



Heterospecific Vocal Interactions in a Frog from the Southern Temperate Forest, *Batrachyla taeniata*

Mario Penna & Nelson Velásquez

Program of Physiology and Biophysics, University of Chile, Santiago, Chile

Correspondence

Mario Penna, Program of Physiology and Biophysics, University of Chile, Independencia 1027, Santiago 70005, Chile.
E-mail: mpenna@med.uchile.cl

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Abstract

Animals using sound communication employ different strategies to overcome interferences from biotic and abiotic sources. However, interactions among acoustically active species have been studied to a very limited extent. The evoked vocal responses of 20 male frogs *Batrachyla taeniata* from the temperate austral forest in Chile were tested with conspecific calls and with the calls of two sympatric species: *B. antartandica* and *B. leptopus*, broadcast at amplitudes of 73, 79, 85, 91 and 97 dB peak SPL. The subjects responded actively to the conspecific call, but only responded weakly to the call of *B. leptopus* at the highest intensity. The preferential responses to conspecific calls could contribute to the typical segregation in monospecific choruses observed in areas where these frogs breed in sympatry.

Introduction

Animals that use sound communication in natural terrestrial environments have developed different mechanisms functional in overcoming interference from noise of biotic and abiotic sources. In the long-term range, vertebrates communicating in natural and urban environments have been reported to produce vocalizations having spectra detuned from the range of the background noise (Dubois & Martens 1984; Feng et al. 2000, 2006; Slabbekoorn & Peet 2003). In the short-term range, various vertebrates increase the amplitude of their vocalizations in the presence of natural or synthetic background noise (e.g. Sinnot et al. 1975; Cynx et al. 1998; Brumm & Todt 2002; Pytte et al. 2003; Brumm 2004). Increases in emission rate and duration of vocalizations also occur in similar circumstances (Potash 1972; Lengagne et al. 1999; Brumm 2004). However, noise interference can also produce decrements in the vocal activity of diverse animals. For instance, reductions in calling rates or adjustments in the timing of vocal emissions to intervals when there is no ongoing interference have been reported for birds

(Popp et al. 1985; Popp & Ficken 1987; Brumm 2006) and soniferous insects (Greenfield 1988; Römer et al. 1989).

Anurans also exhibit different strategies in confronting noises of different nature. Increments and decrements in vocal activity during exposures to natural biotic and abiotic (Schwartz & Wells 1983a,b; Páez et al. 1993; Penna et al. 2005; Penna & Hamilton-West 2007; Wong et al. 2009) as well as to anthropogenic noises (Sun & Narins 2005; Lengagne 2008; Kaiser & Hammers 2009) occur in different species.

Interference of biotic origin arising from acoustic interactions among different anuran species has a widespread occurrence in natural breeding aggregations; however, this ubiquitous phenomenon has been subjected to limited systematic research endeavors.

Contrasting results have also been reported for the responses of animals exposed to this type of interference. Increases in calling activity when presented with calls of sympatric species occur in Central American hyliid frogs which respond augmenting their call rate and synchronizing their responses with

the stimuli (Schwartz & Wells 1984, 1985). Central American frogs *Physalaemus pustulosus* give vocal responses to calls of various congeneric species (Bernal et al. 2007) and to a non-related species as well (Phelps et al. 2006). In contrast, a decrease in calling activity during exposure to heterospecific anuran calls has been reported for other frogs (Littlejohn & Martin 1969; Wong et al. 2009).

The origin and adaptive significance of these different strategies in confronting heterospecific acoustic interference remain unresolved issues, and diverse interpretations for these phenomena have been put forward: responsiveness to heterospecific signals has been interpreted as a means of competition for limited resources (Schwartz & Wells 1984) and as eavesdropping in a predator detection context (Phelps et al. 2006). On the other hand, the suppression or relative low vocal activity in the presence of heterospecific calls has been considered a means to avoid interference (Littlejohn & Martin 1969; Wong et al. 2009) or a mechanism for building up conspecific aggregations (Pfennig et al. 2000).

