Sometimes noise is beneficial: stream noise informs vocal communication in the little torrent frog

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Many animal species use acoustic signals for social communication including attracting mates, defending resources and assessing risks. Nevertheless, a variety of ambient noise sources often interfere with sound communication and efficient decision making. In the present study we identified an exception to this generalization in a streamside species, the little torrent frog (Amolops torrentis) which communicates in an environment in which stream noise is always present. To show that stream noise can act as a biological signal which reflects the character of the microhabitat of the sender, we performed female phonotaxis experiments using synthetic male advertisement calls. Calls with high dominant frequency exceeding the ambient stream noise band and calls with lower dominant frequency centered at the frequency range of best hearing were used. The signal-noise ratio was varied by adding noise to each kind of call. We found that females prefer calls with high amplitude stream noise added to those with low amplitude stream noise added for both the high and low dominant frequency stimulus pairs; however, the sound of running water had no attractiveness in the absence of calls. These results show that stream noise can function as an information source by enhancing the attractiveness of calls in the torrent frog. Stream noise associates closely with rocks, topographies and vegetation; thus the sound of running water may provide useful information to signal receivers about variations in microhabitats and thereby act on sexual selection under some circumstances. These data therefore contribute to our understanding of how the perception of mate attractiveness in heterogeneous ecological environments can evolve.

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Abstract

Many animal species use acoustic signals for social communication including attracting mates, defending resources and assessing risks. Nevertheless, a variety of ambient noise sources often interfere with sound communication and efficient decision making. In the present study we identified an exception to this generalization in a streamside species, the little torrent frog (*Amolops torrentis*) which communicates in an environment in which stream noise is always present. To show that stream noise can act as a biological signal which reflects the character of the microhabitat of the sender, we performed female phonotaxis experiments using synthetic male advertisement calls. Calls with high dominant frequency exceeding the ambient stream noise band and calls with lower dominant frequency centered at the frequency range of best hearing were used. The signal-noise ratio was varied by adding noise to each kind of call. We found that females prefer calls with high amplitude stream noise added to those with low amplitude stream noise added for both the high and low dominant frequency stimulus pairs; however, the sound of running water had no attractiveness in the absence of calls. These results show that stream noise can function as an information source by enhancing the attractiveness of calls in the torrent frog. Stream noise associates closely with rocks, topographies and vegetation; thus the sound of running water may provide useful information to signal receivers about variations in microhabitats and thereby act on sexual selection under some circumstances. These data therefore contribute to our understanding of how the perception of mate attractiveness in heterogeneous ecological environments can evolve.

Keywords: sound communication, stream noise, microhabitat, *Amolops torrentis*, mate attractiveness, sexual selection

Introduction

Acoustic signals can be transmitted over long distances through varied habitats and convey many kinds of messages about species and individual identity, sexual receptivity and spatiotemporal information (Tyack 1998; Marler and Slabbekoorn 2004; Narins et al. 2007). Most terrestrial species rely heavily on acoustic signals to attract mates, assess risks and defend resources (Bernal et al. 2007; Linhart et al. 2012; Halfwerk et al. 2014). However, sound communication is often degraded by various biotic and abiotic sources of environmental noise which interfere with the transmission of acoustic signals as well as the detection and processing of information contained in these signals (Wiley and Richards 1982; Rabin and Greene 2002; Brumm and Slabbekoorn 2005; Brumm and Naguib 2009; Love and Bee 2010). These challenges drive selection pressures resulting in the evolution of specialized morphological, behavioral and physiological adaptations for coping with complex environment noise (Slabbekoorn and Peet 2003; Feng et al. 2006; Fuller et al. 2007; Brumm and Zollinger 2011).

Most research on the impact of noise has focused on the detrimental effects and how animals deal with interference from noise. Nevertheless, noise can also be beneficial to some species depending on the context and how others react to it (Stansbury et al. 2016). For instance, greater mouse-eared bats (*Myotis myotis*) and western scrub jays (*Aphelocoma californica*) have been shown to experience decreased predation pressure when predators avoid increased local noise produced by anthropogenic activity (Schaub et al. 2008; Francis et al. 2009). Anthropogenic noise can be a form of acoustic crypsis and may increase the foraging success of predators by interfering with detection by prey (Chan et al. 2010).

In socially aggregating animals, competing biotic noise can mask vocal communication signals interfering with signal detection, localization and recognition (Lohr et al. 2003; Feng and Schul 2007). However, biotic noise can also be used for orientation in the field because dense choruses can transmit communication sounds over long distances that remain detectable and identifiable (Gerhardt and Klump 1988; Sinsch 1990). The cooperative hypothesis proposes that conspecific background noise (i.e. synchronous calling) may also benefit males by disturbing the localization of individuals by predators and by increasing the group attractiveness to females

(Grafe 1999). Nevertheless, despite possible benefits or anthropogenic and natural biotic noise, there is little evidence that animals can benefit from natural abiotic noise.

The little torrent frog (*Amolops torrentis*) inhabits mountain streams filled with lush vegetation on both sides at altitudes of 80-780 m (Fei et al. 2012). During the breeding season, males prefer to call at sites of high-amplitude stream noise which associate closely with rocks, topographies, vegetation and the running water. Moreover, little torrent frogs have also been found to lay eggs in rocky and fast flowing sites and tadpoles also inhabit in such places. This behavioral preference may enhance survival and reproductive success. For instance, frogs can use stones and running water to avoid predators and to provide a relatively safe environment for early embryo development. Potentially, the noise of the turbulent waters is an indicator for suitable oviposition sites. Thus, we hypothesized that stream noise accompanying male vocalizations may contain information about microhabitat variation useful to females.

