

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

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- Novel system of communication in crickets originated at the same time as bat
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18 Abstract

19 Understanding the evolutionary origins of communication signals requires careful study of 20 multiple species within a known phylogenetic framework. Most cricket species produce low-21 frequency calls for mate attraction, whereas they startle to high-frequency sounds similar to 22 bat echolocation. Male crickets in the tribe Lebinthini produce high-frequency calls, to which 23 females reply with vibrational signals. This novel communication system likely evolved by 24 male sensory exploitation of acoustic startle to high-frequency sounds in females. This 25 behavior was previously described for the Lebinthini from Asia. Here we demonstrate that 26 this novel communication system is found in a Neotropical species, Ponca hebardi, and is 27 therefore likely shared by the whole tribe Lebinthini, dating the origin of this behavior to 28 coincide with the origin of echolocation in bats. Furthermore, we document male duets 29 involving both acoustic and vibratory signals not previously described in crickets, and we 30 tentatively interpret it as competitive masking between males.

31

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

35 Introduction

36 How and why new communication signals evolve are enduring questions in evolutionary 37 biology (Searcy and Nowicki 2005; Bradbury and Vehrencamp 2011). To understand the 38 evolutionary origins of a communication system, studies must test hypotheses with 39 experiments that integrate detailed observations of behavior across multiple species in a 40 phylogenetic framework (Shaw 1995). Evidence from diverse taxa has shown that new mate 41 advertisement signals can arise when novel signals tap into a pre-existing perceptual bias of 42 females (Ryan and Cummings 2013), a process referred to as sensory exploitation. In most 43 cases, males produce signals that are similar to environmental cues that attract females, 44 such as food or shelter (Fleishman 1992; Proctor 1992; Rodd et al. 2002; Christy et al. 45 2003). Mate attraction signals that resemble predator cues are rare, likely because typical 46 responses to predator cues involve freezing or fleeing and not movement towards the cue. 47 Interestingly, the two taxa in which sensory exploitation of predator cues for mating has been 48 documented are both insects in which males produce high-frequency sounds in the range of 49 bat echolocation calls (moths (Nakano et al. 2013); crickets (ter Hofstede et al. 2015)). A key 50 assumption of these studies is that the signal evolved after the evolution of echolocation in 51 bats. Here we compare new behavioral data with dating from previously published 52 phylogenies to support the hypothesis that the timing of high-frequency calls in the cricket 53 tribe Lebinthini coincided with the timing of the origin of echolocation in bats. Convergence in 54 timing would suggest a rapid change in communication at the same time as the emergence 55 of a new and dangerous predator.

56 Males of most cricket species in the family Gryllidae produce low-frequency (3-8 kHz) 57 calling songs as intraspecific communication signals for mate attraction (Bennet-Clark 1989). 58 Female crickets find males by following the sound signal (positive phonotaxis). Alternatively, 59 when crickets hear high-frequency sounds in the range typically produced by bats for 60 echolocation, they show stereotyped anti-predator behaviors, including negative phonotaxis 61 in flight (Wyttenbach et al. 1996) and acoustic startle responses (running or jerking the body) 62 when perched on a surface (ter Hofstede et al. 2015). It is unclear whether crickets benefit

63 from the acoustic startle response on the ground or if it is just a byproduct of the in-flight 64 response to bat calls. A recent study (ter Hofstede et al. 2015) revealed that an alternative 65 communication system evolved in crickets of the Lebinthini tribe (Eneopterinae), involving 66 major changes in every component of the usual cricket system of communication: males 67 produce high-frequency signals (10-28 kHz) (Robillard and Desutter-Grandcolas 2004a), 68 females lack phonotaxis and instead produce vibrational signals in response to male calls, 69 and males locate females via vibrotaxis. The vibrational signal produced by lebinthine 70 females in response to the male's high-frequency call is remarkably similar in latency and 71 structure to the vibrations produced by acoustic startle responses observed in closely related 72 crickets when they hear high-frequency sounds typical of bat calls (ter Hofstede et al. 2015). 73 Therefore, it is hypothesized that the lebinthine communication system evolved through male 74 sensory exploitation of the acoustic startle response to high-frequency sounds in females (ter 75 Hofstede et al. 2015). Lebinthine crickets no longer startle to high-frequency sounds, and 76 females only produce the vibrational signal in response to sound with the temporal pattern of 77 the conspecific male when they are receptive to mating, suggesting that this has evolved into 78 a true communication signal in these species (ter Hofstede et al. 2015).