Frogs *Batrachyla* in southern Chile produce advertisement calls composed of short pulses repeated in species-specific patterns (Barrio 1967; Penna & Veloso 1990; Penna 1997). *Batrachyla antartandica*, *B. leptopus* and *B. taeniata* overlap their geographic distributions extensively in the austral temperate forest region; however, in areas of sympatry, these frogs typically conform conspecific choruses, mixed aggregations being a rare occurrence. Playback experiments examining the selectivity of evoked vocal responses for temporal parameters of sound have revealed divergent preferences for the three species (Penna 1997; Penna et al. 1997; Solís & Penna 1997). In the current study, we explored the responsiveness of male frogs of *B. taeniata* to heterospecific when compared with conspecific advertisement calls, searching for preference patterns that would promote the establishment of monospecific chorusing assemblages observed in nature.

Methods

Study Site

The study was conducted during 2008, from March 18 through 28 at the locality of Tinquilco (39°47'S, 71°46' W, altitude 850 m above sea level), in the vicinity of Huerquehue National Park in southern Chile. The study site was on the shore of Tinquilco lake, in a forest where *Drymis winteri* was the predominant tree. Frogs called from the ground, hidden

underneath fallen *D. winteri* leaves or logs and from inside crevices among *D. winteri* roots.

Experimental Protocol and Stimuli

Playback experiments were conducted nightly between 2100 and 0300 h. Spontaneous vocal activity of each subject was recorded for 2 min approximately, prior and after playback presentations. The loudspeaker through which the stimulus was broadcast was positioned at an average distance of 60 cm (range 55–80 cm) from the experimental subjects. The air and substrate temperatures, measured during recordings with a Digisense 8528-20 thermometer, were on average 12.0°C (range 9.8–14.0°C) and 13.4°C (range 10.5–16.8°C), respectively, and the relative humidity 85% (range 76–86%). Fifteen experimental subjects captured after completing the playbacks had an average weight of 2.5 g (range 2.1–2.9 g) and a snout-vent length of 36 mm (range 34–38 mm).

Stimuli were synthetic imitations of the advertisement calls of *Batrachyla taeniata*, *B. antartandica* and *B. leptopus* made with the Soundmaker 1.0.4 software (Ovolab, Torino, Italy). The stimuli were designed after the typical natural calls of these frogs. The temporal and spectral parameters were close to the average for calls of the three species at about the temperatures at the study sites and as reported in previous field studies (Penna 1997; Penna et al. 1997; Penna & Solís 1998). The elementary unit for the calls of the three species was a 5-ms pulse having rise and fall times of 1 and 4 ms, respectively, and a carrier frequency of 2 kHz. Figure 1 shows the time-wave and the power spectra of the synthetic calls of the three species. The call of *B. taeniata* consisted of 25 pulses repeated with an inter-pulse period of 20 ms. The first pulse had an amplitude of 25%, the second and last pulse an amplitude of 50% and the third pulse an amplitude of 75% relative to the pulses in the mid portion of the call. The total duration of the call was 485 ms (24 inter-pulse periods plus one pulse). The synthetic stimulus was 30-s long and it was obtained by repeating 20 calls with an inter-call period of 1.5 s. The call of *B. antartandica* consisted of 30 pulses repeated with an inter-pulse period of 667 ms. The initial pulse had a 50% of the amplitude of the following pulses and the total duration of the call was 19,348 ms (29 inter-pulse periods plus one pulse). Because of its long duration, a single synthetic call of *B. antartandica* was presented per trial. The call of *B. leptopus* had a more complex temporal structure, namely, it consisted of

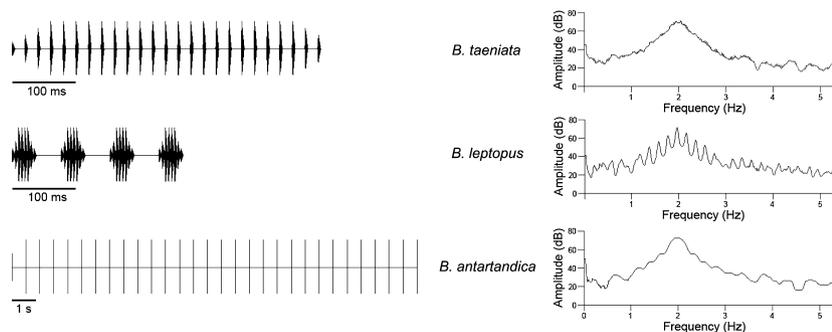


Fig. 1: Synthetic calls of *Batrachyla taeniata*, *B. leptopus* and *B. antartandica*.