The results of a previous study indicate that the dominant frequency of natural male advertisement calls (4.3 kHz) is substantially mismatched with female auditory frequency tuning (1.6 kHz) in little torrent frogs, despite the fact that low-frequency calls with a dominant frequency equal to 1.6 kHz are attractive to females compared to white noise (Zhao et al. 2016, unpublished data). Furthermore, females prefer high-frequency calls (dominant frequency of 4.3 kHz) to low-frequency calls (Zhao et al. 2016, unpublished data). To test the hypothesis that stream noise can be used by females as a cue reflecting information about the microhabitat during mate choice, we tested the females' preferences for stimulus pairs constructed with either synthetic male high-frequency calls or low-frequency calls and stream noise when the signal-noise ratio was varied. In addition, we determined if stream noise alone is attractive to females.

Material and methods

Study site and animal

During the reproductive season, from April to September in 2015, we collected female little torrent frogs in the Mt. Diaoluo Nature Reserve (18.44° N and 109.52° E), Hainan province, China. Daily temperatures varied between 14 and 25 °C during this period. Females found in the stream and nearby shrubs were collected (between 1900 and 2200 hours), placed in containers with water and stones from their capture sites, and brought back to the laboratory for testing as described below. In this species, female of sexual maturity is bigger than male and the ovulated female has obviously plump abdomen. Only ovulated frogs were used in the experiments, to ensure females respond well to acoustic stimuli. The frogs were used for the experiments with the permission of the management office of the Mt. Diaoluo nature reserve. All animal procedures were approved by the Animal Care and Use Committee of the Chengdu Institute of Biology, CAS.

Stimuli

Signal-noise ratio assessments in the natural habitat

Calls of male little torrent frogs (n = 40), from different stream locations, were measured to determine the signal-noise ratio range. After locating a vocalizing male, we recorded call sound pressure levels (dB re 20 μPa) and ambient stream SPLs from a distance of 1 m, using a sound level meter (AWA 6291, Hangzhou Aihua Instruments Co.). The stream was regarded as a noise

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field in which ambient noise intensity was considered virtually constant within the measured distance of 1 m (Preininger et al. 2013). Since sound radiation varies in its directionality, the sound level meter was directed toward the snout-vent orientation of the subject during each recording session. The SPL of the ambient stream noise was recorded simultaneously when recording the calls. To measure the real vocal amplitude accurately, we subtracted the background from that of the signal using logarithmic computation rules (Weißing 1984), in which

$$L_{\text{sig}} = 10 \log_{10} (10^{(L\text{sig + noise}/10)} - 10^{(L\text{noise}/10)}),$$

where $L_{\text{sig + noise}}$ is the total sound pressure level, L_{noise} is the background noise level alone, and L_{sig} is the SPL of the signal (Brumm and Zollinger 2011). Then the dB of signal and noise were transformed to Pa with this formula: SPL = 20 log (P/20μPa). As a result, signal-noise ratios ranged from 1.23 to 18.81 in the natural habitat.

Synthetic stimuli used to create stimulus pairs

For the phonotaxis experiments, acoustic stimuli were synthesized based on the average values of the spectral and temporal properties of calls produced in local populations and stream noise occurring at different habitat locations using Avisoft SAS-Lab Pro (Avisoft Bioacoustics, Berlin) and Adobe Audition 3.0 software (California, USA). All calls have the duration of 6.384 s with 57 short notes (Fig. 1). The dominant frequency of high-frequency stimuli and low-frequency stimuli were 4.3 kHz and 1.6 kHz, respectively, and all other properties remained unchanged. The background noise was combined from recordings obtained from different locations because the noise spectra can vary, and then adjusted so that the amplitude would yield the desired signal to noise ratio. The noise presentation gated on and off with the call stimuli with 5 s interval. To create stimulus pairs for the experiments, the signal-noise ratio was set to either 2:1 or 8:1. Three stimulus categories were used: (1) high dominant frequency call with no noise added (HN), high dominant frequency call with low amplitude noise added (HL: signal/noise = 8:1) and high dominant frequency call with high amplitude noise added (HH: signal/noise = 2:1) (Fig. 1a, b, c), (2) low dominant frequency call with no noise added (LN), low dominant frequency call with low amplitude noise added (LL: signal/noise = 8:1) and low dominant frequency call with high amplitude noise added (LH: signal/noise = 2:1) (Fig. 1d, e, f), and (3) running water (RW), white noise (WN) and silence (S). A total of eight stimulus pairs were constructed using these three categories of stimuli, respectively (Table 1, 2).

Phonotaxis experiments

The three types of stimulus pairs described above were used in experiments 1-3, respectively. Experiment 1 and experiment 2 were conducted in order to determine whether stream noise provides salient information to female little torrent frogs. Two stimulus pairs in experiment 3 were utilized in order to determine whether stream noise alone provides information salient to females.

