactions such as aggressive songs, fighting, phonotaxis, and victory displays are all known in behavioral contexts linked to male rivalry (Shaw et al. 1990; Brown et al. 2006; Bertram et al. 2010; McCarthy et al. 2013). Nevertheless, those interactions almost exclusively rely on acoustic signals occurring at long range, or consist of multimodal short-range aggressive behaviors. The novel long-range male-male bimodal interactions described here significantly increase the behavioral repertoire of cricket male-male communication and adds to the complexity of the communication system of the Lebinthini. Under the hypothesis that the Lebinthini's communication system evolved by sensory exploitation of a startle response in females, it is likely that male vibrational signals originated through a similar mechanism, by tapping into preexisting sensory biases both in male and female receivers (ter Hofstede et al. 2015). These interactions suggest selection pressure in the form of competition among males for detecting female responses and

contending with eavesdropping rival males (Bailey 1991; Mc Gregor 2005; Cocroft et al. 2014).

This study supports an origin of the acoustic-vibratory duet in the ancestor of both the Paleo- and Neotropical Lebinthini clades and demonstrates a potential novel male strategy for thwarting rival males while communicating with a female. Both vibrational and acoustic communication are common and widespread in insects and arthropods (Cocroft et al. 2014), but only a handful of species are known to use bimodal acoustic-vibrational signals in reciprocal interactions between and among sexes (Rajaraman et al. 2015; ter Hofstede et al. 2015). Understanding how these communication systems function can help us understand conditions that favor multimodal communication and competitive interactions within these systems. The presence of the novel acoustic-vibrational duet in the Neotropical lineage of the Lebinthini supports the hypothesis that it evolved in the ancestor of this tribe and provides a time estimate of ~55 Ma for the origin of this novel communication system. This coincides remarkably well with the estimated time for the origin of echolocation in bats (~58 Ma), suggesting a potentially rapid adaptation to a new predator and subsequent effects on communication within crickets. As methods for molecular dating improve, more accurate estimates will reveal how closely these events occurred in time and provide answers about the rate of evolutionary change in a novel communication system.

List of supplementary information

Excel file with datasets: DATA_Ponca.xlsx

SI-Video: Video file of female (Part 1) and male (Part 2) responses to acoustic playback.

Authors' contributions

TR collected the specimens. J.L.B.-L. conducted behavioral recording experiments. All authors contributed to the conception, design, analysis and writing.

Competing interests

We have no competing interests.

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Ethical approval: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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Table 1: Male and female communication signal features for previously studied Asian-Pacific lebinthine species and the Neotropical species *Ponca hebardi*. Values are means $\pm$ standard deviations. Sample sizes are reported in brackets (number of crickets; number of vibrational signals). Values for *A. obscurus*, *C. muria* and *L. luae* from ter Hofstede et al. (2015).

Species	Male dominant frequency (kHz)	Female vibration frequency (Hz)	Female vibration delay (ms)	Male vibration delay (ms)
<i>A. obscurus</i>	15	48 $\pm$ 5 (8; 42)	141 $\pm$ 8 (7; 7)	?
<i>C. muria</i>	14	38 $\pm$ 3 (9; 88)	631 $\pm$ 43 (10; 10)	?
<i>L. luae</i>	17	84 $\pm$ 4 (9; 76)	138 $\pm$ 8 (9; 9)	?
<i>P. hebardi</i>	17	97 $\pm$ 3 (2; 200)	327 $\pm$ 14 (2; 200)	351 $\pm$ 509 (1; 59)

Fig. 1 Evolutionary relationships within the cricket tribe Lebinthini. (a) Phylogenetic tree of the Lebinthini inferred through Bayesian and maximum likelihood approaches based on four mitochondrial and three nuclear gene sequences (modified from Vicente et al. (2017), with arrows pointing to the phylogenetic positions of *Ponca hebardi* and the Asian-Pacific lebinthine species previously analyzed by (ter Hofstede et al. 2015). (b) photo of male *P. hebardi* on vegetation

Fig. 2 Communication signals of the species *Ponca hebardi*. (a, b) Spectrograms (top trace) and oscillograms (bottom trace) of the calling song of *P. hebardi*: (a) three syllables over 8 seconds; (b) detailed view of one syllable. (c) Example of accelerometer recording of a female vibrational reply (upper trace) to the male call (lower trace). The male call is clipped in this recording due to the high gain needed to get a suitable signal-to-noise ratio for the vibrational signal recording, but the call itself was not distorted during playback. Graphs made with the R package 'seewave' (Sueur et al. 2008)

390 **Fig. 3** Results of playback experiments with the species *Ponca hebardi*. (a) Behavioral
391 responses of *P. hebardi* females to a speaker broadcasting conspecific male calling song. (b)
392 Delay between the male call and the female (n = 200) and male (n = 56) vibrational reply
393

394