

Restricted responsiveness to noise interference in two anurans from the southern temperate forest

Mario Penna  | Javiera Cisternas | Jessica Toloza

Programa de Fisiología y Biofísica, Facultad de Medicina, Instituto de Ciencias Biomédicas, Universidad de Chile, Santiago, Chile

Correspondence

Mario Penna, Programa de Fisiología y Biofísica, Facultad de Medicina, Instituto de Ciencias Biomédicas, Universidad de Chile, Santiago, Chile.
Email: mpenna@med.uchile.cl

Funding information

FONDECYT, Grant/Award Number: 1140014

Editor: S. Foster

Abstract

Animals adopt different strategies to communicate by means of sound in noisy environments such that some species increase, while others decrease their vocal activity in the presence of interference. Anuran amphibians from diverse latitudes exhibit both kinds of responses. Recent studies have shown that males of *Batrachyla taeniata* and *Batrachyla antartandica* from the temperate austral forest do not call in response to the presentation of advertisement calls of sympatric congeneric species. In contrast, *Batrachyla leptopus* responds to these signals in a similar way as to conspecific calls. The responsiveness of *B. taeniata* to natural abiotic interference has also been tested and found that noises of such sources produce strong increases in vocal activity. To assess the diversity in responsiveness to acoustic intrusion in this group, we exposed males of *B. leptopus* and *B. antartandica* to prolonged pre-recorded natural abiotic noises of wind, creek, rain, and to a band-pass noise centered at 2,000 Hz, at 67 dB Sound Pressure Level (SPL). The subjects did not increase their vocal activity significantly when exposed to these sounds and to band-pass noise at increasing intensities (55–79 dB SPL). These results contrast with the increase in vocal activity observed previously in *B. taeniata* to continuous abiotic noise and point to the existence of diverse strategies to confront acoustic intrusion among related species. The lack of vocal activation observed also contrasts with the responsiveness of *B. leptopus* to heterospecific signals, but parallels the lack of response to such sounds in *B. antartandica*. Furthermore, the results obtained contrast with the responsiveness of these species to synthetic prolonged sounds observed in previous studies, suggesting that the modes of responses to acoustic intrusion may depend on previous experience, rather than having a species-specific nature.

KEYWORDS

abiotic noise, acoustic interference, anurans, austral temperate forest, sound communication

1 | INTRODUCTION

Sound-communicating animals are subjected to interference from different biotic and abiotic natural sound sources and employ different strategies to confront such intrusions. In the spectral domain, different animals living in syntopy often produce signals tuned to non-overlapping frequency bands (e.g., Ellinger & Hödl, 2003;

García-Rutledge & Narins, 2001; Lenske & La, 2014; Luther, 2009; Schmidt, Römer, & Riede, 2013). Also animals living in environments with permanent abiotic noise sources like creeks or seashores, characterized by low-frequency contents, produce calls having relatively high frequencies, shifted from the background noise range (Douglas & Conner, 1999; Dubois & Martens, 1984; Goutte et al., 2016; Vargas-Salinas & Amezcua, 2013), and the spectral shifts produced

can even reach the ultrasound range (Feng et al., 2006). In the temporal domain, interference from syntopic heterospecific signalers causes transitory reductions in the sound output in a number of species (Brumm, 2006; Brumm & Slabbekoorn, 2005; Greenfield, 1988, 1988; Hart, Hall, Ray, Beck, & Zook, 2015; Latimer & Broughton, 1984; Littlejohn & Martin, 1969; Luther, 2008, 2009; Popp, Ficken, & Reinartz, 1985; Römer, Bailey, & Dadour, 1989; Römer et al., 1989; Schatral & Yeoh, 1990; Stanley, Walter, Venkatraman, & Wilkinson, 2016; Wong, Parada, & Narins, 2009; Zelick & Narins, 1983), although in some cases, increases in call rates have been reported (Symes, Page, & ter Hofstede, 2016). The predominant effect of reduction in acoustic output results in restriction of acoustic emissions to intervals during which the interfering signalers are silent (Brumm, 2006; Greenfield, 1988; Römer et al., 1989).

A reduction in vocal activity during noise exposures would limit energy expenditure to periods during which background levels are lower (e.g., Brumm, 2006; Ophir, Schrader, & Gillioly, 2010). In contrast, increases in amplitude, emission rate, or spectral shifts of vocalizations would result in a preservation of the active space over which animals communicate (e.g., Brumm & Slabbekoorn, 2005).

Frogs from diverse environments use different strategies to confront interference from natural biotic, abiotic, and anthropogenic origin. Some species augment, while others decrease their vocal output when subjected to prolonged exposures to noises of different kinds (Cunnington & Fahrig, 2010; Kaiser & Hammers, 2009; Kaiser et al., 2011; Lengagne, 2008; Love & Bee, 2011; Penna & Hamilton-West, 2007; Penna, Pottstock, & Velásquez, 2005; Sun & Narins, 2005; Vargas-Salinas & Amezcuita, 2013; Vargas-Salinas, Cunnington, Amézquita, & Fahrig, 2014). In particular, in the temperate austral forest, two frogs of the genus *Eupsophus*, inhabiting the same microenvironment, respond differently to noise exposures of moderate to high levels under similar test conditions. The vocal activity of *Eupsophus calcaratus* is enhanced (Penna et al., 2005), whereas *E. emiliopugini* does not alter or decreases its vocal responses when exposed to the same battery of noises (Penna & Hamilton-West, 2007).

Natural abiotic noises are an important component of austral temperate forest night sound environments due to a restricted number of syntopic vocalizing anuran species, as compared to tropical habitats (Penna & Veloso, 1990). Abiotic noises differ in their spectral structure: Wind and sea surf contain predominantly low frequencies and creek and rain relatively high energy in a mid-frequency range. Also, rain has larger amplitude modulations relative to the other noises. The two noises containing higher energy in the mid-frequency range, overlapping the spectral range of frog calls, are more effective to evoke calling in *E. calcaratus* (Penna et al., 2005).

Frogs of the genus *Batrachyla* are distributed throughout the temperate austral forest region, where they breed from the end of the summer through early autumn. Their advertisement calls are composed of short (about 5 ms) pulses produced at different repetition rates depending on the species (Penna & Veloso, 1990). Playback studies have shown that three species of this genus respond in different ways to biotic interference from heterospecific calls. Males of *B. taeniata* and

B. antartandica respond preferentially to conspecific relative to heterospecific signals (Penna & Meier, 2011; Penna & Velásquez, 2011), while *B. leptopus* responds similarly to both kinds of signals over a wide amplitude range (Penna & Toloza, 2014). Furthermore, a recent study (Penna & Zúñiga, 2014) has shown that *B. taeniata* responds with remarkable increases in its vocal activity to interference of continuous abiotic noise, in contrast with the decrease in the vocal output amid interference from heterospecific signals reported formerly for this species (Penna & Velásquez, 2011).