We conducted standard two-speaker phonotaxis tests in a sound-attenuating chamber [2(L)×1 (W) m]. Females were placed in the center of the chamber while the stimulus pairs were broadcast antiphonally from speakers (SME-AFS, Saul Mineroff Electronics, Elmont, NY, USA) placed in the center of each wall opposite one another such that the peak amplitude of each test call was 80 dB SPL (re 20 μPa) at the original place. The subject’s choice and response time were noted when a female approached within 10 cm of one of the two speakers as long as it did not follow the chamber's walls. A female was considered as failing to meet our response criterion if she was motionless or spent more than 10 min roaming the arena without approaching a speaker. In this case the response time was recorded as 10 min. To control for potential side biases, we randomized the speaker assignments for each stimulus pair. Females were never tested more than once in the same experiment. The phonotaxis results showed that there were no side biases.

Statistical analysis

Fisher's exact test and Pearson chi-square were used to evaluate differences in female preference for the stimuli used in this study and for differences in the proportion of females who did not meet the phonotaxis response criterion. The Mann-Whitney rank sum test was used to compare female response times between the noise vs. no added noise stimulus pairs in experiment 1 and between stimuli with high amplitude noise vs. low amplitude noise in experiment 2. All statistical analyses were carried out with SPSS 16.0 software (SPSS Inc., USA) and sigmaplot 11 software program (Systat Software Inc., San Jose, USA). A significance level of $p < 0.05$ was used in all comparisons.

Results

Female call preferences

Female choices for the phonotaxis experiments comparing all pairs of the eight test calls are shown in Table 2. In experiment 1 (i.e. comparing call stimuli of high dominant frequency with no noise, low amplitude noise or high amplitude noise added), both the proportion of subjects choosing the HL vs. HN stimulus in test 1 and the proportion of subjects choosing the HH vs. HN stimulus in test 2 did not differ significantly (Pearson chi-square: test 1, $\chi^2 = 0.19$, $p = 0.663$; test 2, $\chi^2 = 0.439$, $p = 0.508$), however, females strongly preferred HH to HL stimuli in test 3 (Fisher's exact test: $p = 0.014$) (Table 2). In experiment 2, call stimuli of low dominant frequency were used with no noise, low amplitude noise or high amplitude noise added (i.e. LN, LL and LH stimuli). For experiment 2 we found that female call preferences (tests 4-6 of experiment 2) were consistent with the results of experiment 1 (tests 1-3 tests of experiment 1). Thus female preferences between call pairs with the same fundamental frequency but varying noise added were not significantly different in test 3 and test 4 (Pearson chi-square: test 4, $\chi^2 = 0.439$, $p = 0.508$; test 5, $\chi^2 = 0.19$, $p = 0.663$), although LH was more attractive than LL in test 6 (Fisher's exact test: $p = 0.044$) (Table 2).

Female response time

As seen in Fig. 2, female response time was significantly longer in the high-frequency stimulus pairs of experiment 1 in tests 1-2 (Hsp 1-2, median = 8 minutes) compared to that of test 3 (Hsp 3, median = 4.5 minutes) (Mann-Whitney rank sum test: U = 2192.5, $p = 0.037$). Likewise, female response time was longer in the low-frequency stimulus pairs of experiment 2 in tests 4-5 (Lsp 4-5, median = 10 minutes) compared to that of test 6 (Lsp 6, median = 8 minutes), although these differences were not statistically significant (Mann-Whitney rank sum test: U = 2523, $p = 0.089$) (Fig. 2).

Stream noise is not attractive in the absence of advertisement calls

In experiment 3, the proportion of responsive females that chose the sound of running water (RW) over the white noise (WN) or silence (S) stimuli did not differ significantly (Pearson chi-square: test 7, $\chi^2 = 0$, $p = 1.0$; test 8, $\chi^2 = 3.2$, $p = 0.074$) (Table 2). Furthermore, over 50% of the females failed to meet our response criterion in this experiment, which is significantly higher than the proportion in experiment 1 (proportion: 40%; Fisher's exact test: $p = 0.015$) and higher than for experiment 2 (proportion: 45%; Fisher's exact test: $p = 0.076$) (Fig. 3). These results suggest that the sound of running water is not in itself attractive to female frogs.

Discussion

It has been widely known that stream noise can constrain sound communication by interfering with the propagation of acoustic signals and the receiver's perception of the signal and that these phenomena can drive the evolution of sexual signals and perceptual systems (Brumm and Slabbekoorn 2005; Feng et al. 2006; Shen et al. 2008). However, animals are not known to use the fast-flowing stream as a signal. In the present study, female little torrent frogs showed a preference for calls with high amplitude noise compared with low amplitude noise in tests involving both high dominant frequency and low dominant frequency calls while stream noise itself had no attractiveness. These results suggest that stream noise is a significant biological signal that can provide information salient to females of streamside breeding species when listening to male calls.

In many species, males vocalize to attract mates and their calls serve as acoustic beacons to conspecific females as well as to eavesdropping predators and parasites (Tuttle and Ryan 1981;

Tuttle et al. 1985; Dapper et al. 2011). Prey can use ambient noise to avoid predators, for instance, masking background noise may benefit prey species because it can reduce the foraging success of predators (Barber et al. 2009). Apart from natural biotic noise, animals also can make use of abiotic noise as a signal in orientation. Studies on marine mammals suggest that ocean noise caused by waves or currents plays an important role in migration and orientation behavior (Richardson et al. 1995). Moreover, many reproductive sites such as borrows, holes, nests and hides provide safety and security for mating, egg laying or the raising of offspring. Information about these microhabitats can be encoded by sounds. For instance, male Emei music frog calls convey information about the geometry of nest burrows which is salient to females (Cui et al. 2012). Interestingly, male little torrent frogs often vocalize at rocky and fast-flowing sites where amplexus and spawning occur in hidden holes and gaps, while females often inhabit the forested areas along the sides of streams during the breeding season. Thus it is possible that stream noise can be beneficial for avoiding predators and orienting in stream-breeding species.