four notes, each having a duration of 40 ms, containing eight pulses repeated with an inter-pulse period of 5 ms and separated by inter-note intervals of 40 ms. The initial and final pulses of each note had an amplitude of 25%, the second and seventh pulse had an amplitude of 50% and the four central pulses had a 100% amplitude. The total duration of the call was 280 ms. The synthetic stimulus was 25-s long and it was obtained by repeating 20 calls with an inter-call period of 1.25 s. The bouts of stimuli of the three species were repeated successively, leaving 60-s intervals in between presentations.

Stimuli were broadcast with a portable compact disc player (Sony D-E356 CK, Sony Electronics, Inc., San Jose, CA, USA) connected to a custom-made impedance-matched operational amplifier, attenuators (Hewlett-Packard 355 C and D, Hewlett-Packard, Loveland, CO, USA), a power amplifier (Alpine 3540, Alpine Electronics of America, Torrance, CA, USA) and a 10-cm diameter loudspeaker, positioned 0.8–1.0 m in front of the experimental subject. Evoked vocal responses (EVRs) were recorded with a directional microphone (Sennheiser ME 66, Sennheiser Electronic GmbH & Co., KG, Wedemark, Germany), the tip of which was placed 0.2–0.4 m in front of the subject. EVRs were recorded on the left channel of a cassette recorder (Sony TC-D5M, Sony Electronics, Inc., San José, CA, USA). The line output of the acoustic stimulus was recorded on the right channel of this recorder.

Before starting recordings, the amplitude of the three stimuli at the position of the experimental subject was adjusted with the attenuator to 85 dB SPL (peak) by placing the microphone of a sound-level meter (Bruel & Kjaer 2230, Brüel & Kjaer Instruments, Inc., Boston, MA, USA; linear weighting scale) just above the frog position, making efforts to avoid disturbing the animal. This SPL was within the range of amplitudes of the calls of nearest neigh-

bors at the position of focal subjects (Penna & Solís 1998; M. Penna and R. Solís, unpublished data). The fast RMS SPLs of the synthetic calls of *B. taeniata*, *B. leptopus* and *B. antartandica* were 16, 15 and 23 dB below their peak values, respectively.

To avoid interferences during the playback experiments, nearby neighbors were silenced by capturing or disturbing them with gentle vibrations of the substrate. The basal calling activity of the experimental subject was recorded during an interval of two minutes approximately, after which a bout of the conspecific stimulus was presented, and if the frog responded, the playback experiment proceeded thereafter. The experimental sequence started with a series of synthetic calls of the three species presented at 85 dB SPL. Subsequently, series of stimuli with the heterospecific synthetic calls at different levels were presented in an order of increasing amplitude: 73, 79, 91 and 97 dB SPL, using the corresponding attenuator settings. Bouts of conspecific synthetic calls at 85 dB SPL were presented before and after two consecutive heterospecific stimuli to compare the responses to these different stimuli at a proximate time. At the end of the experimental sequence, the basal calling activity of the experimental subject was recorded as at the beginning of the experiment, during an interval of about two minutes. The total duration of the experimental sequence from the onset of the initial conspecific bout of synthetic calls to the end of the final conspecific bout of synthetic calls was 23 min and 15 s. The heterospecific synthetic calls were broadcast following two presentation orders: for 10 frogs the sequence was *B. leptopus* first, *B. antartandica* second, and for the other 10 subjects the presentation followed the reverse order. For graphical representation and for the statistical analysis performed (see below), the correspondence of the intervals preceding the synthetic heterospecific calls was maintained, so that the silent interval

preceding the bout of synthetic calls of *B. leptopus* and that of the synthetic call of *B. antartandica* were labeled silent interval 2 and 3, correspondingly, irrespective of the actual presentation order of the stimuli of each species.