In this study, we evaluate the effects of continuous noises of abiotic origin and a band-pass noise centered at the typical frequency of the calls of *Batrachyla* on the vocal responses of *B. leptopus* and *B. antartandica*, allowing comparisons with the responses to stereotyped biotic signals studied previously in these species. In particular, the similarity of the responsiveness to biotic signals by males of *B. antartandica* and *B. taeniata*, with evoked calling selective for conspecific calls (Penna & Meier, 2011; Penna & Velásquez, 2011), suggests that when confronted with prolonged abiotic noise, the untested species will respond with vocal activation, as *B. taeniata* does in the presence of this intrusion (Penna & Zúñiga, 2014). Such a response would point to a common strategy to confront interference from noises of different origin in related species. The exploration of responsiveness to prolonged abiotic noise in *B. leptopus*, a species that differs from the other two in its reaction to biotic interference, responding to conspecific as well as to heterospecific signals, is an opportunity to learn how different strategies in exposures to biotic interference are related to tactics used when facing acoustic interference of abiotic origin. Because it is not known how the two species of *Eupsophus* that respond to continuous abiotic noise differently (Penna & Hamilton-West, 2007; Penna et al., 2005) react to heterospecific signals, an overview of responses to noises of biotic and abiotic nature is not available for these anurans.

By extending the exploration of the responses of two other species to abiotic noise interference, we sought to contribute an assessment of the adaptive values of different strategies for confronting acoustic intrusion. In recent years, numerous studies exploring the effect of anthropogenic noise on sound-communicating animals have been published (e.g., Barber, Crooks, & Fristrup, 2010; Lampe, Reinhold, & Schmoll, 2014; Luther & Derryberry, 2012). Also, assessments of the relevance of biotic components of acoustic environments for sound communication of different animals have been addressed (Hart et al., 2015; Stanley et al., 2016; Symes et al., 2016), and the relevance of biotic components of sound environments for evolutionary changes in sound communication systems has been extensively documented (Amézquita, Flechas, Lima, Gasser, & Hödl, 2011; Hoskin & Higgie, 2010; Okamoto & Grether, 2013). However, the relevance of natural abiotic noises for animal sound communication has been subjected to relatively limited explorations (e.g., Dunlop, 2016; Feng et al., 2006; Goutte et al., 2016; Vargas-Salinas & Amezcuita, 2013), in spite of their ubiquitous presence in evolutionary time and environments, which positions these sounds of different spectral and temporal structure as significant potential shapers of animal communication signals.

2 | MATERIALS AND METHODS

2.1 | Study site

The experiments with *B. leptopus* were conducted from Mar. 5, 2009, to Mar. 13, 2009, in Huerquehue (39°08'S, 71°42'W) in Southern Chile. The study site was located in a forest of *Podocarpus nubigenus* where males of *B. leptopus* called from inside crevices among mosses (*Rachomytrium* sp.) and ferns (*Hymenophyllum secundum* and *H. tortuosum*). Climbing plants (*Asteranthera ovata* and *Luzuriaga radicans*) were also abundant. At this site, a monospecific *B. leptopus* assemblage congregates typically every year.

The experiments with *B. antartandica* were conducted from Nov. 11, 2009, to Nov. 23, 2009, at La Picada (41°02'S, 72°30'W), within the Vicente Pérez Rosales National Park in Southern Chile. The study site was a bog of volcanic substrate, where males of *B. antartandica* called from inside crevices and small burrows along the borders of small streams or pools among vegetation composed mainly of mosses (*Rachomytrium* sp.), grasses (*Scyrcus* sp. and *Myrteola* sp.), and ferns (*Blechnum* sp.).

The intent of this study was to offer a comparison of the vocal activity of these two species under noise exposure with work published in an earlier manuscript on a related species (Penna & Zúñiga, 2014). The methods have been published in that article, but we repeat them, here, with slight textual modification to enable readers to judge the methods in this study without recourse to the earlier publication.

2.2 | Synthetic stimuli and noises

Synthetic calls imitating the advertisement calls of *B. leptopus* and *B. antartandica*, as reported in previous studies (Penna, 1997; Solís & Penna, 1997), were designed using SOUNDMAKER 1.0.4. software (Ovolab, Torino, Italy). The synthetic calls have been described in detail elsewhere (Penna & Meier, 2011; Penna & Toloza, 2014; Penna & Velásquez, 2011). Briefly, the elementary unit for the calls of the two species was a 5-ms pulse having rise and fall times of 1 and 4 ms, respectively, and a carrier frequency of 2 kHz, which is close to the average dominant frequency of the calls of the populations, was studied. The call of *B. leptopus* had a relatively complex temporal structure; namely, it consisted of four notes, each containing eight pulses repeated with an interpulse period of 5 ms. Internote intervals lasted 40 ms, and the total duration of the call was 280 ms. The call of *B. antartandica* consisted of 45 pulses repeated with an interpulse period of 667 ms, and the total duration of the call was 30 s. Because of its long duration, a single synthetic call of *B. antartandica* was presented per trial, and the synthetic call of *B. leptopus* was presented in bouts of 24 calls at an intercall period of 1.25 s. These call rates were within the ranges measured in natural aggregations (Penna, 1997). Figure 1 shows the waveform and spectra of these stimuli.

Stimuli were broadcast using the same instrumentation detailed in Penna and Velásquez (2011) and Penna and Meier (2011). Recordings of evoked vocal responses (EVRs) during Jan. 2009 were conducted using a directional microphone (Sennheiser ME 66), the tip