In tests 1-2 and tests 4-5, female preferences were not significantly different for either the HH vs. HN or HL vs. HN stimulus pairs or for the LH vs. LN and LL vs. LN stimulus pairs (Table 2). These results show that females do not prefer stream noise in itself, but use it as an information source insofar as females prefer HH to HL and LH to LL stimuli. It is important to note that a growing body of research indicates that sexual selection can fluctuate over time, space and variations in the ecological environment and need not be strong and consistent (Amcoff et al. 2013; Gillespie et al. 2014). Stream noise is one of the most important ecological factors for turbulent species, whose presence or absence affects female perception and preference as shown by the results of the experimental manipulations in this study.

In the present study, HN and LN sounds may be considered novel stimuli for frogs because males call only in the presence of running water in their natural habit. Many studies indicate that songbirds and frogs are more sensitive initially to the playback of a novel stimulus. In such cases the animals manifest changes in virtually many aspects of observable behaviors such as staying closer to the speaker in playback experiments or flying short distances more frequently (Davis 1987; Blanchard 1941; Verner and Milligan 1971; Owen and Perrill 1998; Kroodsma 2005). These behaviors are responses to novel stimuli which typically habituate therefore representing sensitization and habituation.

The results of the present study in which females did not prefer male calls with noise over the HN or LN stimuli may reflect the effects of sensitization and habituation. In the absence of stream noise, higher signal-noise ratio calls are easier to process and easier for females to perceive, although this condition does not normally occur in their natural habitat. The response to HN and LN stimuli would be enhanced by sensitization to novel stimuli and by the advantage such stimuli would have for female perception. This idea is supported by the fact that female response time was longer in tests 1-2 than in test 3 and longer in tests 4-5 than in test 6 (Fig. 2), implying that female choice is more difficult when it involves novel calls with no added noise compared to female choice involving call pairs in which both contain running water noise added since such calls are typical in the natural habitat.

Taken together, our results demonstrate that stream noise can be a significant biological signal that is salient to females. Stream noise in the context of male vocalization may inform females about microhabitats in streamside species. Our data also provide experimental evidence supporting the idea that female mate choice is influenced by variation in ecological factors not strictly related to male phenotypes. Ecological variation is common in the field. Therefore this work can increase our understanding of how sexual selection influences female perception of mate attractiveness in complex and diverse environments.

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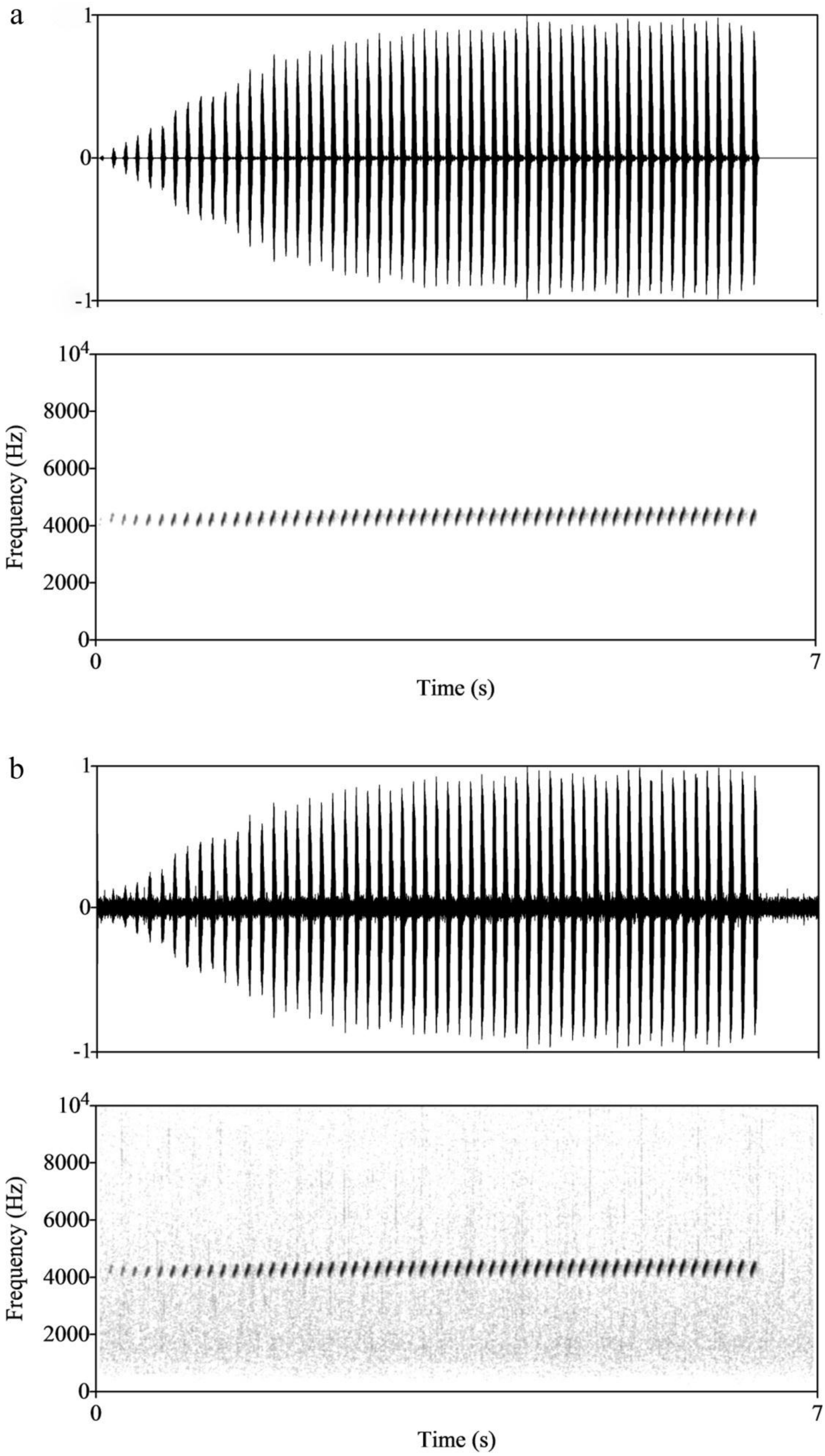
Figure 1(on next page)