Upon completion of the recordings, substrate and air temperature and relative humidity were measured and whenever possible, the experimental subjects were captured and their snout-vent lengths (SVLs) and body weights were measured.

The measures applied to the evoked vocal responses were call rate (calls/min) and call duration (ms). The two measures were computed for calls produced by the experimental subject in response to bouts of synthetic calls of *B. taeniata* and *B. leptopus*, to a single call of *B. antartandica* and to the no-stimulus ('silent') intervals in between presentations of stimuli of the three species. The time interval during which responses to a bout of calls of *B. taeniata* and *B. leptopus* were considered to occur, started at the onset of the first stimulus of the bout and ended 1.5 and 1.25 s (the corresponding stimulus repetition periods) after the onset of the 20th stimulus repetition (30 and 25 s, respectively). The time interval during which responses to the *B. antartandica* call were computed started at the onset of the first pulse of the stimulus and ended 667 ms (the pulse repetition period) after the onset of the 30th pulse (20 s).

Recordings of frog vocalizations and stimuli were digitized with a Motu 828 interface and a Macintosh G4 computer using Peak 4.0 software (Bias, Inc., Petaluma, CA, USA), at a sampling rate of 44 kHz. Onset and end times of evoked calls and stimuli were measured with Signalyze 3.12 software (Infosignal, Inc., Charlestown, MA, USA). The call's dominant frequency during the initial period of basal activity was measured from power spectra (0–5500 Hz, frequency resolution: 20 Hz).

We used General Linear Model (GLM) statistics. Logarithmic and square-root transformations were applied to some data sets to attain normality criteria. We carried out five kinds of statistical analyses. First, the dependence of call rate and call duration on air and substrate temperature and of dominant frequency on weight and SVL was explored with GLM multiple regressions ($p < 0.05$). Second, GLM repeated-measures ANOVAs ($p < 0.05$) were used to compare the basal calling activity during the initial and last 2 min of vocal recording. Third, GLM repeated-measures ANOVAs ($p < 0.05$) were performed on the vocal responses to the six bouts of conspecific calls, to test the hypotheses that vocal

activity did not change during the experiment as an effect of repeated stimulation. Fourth, GLM one-way ANOVAs ($p < 0.05$) were used to compare vocal responses to one heterospecific call when it was presented either before or after the other heterospecific call. For these comparisons, the differences in call rate and call duration evoked by a stimulus bout and the preceding silence were computed, and compared between the two sequences of stimuli presentation. Fifth, GLM repeated-measures ANOVAs ($p < 0.05$) were used to compare vocal responses to conspecific and heterospecific calls. For this analysis, responses among six time intervals: the intervals of presentation of a bout of *B. taeniata* synthetic call and the two following heterospecific call stimuli, and the silent intervals preceding each of these three stimuli. Five of such GLM repeated-measures ANOVAs were performed, one for each series of heterospecific stimuli presented at intensities of 85, 73, 79, 91 and 97 dB SPL. Post-hoc comparisons among the six time intervals (three bouts of stimuli and their corresponding preceding silences) were performed using Tukey tests ($p < 0.05$).

Results

Basal Activity

Previous to the presentation of the series of stimuli, the calls produced by the experimental subjects were recorded during an average interval of 194.8 s (range 39–319 s). Ten frogs did not call during the initial time interval. For the 10 frogs that called, the average call rate was 10.6 calls/min (range 1.1–26.7 calls/min) and the average call duration was 419 ms (range 307–452 ms). Upon completion of the experimental series, the basal vocal activity was recorded again during an average interval of 152.4 s (range 105–206 s). Fourteen frogs called during this time interval. The dominant frequency was measured for the 20 experimental subjects in the calls emitted in response to the first bout of the conspecific stimulus, and yielded an average of 2060 Hz (range 1816–2266 Hz).