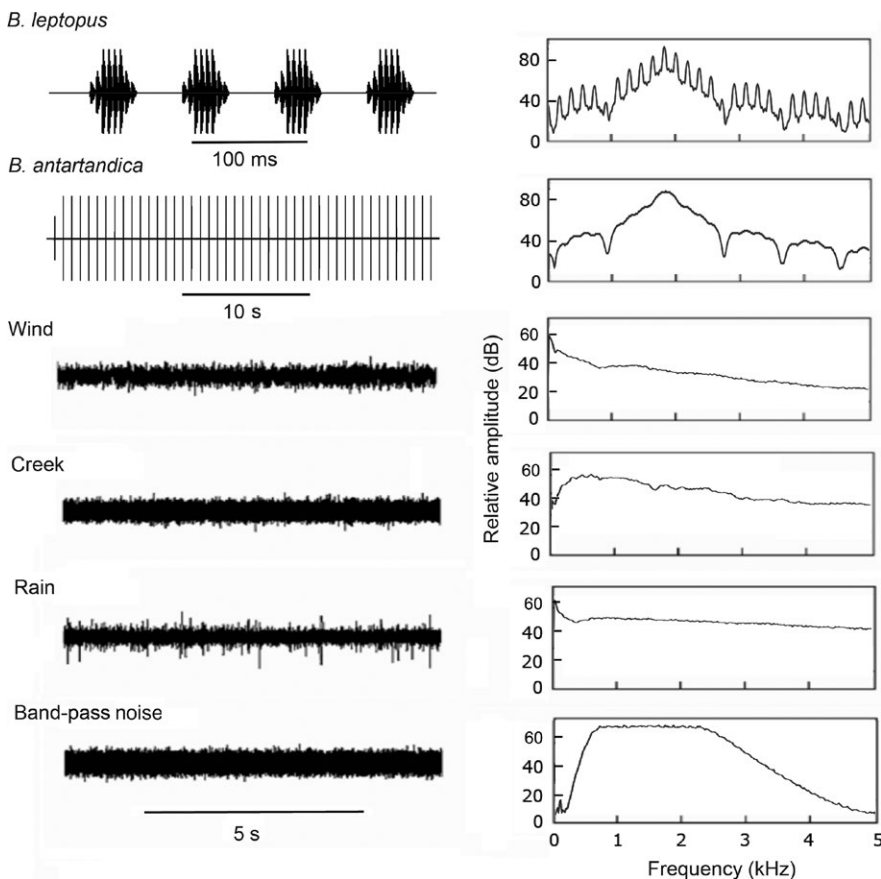


FIGURE 1 Oscillograms and power spectra of the synthetic advertisement calls of *Batrachyla leptopus* and *Batrachyla antartandica* and natural noises and a band-pass noise used to create the sound tracks presented to the experimental subjects. Power spectra of the synthetic call are averaged over 500 ms, and noise spectra are averaged over 10 s (bandwidth: 20 Hz)

of which was placed at 0.2–0.4 m in front of the subject and a digital tape recorder (Sony TC D10 PROII, Sony Electronics Inc., San José, California, USA). During Mar. 2011, the same microphone and a digital solid-state recorder (Tascam DR 100) were used.

Natural pre-recorded noises of wind, rain, and creek used in this study were the same used in previous field playback studies. The recording and editing procedures are described in Penna et al. (2005) and Penna and Zúñiga (2014). Briefly, recordings of these environmental sounds were carried out in the region where the study was conducted. Recordings were conducted in the absence of other interfering sounds with a sound level meter (Brüel & Kjaer 2230; Brüel & Kjaer Instruments, Boston, Massachusetts, USA), connected to a digital tape recorder (Sony TC D10 PROII). Segments of 10-s duration having spectra representative of each kind of noise were selected and pasted to obtain noise durations of 150 s. These noises were digitized as the recordings of vocal responses of the experimental subjects in this study (see subsection: Analysis of evoked vocal responses). In addition to the natural recorded sounds, a band-pass noise was obtained filtering a white noise between 1,000 and 3,000 Hz. This spectrum encompasses the dominant frequency range of the advertisement calls of *Batrachyla*. This noise was generated using a wave generator (WG1, Tucker-Davis Technologies) and a programmable filter (PF1, Tucker-Davis Technologies). The total duration of each noise was 150 s. Oscillograms and power spectra of the synthetic calls and of the noises are shown in Figure 1.

2.3 | Experimental protocols

Synthetic stimuli and noises were recorded on different channels of an audio player (iPod nano; Apple Computer Inc., Cupertino, California, USA), in successive tracks. On track 1, which lasted 120 s, the left channel contained no stimuli, and on the right channel, the first 30 s contained either 24 repetitions of the synthetic advertisement call of *B. leptopus* with a repetition period of 1.25 s

or a single synthetic call of *B. antartandica*, composed of 45 pulses with a repetition period of 667 ms. This stimulus interval was followed by 90 s of silence, as shown in Figure 2. Four subsequent tracks, each lasting 240 s, shared a similar structure, as shown for track 2 in Figure 2. In this track, the left channel started with 150 s of noise followed by 90 s of silence, and on the right channel, a bout of 20 synthetic calls lasting 30 s started 60 s after the noise onset on the left channel and was followed by 150 s of silence. Track 1 schematized in Figure 2 was delivered at the beginning and repeated at the end of each experiment, and for schematic track 2, the noise structure or amplitude was modified in subsequent presentations (see below).

Two experiments were conducted for each species: A “Noise-structure Experiment” in which four tracks containing corresponding noises of different structure were played in two orders; for sequence A, the order was wind, creek, rain, and band-pass noise, and sequence B contained the reverse order. Each sequence was broadcast to half of the experimental subjects. The rationale for using two different orders was to control for the influence of the order of presentation of noises of different structure on the evoked vocal responses (EVRs). After the presentation of the fourth noise track (i.e., fifth track of the sequence), a sixth track identical to the first one, containing a bout of 20 synthetic calls followed by 90 s of silence on the right channel and comprising 120 s of silence on the left channel, was presented as a control for changes in vocal output throughout the experiment. Upon completing this first experiment, the basal vocal activity was recorded in absence of any broadcast sound for 2 min. Following this recording period, the second, “Noise-level Experiment” proceeded, starting with a track identical to the first track of the first experiment and thereafter, a band-pass noise track identical to the one used in the first experiment was presented five times at increasing amplitudes (see next subsection). The rationale for presenting an order of increasing noise levels was to minimize the effect of presentations of high-amplitude noise on vocal activity during following exposures.

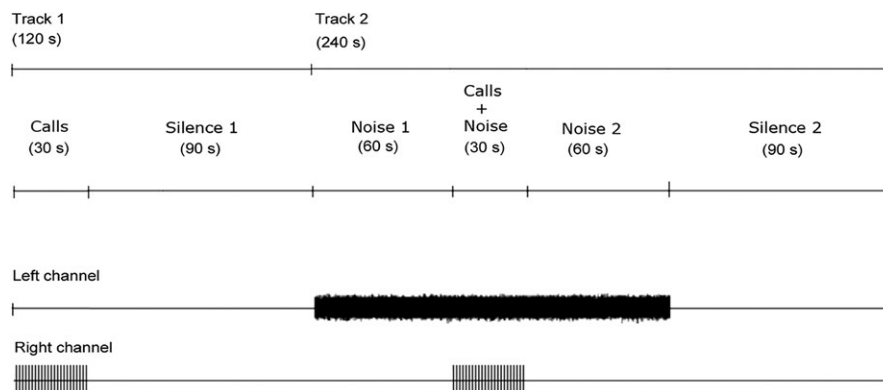


FIGURE 2 Schematic diagram of the time intervals for which measures of evoked vocal responses (EVRs) were compared during exposures to different kinds of noise and to band-pass noise at different levels. Track 1 contains silence during the 120 s on the left channel and a bout of 20 calls lasting 30 s followed by 90 s of silence on the right channel. Track 2 contains noise during 150 s followed by 90 s of silence on the left channel and, on the right channel, 60 s of silence followed by a bout of 20 calls lasting 30 s and 150 s of silence. Silence 1, noise 1, calls + noise, noise 2, and silence 2 are the five intervals for which vocal activity in terms of call rate, call duration, and call amplitude was compared with the exposures to noise (see text)