Waveforms (top panel) and spectrograms (bottom panel) of the six acoustic stimuli used in this study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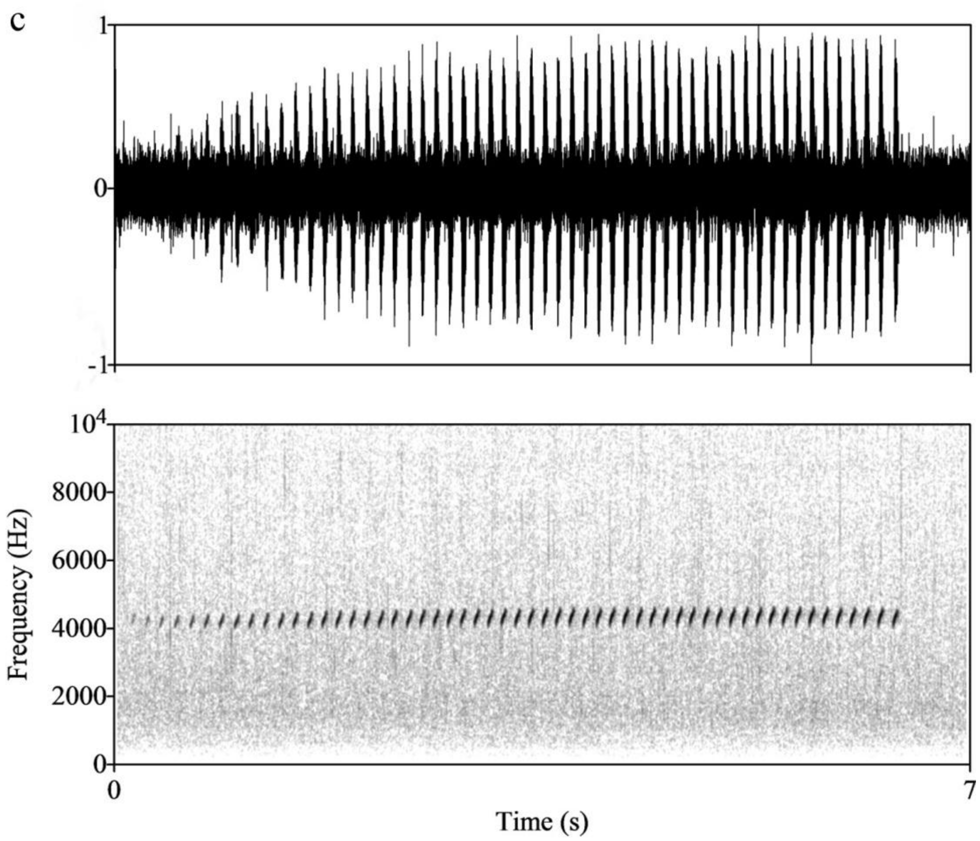
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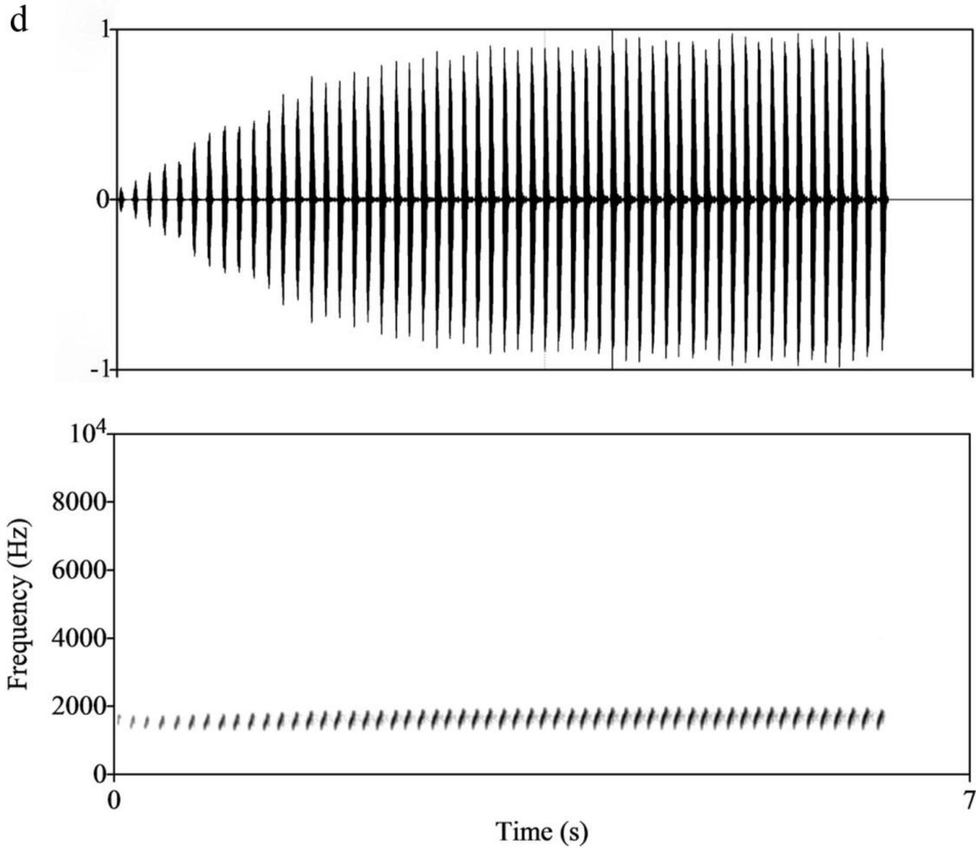
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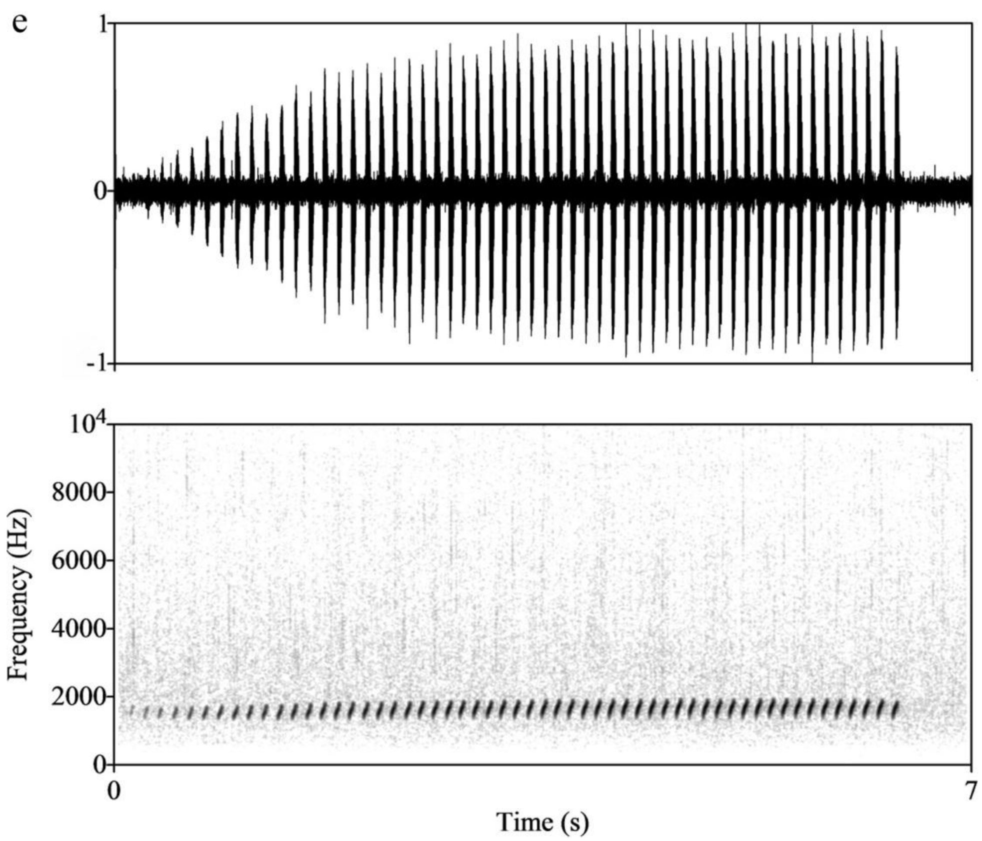
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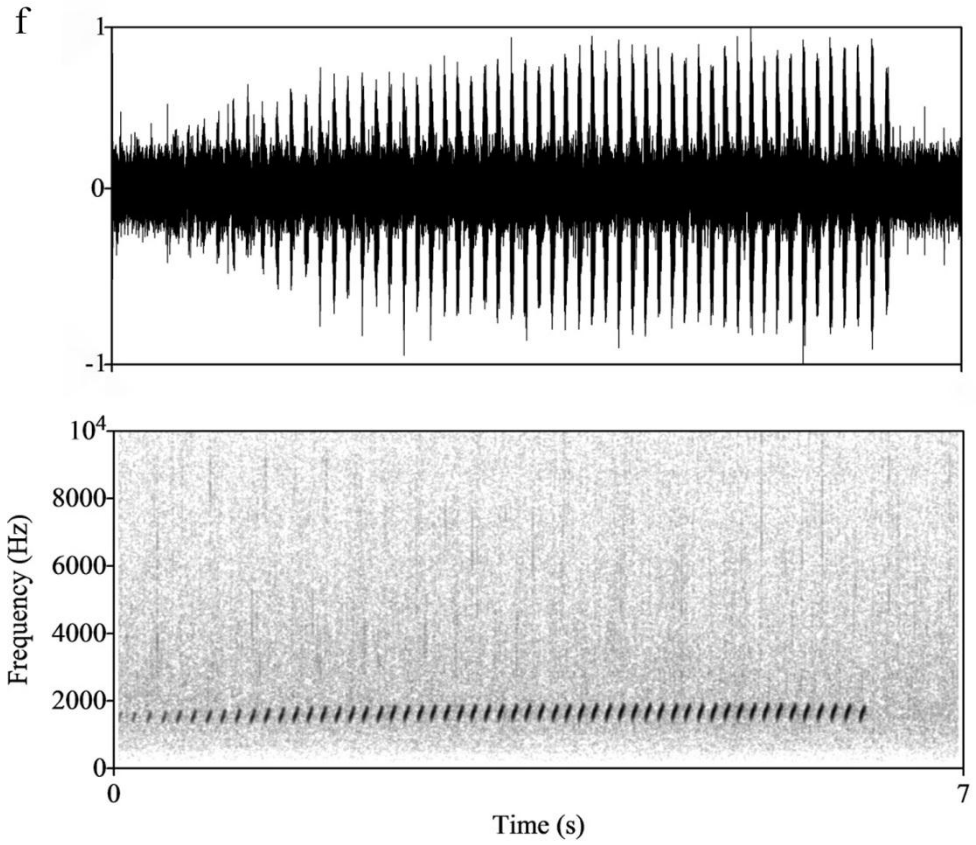
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Fig. 1 Waveforms (top panel) and spectrograms (bottom panel) of the six acoustic stimuli used in the female phonotaxis experiments. Experiment 1: a (HN), b (HL), c (HH); Experiment 2: d (LN), e (LL), f (LH). HN, high dominant frequency call with no noise added; HL, high dominant frequency call with low amplitude noise added; HH, high dominant frequency call with high amplitude noise added; LN, low dominant frequency call with no noise added; LL, low dominant frequency call with low amplitude noise added; LH, low dominant frequency call with high amplitude noise added.