79 The lebinthine communication system was previously described for three species of 80 different genera from Asia and islands from the Pacific region (Fig. 1). The second major 81 branch of the Lebinthini, however, is found in the Neotropics (Fig. 1) (Vicente et al. 2017), but 82 communication has not been studied in these species. If species in the neotropical clade 83 demonstrate the same acoustic-vibrational duet as seen in the Asian-Pacific species, it would 84 support the hypothesis that this novel communication system evolved in the ancestor of the 85 entire tribe. The tribe Lebinthini is estimated to have diverged ~55 million years ago (Ma) 86 (95% highest posterior density: 44.43–69.53 Ma (Vicente et al. 2017)), which coincides with 87 the time estimated for the origin of an echolocating ancestor in bats ~58 Ma (Shi and 88 Rabosky 2015; Thiagavel et al. 2018). Here, we test whether the species Ponca hebardi 89 Robillard, 2005 from the Neotropical Lebinthini lineage (Fig. 1) demonstrates the alternative 90 acoustic-vibrational communication system found in species from the Asian-Pacific clade of

91 the Lebinthini. We recorded the calling song of this species for the first time and used the

92 recorded calls for playback experiments to test the behavioral responses of both sexes.

93

94 Methods

95 Study animals

96 Ponca hebardi is a nocturnal eneopterine cricket species (Fig. 1) previously known by only 97 two type specimens collected in 1954 on Barro Colorado Island, Panama (Robillard and 98 Desutter-Grandcolas 2005). We collected juveniles in the same locality in March 2017 and 99 maintained them in the laboratory. Crickets were separated by sex before final moult and 100 were tested in playback experiments two to four weeks after final moult. All male call 101 recordings and playback tests were conducted in a room lined with sound-attenuating foam 102 at controlled temperature and humidity conditions (temperature: 23.5 ± 1 °C, humidity: 60 ± 103 15 %). Specimens were deposited in the Muséum national d'Histoire naturelle, Paris (MNHN-104 EO-ENSIF4124-4127) and recorded .wav files were deposited in the sound library of MNHN 105 under accession numbers MNHN-SO-2019-87 to MNHN-SO-2019-90 106 (https://sonothegue.mnhn.fr/).

107

108 Male recordings and acoustic analysis

109 Call recordings were obtained from four males with a modified condenser microphone 110 (CM16, Avisoft Bioacoustics, Berlin, Germany) with a frequency range of 3-150 kHz \pm 6 dB 111 (R. Specht, pers. comm.). Each male was put individually in a suspended textile net cage 112 overnight with the lights off and the microphone suspended 30 cm above the cage. Sound-113 triggered recordings were made using Avisoft Recorder software version 2.97 (Specht 2008) 114 and an 8-Pro MOTU sound card at a sampling rate of 96 k-samples per second (16 bit). To 115 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 116 117 frequency response. Temporal and spectral song features were measured using the 118 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).

122

123 Playback experiments

124 The responses of female and male *P. hebardi* to male calls were tested within a dark arena 125 (1.54 m x 0.65 m). Playback experiments were conducted using an UltraSoundGate Player 126 216H with Avisoft recorder USGH software and Avisoft Ultrasonic Dynamic Speaker Vifa. We 127 selected five calls from one male recording with acoustic parameters similar to the mean 128 values of the four recorded males. These calls were broadcasted at an amplitude of 65 dB at 129 the cricket, matching the natural amplitude of the call at 80 cm, measured with an 130 SVAN971/Svantek sonometer. Playback experiments were monitored using a SONY 131 Handycam HDR-HC3 video camera using the night-shot vision function.