2.4 | Instrumentation and experimental setting

Stimuli and noises were played back with an iPod nano audio player connected to a two-channel impedance-matched operational amplifier and two attenuator sets (Hewlett-Packard 355 C and D for synthetic calls and Hewlett-Packard 350 D for noises; Hewlett-Packard, Loveland, Colorado, USA). The synthetic call and noises were combined with an electronic adder and fed into a power amplifier (Alpine 3540; Alpine Electronics of America, Torrance, California, USA) and a two-way loudspeaker (Dynaudio BM6, frequency response: 38–20,000 Hz; Dynaudio Acoustics, Risskov, Denmark). The loudspeaker was positioned at a distance of 0.6–1.0 m in front of each experimental subject. Evoked vocal responses were recorded with a directional microphone (Sennheiser ME 66; Sennheiser Electronic GmbH & Co., KG, Wedemark, Germany) connected to the left channel of a digital tape recorder (Sony TC D10 PROII). During the experiments, the synthetic advertisement calls were recorded on the right channel of the digital recorder from the iPod audio player through a connection cable, to obtain a temporal relationship between the stimuli and the EVRs. During playbacks, special care was taken to suppress vocal activity of neighboring frogs by gently tapping the substrate near their positions so that the EVR of the focal frog was recorded without this interference.

The synthetic calls were presented at 70 dB SPL RMS (Sound Pressure Level root-mean-square, fast weighting scale, linear frequency weighting) at the position of the experimental subject in the first and second experiments. The noises were presented at 67 dB SPL RMS in the Noise-structure Experiment, and at five different levels in the Noise-level Experiment. The value of the synthetic calls was close to the average level of the calls of nearest neighbors in natural aggregations of this species (MP, unpublished data), and the noise level was well above the background noise, which, at the study sites, was typically below 40 dB SPL on nights with calm atmosphere (see Section 3). However, during stormy weather, levels of wind, rain, and creek noise of up to 70–76 dB SPL RMS occur in these habitats (Penna et al., 2005). The 3-dB signal-to-noise ratio has been appropriate to evoke consistent vocal responses to synthetic calls in previous studies with other anurans in the temperate austral forest (Penna & Hamilton-West, 2007; Penna & Zúñiga, 2014; Penna et al., 2005). Before starting an experimental session, the SPLs of the synthetic calls and noises were measured by placing the tip of the microphone of a sound level meter (Brüel & Kjaer 2230) as close as possible to the head of the experimental subject, without causing disturbance. These measurements allowed us to adjust the attenuator settings in order to maintain a constant SPL during playback of the synthetic call and noises for each individual. The range of SPLs used for the Noise-level Experiment for exposures to band-pass noise at five increasing amplitudes in 6-dB steps (55, 61, 67, 73, and 79 dB SPL) encompassed levels effective in altering frog vocal activity in previous studies (Penna & Hamilton-West, 2007; Penna & Zúñiga, 2014; Penna et al., 2005).

Experimental sessions were conducted at night, between 21:00 and 05:00 hr, comprising the period during which natural choruses build up and fade away. The total duration of the Noise-structure

Experiment and Noise-level Experiment was 20 and 24 min, respectively. Basal vocal activity in absence of any stimulation was recorded for 2 min before and after the Noise-structure Experiment and Noise-level Experiment were completed. At the end of the experimental session, the environmental noise level was measured by placing the microphone of the sound level meter at the position of subject. Air and substrate temperature were measured with a thermometer (Digi-sense 8528-20) and the relative humidity with a hygrometer (Bacharach sling psychrometer). Whenever possible, experimental subjects were captured, and their snout-vent length and body weight were measured.

2.5 | Acoustic analysis of evoked vocal responses

Recordings were digitized with a Macintosh computer (Macintosh G4), using PEAK 2.52 software (Bias, Inc., Petaluma, California, U.S.A.) at a 44.1 kHz sampling rate, an anti-aliasing filter (FT6-2, Tucker-Davis Technologies), and an analogue digital interface (Motu 828). Recordings were analyzed using RAVEN PRO 1.3 software (Cornell Laboratory of Ornithology, Ithaca, New York, USA), and three measures of the frogs' EVRs were quantified for each species: call rate, call duration, and call amplitude for *B. leptopus*, and pulse rate, multiple pulses proportion, and call amplitude for *B. antartandica*. Multiple pulses composed of 2–3 emissions in fast succession are occasionally produced within the call of this species, interspersed along prolonged sequences of single pulses emitted at a lower rate (Penna & Meier, 2011).

Because EVRs recorded during the presentation of noises were embedded in the broadcast noise, we corrected the amplitude values of these vocalizations with the following procedure: In the recordings, we measured the RMS amplitude of an interval containing the noise broadcast through the loudspeaker but free of evoked calls, and added it to the RMS value of a call recorded at a preceding interval free of broadcast noise to calculate the predicted amplitude resulting of adding the two sounds (Bradbury & Vehrencamp, 1998, pp. 34–35). Then, we corrected the RMS amplitude measured for the recorded calls embedded in noise by subtracting the predicted amplitude increment calculated. An experimental checking of the accuracy of this procedure has been conducted previously (Penna & Zúñiga, 2014).

2.6 | Statistical analysis

The effects of exposure to noises of different structure broadcast at the same SPL (Noise-structure Experiment) were analyzed with Friedman nonparametric ANOVAs for repeated measures (STATISTICA 6.0 software, Statsoft, Inc., Tulsa, Oklahoma, U.S.A.; significance level $p < .05$) and post hoc multiple comparisons (Siegel & Castellan, 1988, pp. 180–181) for the three EVR measures. The five time intervals within a noise exposure were considered as treatments: the no-playback interval preceding the noise presentation (90 s), the noise exposure before synthetic call onset (60 s), the noise exposure during the presentation of the bout of synthetic call (30 s), the noise exposure after the presentation of the synthetic call (60 s), and the no-playback interval after noise exposure (90 s). We refer to these

five time intervals as S1 ("silence 1"), N1 ("noise 1"), CN ("call and noise"), N2 ("noise 2"), and S2 ("silence 2"), respectively. A no-playback interval between two noise exposures was considered as S2 for the preceding exposure and as S1 for the subsequent exposure. The EVRs to the two sequences of exposures to noise of different structure (A and B) employed for the Noise-structure Experiment were analyzed separately.

To assess the effects of band-pass noise broadcast at increasing levels (Noise-level Experiment), nonparametric Friedman ANOVAs and multiple comparisons tests were performed as for the Noise-structure Experiment.