Figure 2(on next page)

Female response time

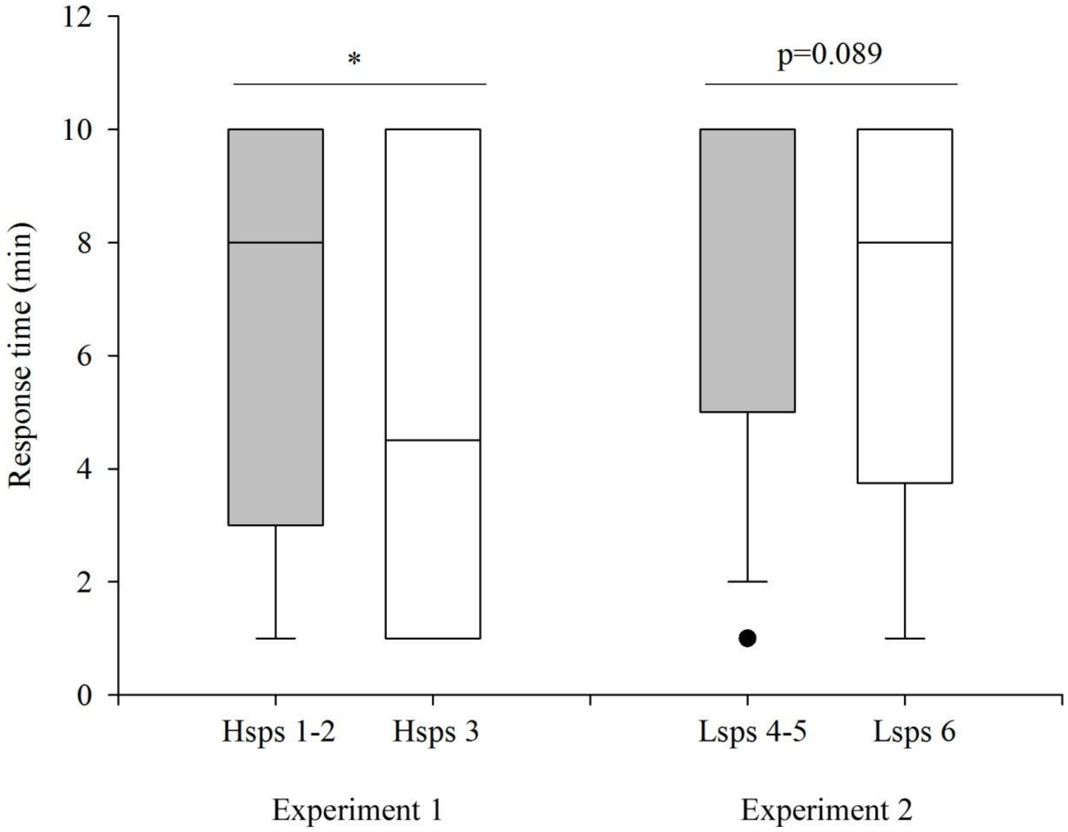

Fig. 2 Female response time in phonotaxis experiment 1 (Hsp 1-2, n = 146; Hsp 3, n = 38) and experiment 2 (Lsp 4-5, n = 159; Hsp 6, n = 38). Box plots show the median response with interquartile range and the 25th and 75th percentile. *$p < 0.05$. Hsps, high-frequency stimulus pairs of experiment 1; Lsps, low-frequency stimulus pairs of experiment 2.