The dependence of call rate and call duration on air or substrate temperature for the 10 males that called during the initial period of basal activity recording was explored with GLM multiple regressions. Call rate was significantly related ($F_{2,9} = 4.79$, $p = 0.04900$), but call duration was not related ($F_{2,9} = 2.40$, $p = 0.15300$) to these environmental factors. Dominant frequency was not dependent on weight or SVL, as examined for the 15 experimental

subjects that were captured (GLM multiple regression: $F_{2,14} = 0.03$ and $p = 0.96900$).

Call rate and call duration, analyzed for 19 of 20 experimental subjects (one individual stopped responding after the first experimental series, see below), did not differ between the initial and final periods of recording of basal activity (GLM repeated measures ANOVA: $F_{1,18} = 0.96$, $p = 0.34067$ and $F_{1,18} = 1.36$, $p = 0.25825$, respectively).

Evoked Vocal Responses to Synthetic Calls

All 20 frogs responded to the initial bout of 20 repetitions of the conspecific stimulus with an average call rate of 29.2 calls/min (range 8.0–50.2 calls/min) and an average call duration of 511 ms (range 345–687 ms) and gave similar responses to subsequent presentations of bouts of the conspecific stimulus throughout the experimental sequence. Call rate and call duration evoked during the presentation of the six bouts of conspecific stimuli did not differ significantly (GLM repeated measures ANOVA: $F_{5,90} = 0.38$, $p = 0.85987$ and $F_{5,90} = 1.17$, $p = 0.33139$, respectively).

One frog ceased responding after the presentation of the second bout of conspecific stimuli and thus only its responses to the first series of stimuli – presented at 85 dB SPL – were computed. In addition, two experimental subjects did not respond to the presentation of two bouts of conspecific stimuli (one frog to bouts 2 and 3 and the other to bouts 4 and 6), one experimental subject did not respond to bout 3 and another to bout 5.

In general, no differences occurred between evoked vocal responses to the corresponding stimuli presented in the two experimental sequences in which the presentation of the heterospecific calls was reversed. Just one significant difference in call duration occurred between the two sequences for the *B. leptopus* stimulus presented at 73 dB SPL. In this case, call rate and call duration were larger for the sequence in which the synthetic call of this species was presented first (GLM One-way ANOVAs $F_{1,17} = 5.58$, $p = 0.03033$ and $F_{1,17} = 13.31$, $p = 0.00199$, respectively).

Responses to the heterospecific calls occurred only at the higher intensities. EVRs of the experimental subjects differed significantly in terms of call rate and call duration among stimuli and inter-stimuli intervals within each of the five experimental series (GLM repeated measures ANOVAs, Table 1, Fig. 2).

The frogs responded to the conspecific stimulus with call rates significantly higher than those pro-

duced during the three silent intervals and during the presentation of the heterospecific calls in the five experimental series. The call rate in response to the *B. leptopus* call during the experimental series with heterospecific calls at 91 dB SPL was significantly higher than that during silent intervals S1 and S2, and that during the series with heterospecific calls at 97 dB SPL was significantly higher than that during the three silent intervals (Table 1). The call rate in response to the *B. antartandica* call during the experimental series with heterospecific calls at 79 dB SPL was significantly higher than that during silent interval S1 and that during the series with heterospecific calls at 97 dB SPL was significantly higher than that during S1 and S3.

The frogs also responded to the conspecific stimulus with calls having durations longer than those produced during the three silent intervals and in response to the call of *B. antartandica* in the five experimental series. Duration of calls in response to the conspecific stimulus was longer than that in response to the call of *B. leptopus* in the first three experimental series (heterospecific calls at 85, 73 and 79 dB SPL), but no significant differences between the two stimuli occurred in the experimental series in which the call of *B. leptopus* was presented at 91 and 97 dB SPL. In addition, the call of *B. leptopus* at 97 dB SPL evoked calls having longer duration than those produced during the three silent intervals (Table 1, Fig. 2).