For all the analyses performed, the absence of calls during a given time interval was quantified as a 0 call rate in *B. leptopus* and as 0 pulse rate in *B. antartandica*; however, for call duration, multiple pulses proportion, and call amplitude, these were considered as missing data. To compare graphically the EVRs of different subjects during the five time intervals, the three EVR measures were normalized to the maximum response for each individual; namely, the value of call rate, call duration, and call amplitude for a given subject during a particular interval was divided by the maximum value of that measure produced by the frog across all intervals.

3 | RESULTS

3.1 | Environmental conditions and basal vocal activity

Averages and standard deviations for the environmental variables at the study site of *B. leptopus* were as follows: air temperature: 13.0 ± 3.8 , substrate temperature: $13.4 \pm 3.0^\circ\text{C}$, air relative humidity: $83.1 \pm 16.3\%$, and the distance between the 14 experimental subjects and their nearest neighbors: 3.0 ± 1.7 m. The body measures for nine males captured were size: 33.2 ± 0.9 mm and weight: 2.6 ± 0.2 g. The abiotic noise at the location of the experimental subjects was 33.2 ± 7.5 dB RMS SPL, and during quiet nights, the range was 35–40 dB SPL. During a single night in which a moderate wind blew, 48 dB SPL was measured.

Averages and standard deviations for the environmental variables at the study site of *B. antartandica* were as follows: air temperature: 5.4 ± 2.4 , substrate temperature: $7.6 \pm 1.9^\circ\text{C}$, air relative humidity: $96.6 \pm 2.8\%$, and the distance between 12 experimental subjects and their nearest neighbors: 2.5 ± 1.0 m. The body measures for nine males captured were size: 38.1 ± 1.4 mm and weight: 3.3 ± 0.3 g. The abiotic background noise at the location of the experimental subjects was 37.7 ± 3.6 dB RMS SPL, and during quiet nights, the range was 30–37 dB SPL. During a single night in which a moderate wind blew, 40 and 54 dB SPL were measured.

For 14 males of *B. leptopus*, the averages and standard deviations of the acoustic variables measured during the initial two minutes of basal vocal activity recording were call rate: 9.6 ± 7.1 calls/min and call duration: 221 ± 59 ms, and in response to the initial 20 repetitions of the synthetic call preceding noise broadcast, these variables were 19.8 ± 11.7 calls/min, call duration: 306 ± 81 ms.

For 12 males of *B. antartandica*, the averages and standard deviations of the acoustic variables measured during the initial two minutes of basal vocal activity recording were pulse rate: 20.3 ± 17.9 pulses/min and multiple pulses proportion: 0.15 ± 0.13 , and in response to the initial synthetic call preceding noise broadcast, these variables were 0.17 ± 0.58 pulses/min and 0.0 ± 0.0 , respectively. The low values obtained for these measures during the 20 s of presentation of the synthetic call are because males of this species typically respond to conspecific advertisement calls with relatively long latencies of about 15 s, and in previous studies, the evoked vocal responses to synthetic stimuli have been computed during the 20-s stimulus and a 30-s silent interval following the cessation of the stimulus (Penna, Feng, & Narins, 1997; Penna & Meier, 2011). In this study, we chose to compute the responses during time of presentation of the stimulus, considering that this signal had a duration of 30 s, longer than the synthetic calls used in previous studies.

3.2 | Noise-structure experiment, *Batrachyla leptopus*

Fourteen males were subjected to this experiment, seven following the presentation order: wind, creek, rain, and band-pass noise (sequence A), and seven following the reverse order (sequence B). In general, the frogs vocalized consistently throughout the experimental session. For sequence A, call rate differed significantly among the intervals S1, N1, CN, N2, and S2 during exposures to wind, creek, and band-pass noises. It was not possible to analyze call duration and call amplitude because only one of the seven individuals called during all the five time intervals considered in the analysis (Table S1 and Figure 3).

For sequence B, call rate differed significantly among the intervals S1, N1, CN, N2, and S2 during exposure to band-pass noise only. It was not possible to analyze call duration and call amplitude for wind, rain, and band-pass noises because only one of the seven individuals called during all the five time intervals considered in the analysis. For creek noise, call duration and call amplitude did not differ significantly among the five intervals analyzed (Table S1 and Figure 3).

Multiple comparisons showed that for sequence A, call rate was higher during CN than during S1 for band-pass noise, higher during CN than during N1 for wind noise, higher during CN than during N2 for wind and creek noise, and higher during CN than during S2 for creek noise (Table S2 and Figure 3). For sequence B, call rate was higher during CN than during S1, N1, and S2 for band-pass noise (Table S2 and Figure 3).

3.3 | Noise-structure experiment, *Batrachyla antartandica*

Twelve males were subjected to this experiment: six following the presentation order: wind, creek, rain, and band-pass noise (sequence A), and six following the reverse order (sequence B). In general, the frogs vocalized consistently throughout the experimental session. For sequence A, pulse rate differed significantly among the intervals S1, N1, CN, N2, and S2 during exposures to wind, creek, rain,