132 Six unmated females were tested for behavioral responses to male calls. In a first set 133 of experiments, phonotactic response was assessed with free moving individuals in an 134 arena. The floor of the arena was covered by white filter paper that was changed after each 135 experiment to remove any odor cues left by previously tested individuals. We placed each 136 cricket in the middle of the arena, broadcasted male calls for 10 minutes and observed 137 whether the female walked towards the speaker (positive phonotaxis). In a second set of 138 experiments, females were placed on a foam base covered by a layer of filter paper and 139 covered by a nylon mesh cage. For two of the six females, a custom accelerometer was 140 placed underneath the filter paper to record vibrational signals. Using a microphone pointed 141 at the speaker and the accelerometer below the female, we simultaneously recorded the 142 male call playback and the female vibrational responses on two channels using Avisoft 143 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 144 145 vibrational signals using Avisoft-SASLab Pro.

146 In a third set of experiments, two unmated males were tested for behavioral responses 147 to male calls. Males were placed in the middle of the arena and covered by a nylon mesh 148 cage. A microphone was pointed at the cricket to record both the calls of the focal cricket and 149 the playbacks from the speaker behind the male. Due to the microphone orientation, the 150 focal male's calls and the broadcasted calls differed in amplitude on the oscillogram. From 151 these recordings, we measured the dominant frequency (kHz), duration (ms) and time delay 152 after the playback (ms) of the male calls using Avisoft-SASLab Pro. Videos monitoring 153 playback experiments were analyzed frame by frame to document the timing of the vibration 154 behavior of the focal male.

155

156 **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 \pm 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).

176

177 **Discussion**

178 Our data show that the Neotropical lebinthine species P. hebardi exhibits the same 179 type of communication behavior as the lebinthine species of the Asian-Pacific clade. The call 180 of *P. hebardi* consists of a single syllable with a high dominant frequency corresponding to 181 the third harmonic peak (Fig. 2A-B). The frequency structure is similar to other Lebinthini 182 species, and the call particularly resembles that of the species Cardiodactylus muria (ter 183 Hofstede et al. 2015). Playback experiments revealed that female P. hebardi produce 184 vibrational signals at a specific time interval after male calls and show no phonotactic activity 185 (SI-Video_part1). The female vibrational signal occurs after the males's call with a similar 186 delay and dominant frequency as previously studied Lebinthini species (Table 1). Therefore, 187 this novel communication system consisting of high-frequency male acoustic signals and 188 female vibrational replies likely evolved in the ancestor of the Lebinthini tribe, representing a 189 key innovation leading to the evolutionary diversification of these crickets (Robillard and 190 Desutter-Grandcolas 2004b; ter Hofstede et al. 2015).

191 A fascinating and unexpected result of the playback experiments demonstrated that 192 male P. hebardi also respond to calls of other males, both by alternating their own call 193 between playbacks and by producing vibrational signals similar to those documented in 194 females. These male vibrational signals have not been looked for in previously studied 195 species. The mean delay between a male call and the male vibrational signal was similar to 196 the delay measured for female signals, but was much more variable compared to the delay 197 between male call and female vibrational signals. Interestingly, most of the male vibrational 198 signals (49 of 59, 83 %) had shorter delays than the mean female delay, with five very long 199 delays generating the higher mean and much larger standard deviation for male than female 200 delays.