Figure 3(on next page)

Proportions of females that met and did not meet the phonotaxis response criterion

Fig. 3 Proportions of females that met and did not meet the phonotaxis response criterion in the Hsps, Lsps and Rwsps experiments (Hsps, total n = 184; Lsps, total n = 197; Rwsps, total n = 171). *p < 0.05. n.s., not statistically significant. Hsps, high-frequency stimulus pairs of experiment 1; Lsps, low-frequency stimulus pairs of experiment 2; Rwsps, the running water stimulus pairs of experiment 3.

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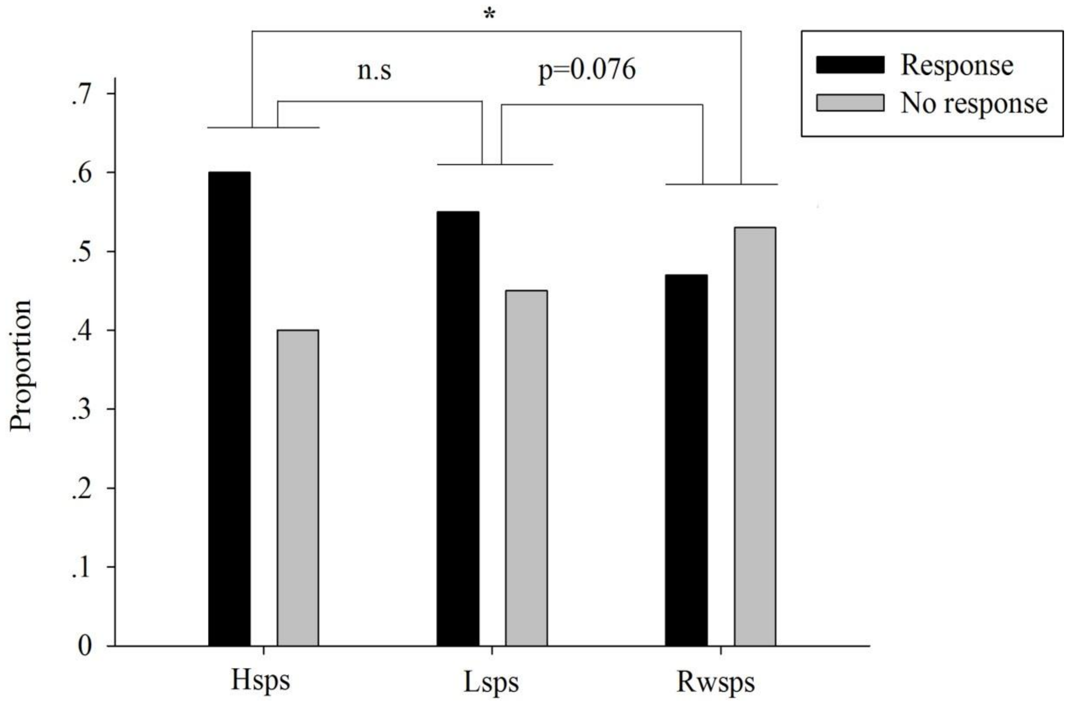

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Table 1(on next page)

Table 1. All eight stimulus pairs constructed in this study.

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Stimulus pairs	Stimulus 1		Stimulus 2	
	Frequency type	Signal/noise	Frequency type	Signal/noise
1	high-frequency	8:1	high-frequency	/
2	high-frequency	2:1	high-frequency	/
3	high-frequency	2:1	high-frequency	8:1
4	low-frequency	8:1	low-frequency	/
5	low-frequency	2:1	low-frequency	/
6	low-frequency	2:1	low-frequency	8:1
7	running water	/	white noise	/
8	running water	/	silence	/

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Table 2(on next page)

Table 2. Summary of outcomes from the phonotaxis tests of experiments 1-3.

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Table 2. Summary of outcomes from the phonotaxis tests of experiments 1-3.

		Stimuli		Choices		
Experiment	Test	A	B	A	B	*P*
1	1	HL	HN	22	20	0.663
	2	HH	HN	19	22	0.508
	3	HH	HL	18	9	0.014
2	4	LL	LN	19	22	0.508
	5	LH	LN	20	22	0.663
	6	LH	LL	16	9	0.044
3	7	RW	WN	20	20	1.000
	8	RW	S	16	24	0.074

Note: The choices represent the number of females attracted to each stimulus in each experiment in each test. Statistical p values are the probability of rejecting the null hypothesis using the Pearson chi-square or Fisher's exact tests. HN, high dominant frequency call with no noise added; HL, high dominant frequency call with low amplitude noise added; HH, high dominant frequency call with high amplitude noise added; LN, low dominant frequency call with no noise added; LL, low dominant frequency call with low amplitude noise added; LH, low dominant frequency call with high amplitude noise added; RW, the running water; S, silence.

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