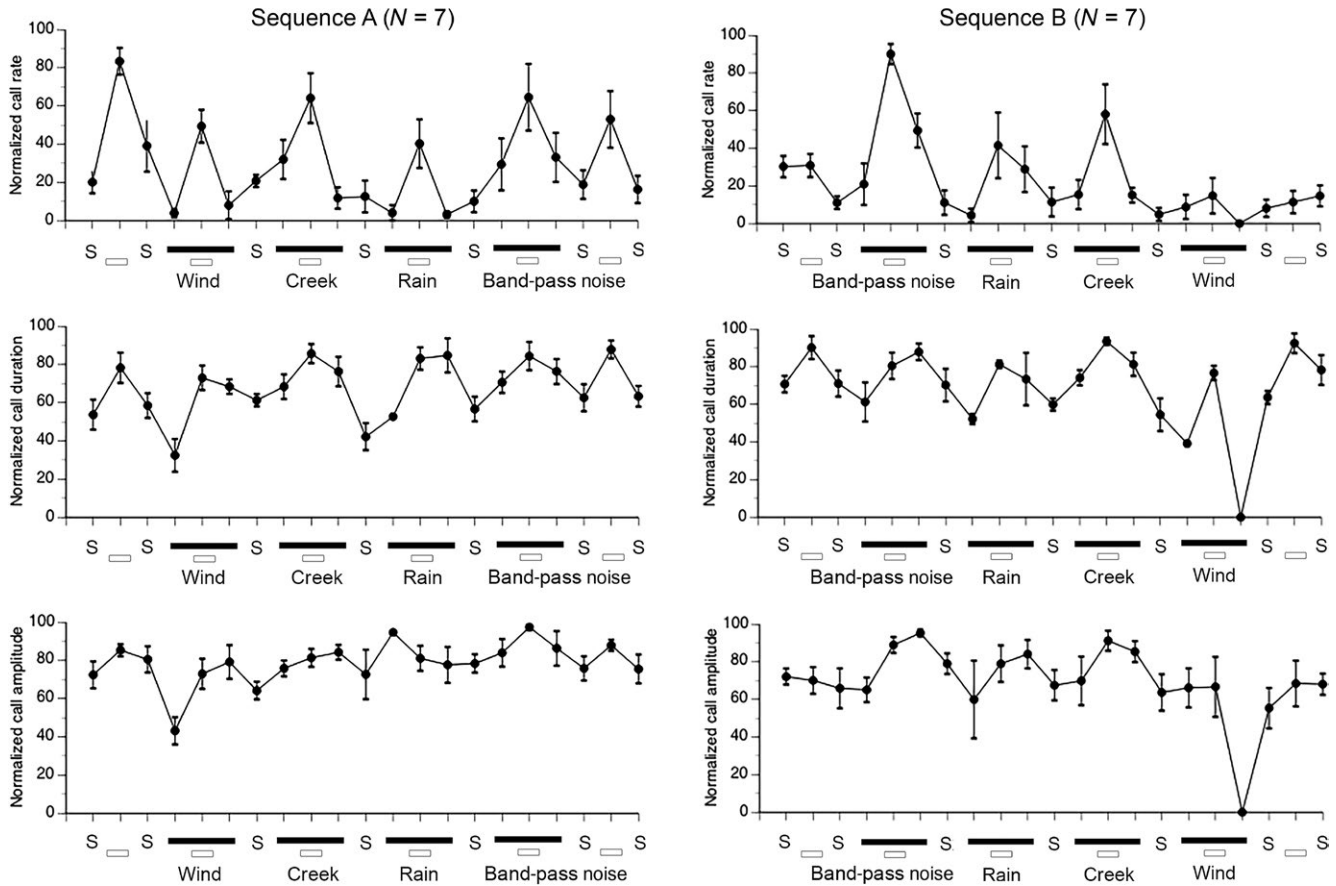
B. leptopus

FIGURE 3 Normalized measures of EVRs: call rate, call duration, and call amplitude of 14 males of *Batrachyla leptopus* during the presentation of sequences A and B (see Section 2) of exposures to noises of different structure. Empty rectangles on the horizontal axis indicate presentations of bouts of synthetic calls, having a duration of 30 s. Filled rectangles indicate the presentation of different noises, having a duration of 150 s. Intervals of silence lasting 90 s, before, between, and after presentation of noises are indicated by S between horizontal rectangles. The three measures of evoked call response were normalized to the maximum response for each individual; namely, the value of call rate, call duration, and call amplitude for a given subject during a particular interval was divided by the maximum value of that measure produced by the frog across all intervals. Filled circles and whiskers represent averages and standard errors, respectively

and band-pass noises. It was not possible to analyze multiple pulses proportion and call amplitude for rain noise because only one of the six individuals called during all the five time intervals considered in the analysis. For wind, creek, and band-pass noise, multiple pulses proportion and call amplitude did not differ significantly among the five intervals analyzed (Table S3 and Figure 4).

For sequence B, call rate and multiple pulses proportion differed significantly among the intervals S1, N1, CN, N2, and S2 during exposure to band-pass noise only. It was not possible to analyze multiple pulses proportion and call amplitude for wind noise because only one of the six individuals called during all the five time intervals considered in the analysis. For creek and rain noises, multiple pulses proportion and call amplitude did not differ significantly among the five intervals analyzed (Table S3 and Figure 4).

Multiple comparisons showed that for sequence A, pulse rate was higher during N2 than during S1 for creek and band-pass noise, higher during N2 than during N1 for wind, rain, and band-pass noise (Table S4 and Figure 4). For sequence B, pulse rate was significantly higher

during N2 than during S1 and N1 for band-pass noise. For sequence B, multiple pulses proportion was higher during CN than during S1 for band-pass noise (Table S4 and Figure 4).

3.4 | Noise-level experiment, *Batrachyla leptopus*

Thirteen males were subjected to this experiment because one animal stopped responding after the completion of the Noise-structure experiment. The experimental subjects in general vocalized consistently throughout the experimental session. Call rate differed significantly among the intervals S1, N1, C, N2, and S2 during exposures at 55, 67, 73, and 79 dB SPL. The analysis of call duration and call amplitude showed differences among the five intervals analyzed for the exposure at 55 dB SPL. No significant differences for call duration occurred for the exposures at 67, 73, and 79 dB SPL, and because no individuals produced calls during all the five time intervals during the 61 dB SPL exposure, the ANOVA could not be applied to call duration and call amplitude (Table S5 and Figure 5).