Discussion

The consistency and persistence of the vocal activity evoked by the conspecific call in males of *B. taeniata* indicate that the experimental conditions chosen approximate those of natural interactions in breeding aggregations. The lack of responses to heterospecific calls presented at low to moderate levels reveal a condition different from other frogs which respond to heterospecific calls to a lesser extent than conspecific calls, but at calling levels higher than those observed during intervals in which no stimuli are presented (Bernal et al. 2007; Phelps et al. 2006). Only at the two higher intensities employed, the *B. leptopus* stimulus evoked an activity different from that of silent intervals in terms of call rate and at the highest intensity, there was a clear increase in call duration, relative to the silent intervals. The *B. antartandica* stimulus also evoked a higher call rate relative to that of silent intervals at 79 and 97 dB SPL. The relatively restricted increase in calling activity to the *B. antartandica* stimulus at high inten-

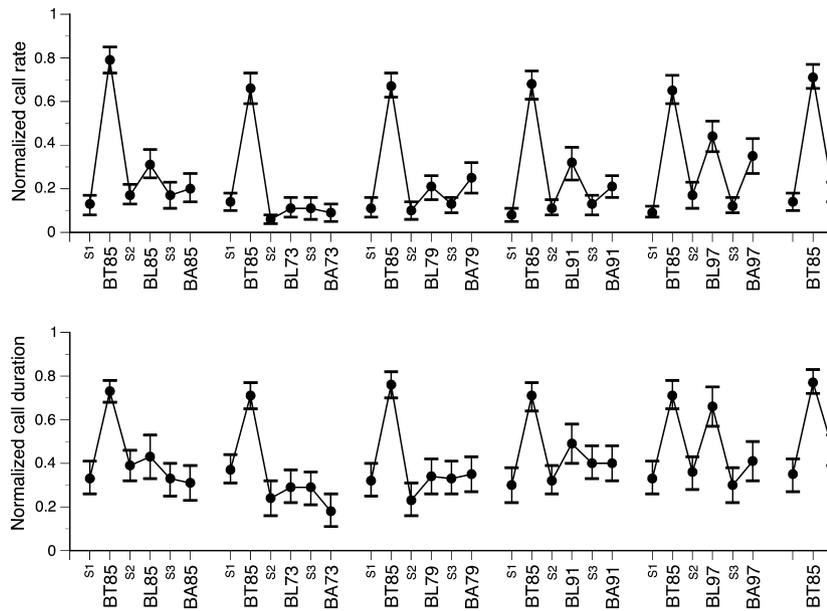


Fig. 2: Normalized call rate and call duration of males of *Batrachyla taeniata* during the sequence of presentation of conspecific and heterospecific calls and during 1-min inter-stimuli intervals. The two measures of evoked call response were normalized to the maximum response for each individual. Namely, the value of call rate and duration for a given subject in response to a particular bout of stimuli or silent interval was divided by the maximum value of that measure produced by the frog to any bout of stimuli and multiplied by 100. Filled circles correspond to averages and bars to standard errors. Stimuli abbreviations: BT: *Batrachyla taeniata*, BA: *B. antartandica*, BL: *B. leptopus*.

sounds. In fact, studies in Central American hylids have reported contrasting results with exposure to heterospecific calls within the same species. Exposures to prolonged and intense chorusing noise lacking a fine temporal structure produce suppression of vocalization by males of *Hyla ebraccata* (Schwartz & Wells 1983a,b), whereas heterospecific signals having stereotyped temporal structure elicit evoked calling by this frog and *H. microcephala* (Schwartz & Wells 1984, 1985). Interestingly, our results with *B. taeniata* show an opposite trend; temporal patterned heterospecific signals do not elicit vocal responses, whereas continuous prolonged noise causes vigorous responses (M. Penna and D. Zúñiga, in preparation). An adaptive interpretation for this contrast could be proposed, considering that in the tropics noise sources of biotic origin, likely having temporal structured patterns, typically predominate. By contrast, in temperate environments, noises of abiotic sources generally lacking a fine or stereotyped temporal structure have a larger importance relative to abiotic noises.

The current study contributes to the relatively overlooked issue of the diversity of response strategies to interfering biotic sounds produced by related taxa, and complements recent research on the influence of the abiotic sound environment on anuran

sound communication (Narins et al. 2004; Penna et al. 2005; Feng et al. 2006; Penna & Hamilton-West 2007).

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