201 Considering that *P. hebardi* male vibrational signals are similar to female responses 202 and occur in response to male calls, we suggest that the male vibrational signal evolved to 203 mask female replies to a rival male's calls, thereby preventing rival males from detecting and 204 locating females. This disruptive male strategy of mimicking the female signal in response to 205 another male's signal has been documented in other vibrationally duetting insects (Tauber 206 2001; Bailey et al. 2006; Mazzoni et al. 2009a, b; Legendre et al. 2012; Polajnar et al. 2014). 207 The delay between male call and male vibration signal was usually shorter than the delay 208 measured in females, perhaps ensuring that the male signal reaches the rival male before 209 the female reply. However, males occasionally produced vibrational signals at very long 210 intervals after another male call, suggesting that spontaneous vibrational signaling might also 211 be part of this species' signaling repertoire. In addition, P. hebardi males produce their own 212 acoustic signal between acoustic signals of the rival male, allowing them to maintain a duet 213 with the female. This behavior has the potential to increase a male's mating success if the 214 male can produce a masking signal that increases the time required by the rival male to 215 reach the female (Bailey et al. 2006; Legendre et al. 2012; Cocroft et al. 2014) without 216 decreasing his own call production (Bailey et al. 2006; Legendre et al. 2012).

217 In crickets, male-male interactions such as aggressive songs, fighting, phonotaxis, and 218 victory displays are all known in behavioral contexts linked to male rivalry (Shaw et al. 1990; 219 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 220 221 multimodal short-range aggressive behaviors. The novel long-range male-male bimodal 222 interactions described here significantly increase the behavioral repertoire of cricket male-223 male communication and adds to the complexity of the communication system of the 224 Lebinthini. Under the hypothesis that the Lebinthini's communication system evolved by 225 sensory exploitation of a startle response in females, it is likely that male vibrational signals 226 originated through a similar mechanism, by tapping into preexisting sensory biases both in 227 male and female receivers (ter Hofstede et al. 2015). These interactions suggest selection 228 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).

231 This study supports an origin of the acoustic-vibratory duet in the ancestor of both the 232 Paleo- and Neotropical Lebinthini clades and demonstrates a potential novel male strategy 233 for thwarting rival males while communicating with a female. Both vibrational and acoustic 234 communication are common and widespread in insects and arthropods (Cocroft et al. 2014), 235 but only a handful of species are known to use bimodal acoustic-vibrational signals in 236 reciprocal interactions between and among sexes (Rajaraman et al. 2015; ter Hofstede et al. 237 2015). Understanding how these communication systems function can help us understand 238 conditions that favor multimodal communication and competitive interactions within these 239 systems. The presence of the novel acoustic-vibrational duet in the Neotropical lineage of the 240 Lebinthini supports the hypothesis that it evolved in the ancestor of this tribe and provides a 241 time estimate of ~55 Ma for the origin of this novel communication system. This coincides 242 remarkably well with the estimated time for the origin of echolocation in bats (~58 Ma), 243 suggesting a potentially rapid adaptation to a new predator and subsequent effects on 244 communication within crickets. As methods for molecular dating improve, more accurate 245 estimates will reveal how closely these events occurred in time and provide answers about 246 the rate of evolutionary change in a novel communication system.

247

- 248 List of supplementary information
- 249 Excel file with datasets: DATA_Ponca.xlsx

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

251

252 Authors' contributions

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

255

256 Competing interests

257 We have no competing interests.

258

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263

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270

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

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- 363
- 364

- Table 1: Male and female communication signal features for previously studied Asian-Pacific
 lebinthine species and the Neotropical species *Ponca hebardi*. Values are means ± standard
- 367 deviations. Sample sizes are reported in brackets (number of crickets; number of vibrational
- 368 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)
A. obscurus	15	48 ± 5 (8; 42)	141 ± 8 (7; 7)	?
C. muria	14	38 ± 3 (9; 88)	631 ± 43 (10; 10)	?
L. luae	17	84 ± 4 (9; 76)	138 ± 8 (9; 9)	?
P. hebardi	17	97 ± 3 (2; 200)	327 ± 14 (2; 200)	351 ± 509 (1; 59)

370

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



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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)



387

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