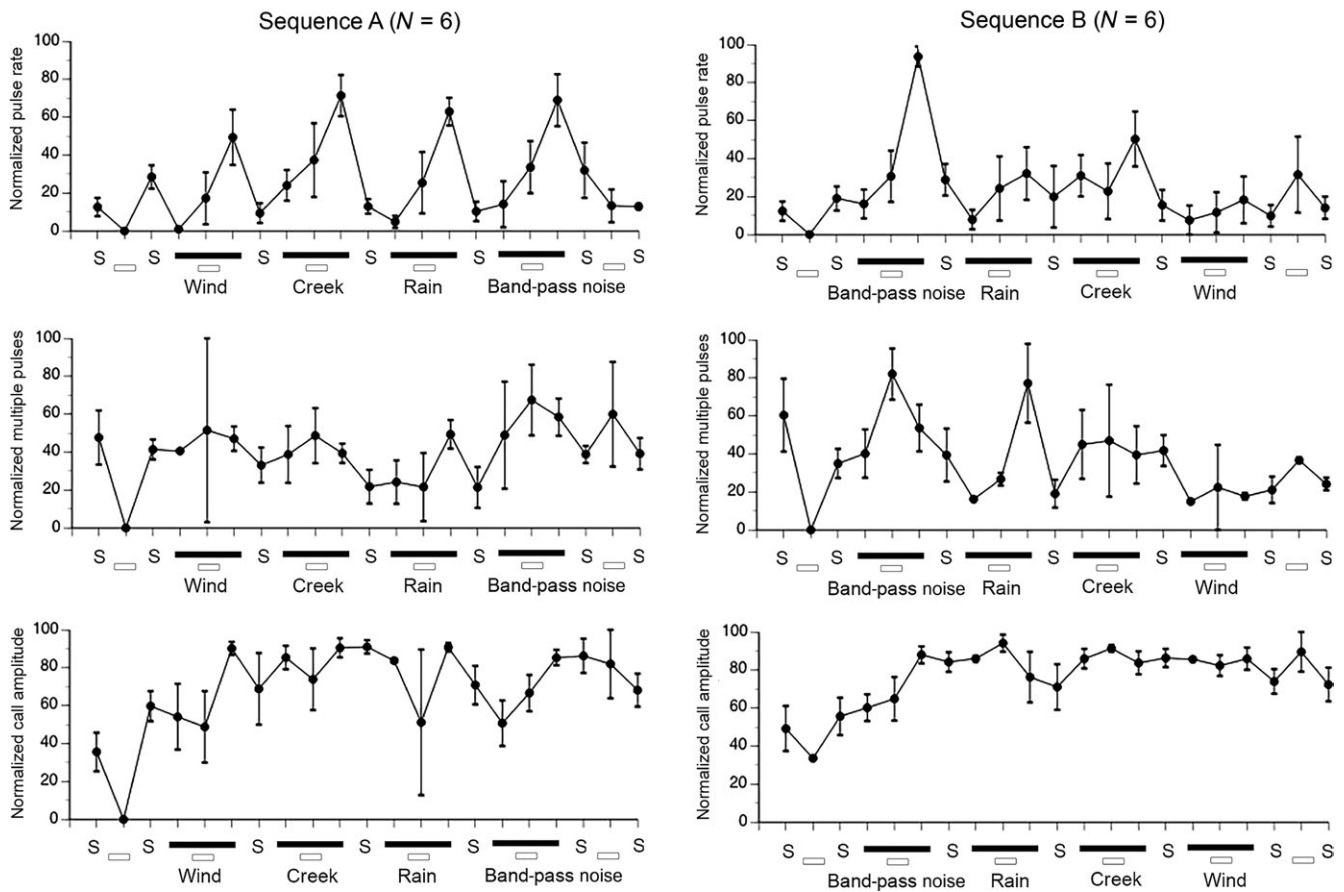
B. antartandica

FIGURE 4 Normalized measures of EVRs: pulse rate, multiple pulses proportion, and call amplitude of 12 males of *Batrachyla antartandica* during the presentation of sequences A and B (see Section 2) of exposures to noises of different structure. Symbols as in Figure 3

Multiple comparisons showed that call rate was significantly higher during CN than during S1 for noise exposures at 61, 67, 73, and 79 dB SPL and also higher during CN than during S2 for noise exposures at 55, 61, 67, and 79 dB SPL (Table S2 and Figure 5). Multiple comparisons also showed that call duration was significantly longer during CN than during N2 and S2 for the exposure at 55 dB SPL. Multiple comparisons did not yield significant differences in call amplitude for any of the exposure levels (Table S2 and Figure 5).

3.5 | Noise-level experiment, *Batrachyla antartandica*

Eleven males were subjected to this experiment because for one animal, the session was suspended after the completion of the Noise-structure Experiment due to technical and weather conditions. The experimental subjects vocalized consistently throughout the experimental session. Pulse rate differed significantly among the intervals S1, N1, C, N2, and S2 during exposures at 55, 61, 67, 73, and 79 dB SPL. Multiple pulses proportion differed significantly among the five intervals analyzed for the exposure at 67 dB SPL only, and call amplitude differed significantly among the five intervals analyzed for the exposure at 61 dB SPL only (Table S5 and Figure 6).

Multiple comparisons showed that pulse rate was significantly higher during N1 than during S1 for the noise exposure at 61 dB SPL and higher during N1 than during S2 for the exposure at 55 dB SPL. In addition, pulse rate was higher during N2 than during S1 for exposures at 61, 67, 73, and 79 dB SPL, higher during N2 than during N1 for the exposures at 67, 73, and 79 dB SPL, higher during N2 than during CN for the exposure at 61 dB SPL, and higher during N2 than during S2 for the exposures at 55 and 67 dB SPL. Multiple comparisons showed that multiple pulses proportion was higher during CN than during S1 for the exposure at 67 dB SPL. No significant differences occurred for call amplitude (Table S4 and Figure 6).

In this experiment as in the Noise-structure Experiment, the restricted statistical significance of multiple comparisons for call duration and call amplitude in *B. leptopus* and for multiple pulses proportion and call amplitude in *B. antartandica* was due to missing cases for these two variables.

4 | DISCUSSION

Results of this study show that the vocal activity of males of *B. leptopus* and *B. antartandica* is not altered significantly in the presence

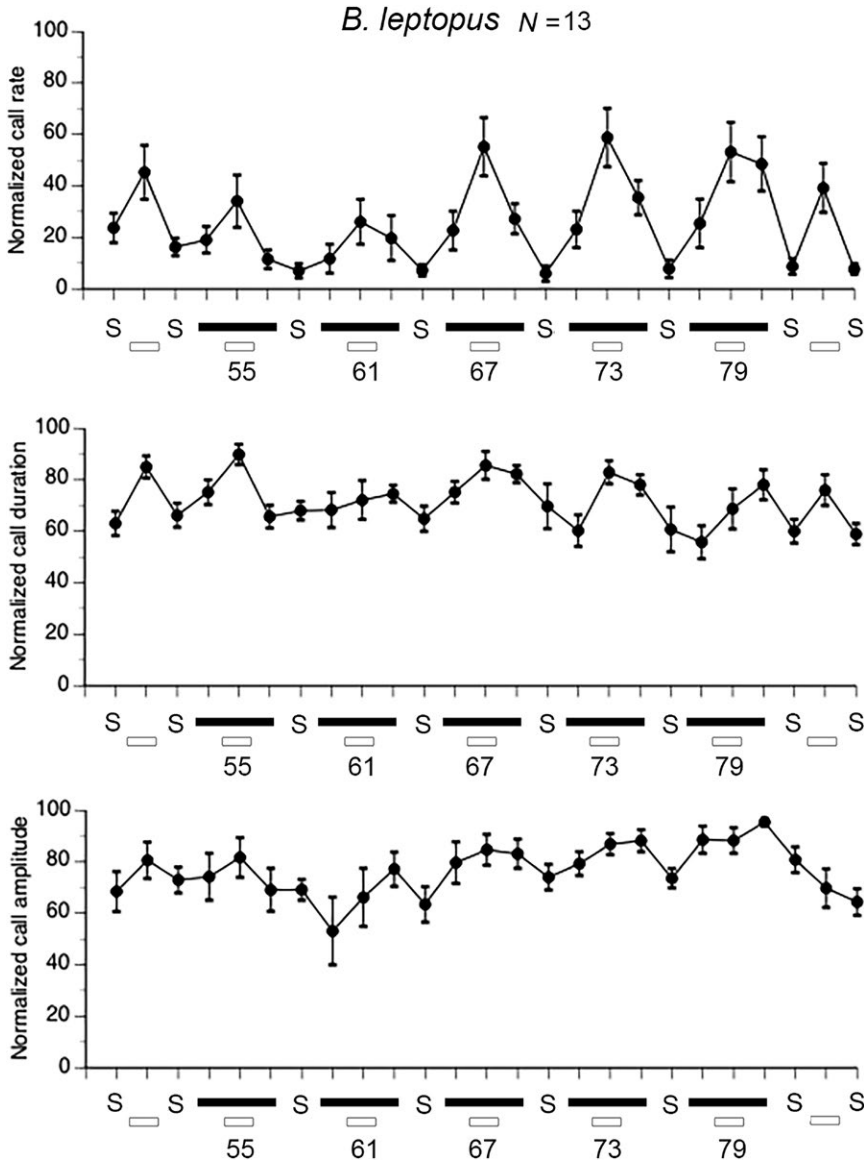


FIGURE 5 Normalized measures of EVRs: call rate, call duration, and call amplitude of 13 males of *Batrachyla leptopus* during the sequence of exposures to band-pass noise (center frequency: 2,000 Hz; cutoff frequencies: 1,000 and 3,000 Hz) at different amplitude levels. Empty rectangles on the horizontal axis indicate the presentation of bouts of synthetic calls, having a duration of 30 s. Filled rectangles indicate the presentation of band-pass noise at different levels, having a duration of 150 s. Intervals of silence lasting 90 s are indicated by S between horizontal rectangles (see Section 2). Numbers below rectangles indicate levels of noise exposures in dB SPL. Other symbols as in Figure 3

of natural abiotic noises of different origin and a band-pass noise encompassing the dominant frequency range of the advertisement call of these species. Significant increases in measures of vocal activity during noise occur mostly during the presentation of the conspecific stimulus, and these affect call rate in *B. leptopus* and pulse rate and multiple pulses proportion in *B. antartandica*. In *B. leptopus*, the seven and eight significant differences in call rate between the time intervals analyzed in the Noise-structure Experiment and in the Noise-level Experiment, respectively, correspond to differences between the CN interval and other intervals. In *B. antartandica*, all seven significant differences in pulse rate between the time intervals analyzed in the Noise-structure Experiment correspond to differences between the N2 interval and other intervals. In the Noise-level Experiment for this species, 10 of 12 significant differences in pulse rate correspond to differences between the N2 interval and other intervals. In this species, the response to the stimulus is typically delayed, often starting at about the end of the stimulus (Penna & Meier, 2011; Penna et al., 1997), and therefore, the responses to the synthetic calls are

computed during N2, the interval following C, so the increase in vocal output during the noise exposure following the call delivery is likely activated by the biotic signal.

Comparisons particularly relevant to test the effect of noise are those between the intervals with noise alone before the presentation of conspecific calls and the preceding silent interval, that is, N1 vs. S1. Of all such comparisons for three EVR measures in the two species, only the pulse rate in *B. antartandica* was significantly higher during the N1 interval than during S1 for the band-pass noise exposure at 61 dB SPL (see Table S4 and Figure 6). These results also point to a lack of dependence of vocal activation on noise in the two anurans considered in the current study.

The effect of exposures to sounds on call duration in *B. leptopus*, multiple pulses proportion in *B. antartandica*, and call amplitude in both species is difficult to assess, due to the number of missing cases in the computation of these variables. In the Noise-structure Experiment, only one comparison yielded significant differences for multiple pulses proportion in *B. antartandica* (see Table S4), and in

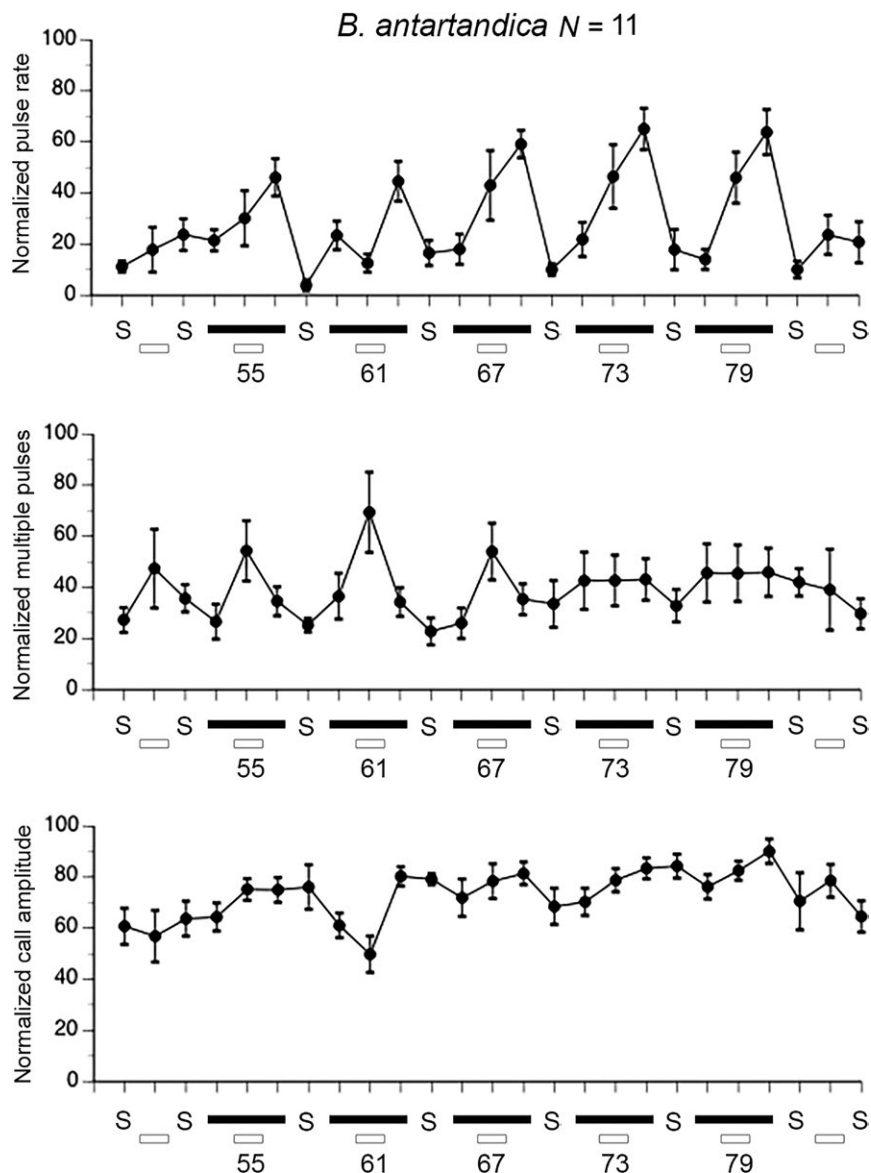


FIGURE 6 Normalized measures of EVRs: pulse rate, multiple pulses proportion, and call amplitude of 12 males of *Batrachyla antartandica* during the sequence of exposures to band-pass noise (center frequency: 2,000 Hz; cutoff frequencies: 1,000 and 3,000 Hz) at different amplitude levels. Symbols as in Figure 5

the Noise-level Experiment only two comparisons yielded significant differences for call duration in *B. leptopus* (see Table S2), and two comparisons yielded a significant difference for multiple pulses proportion in *B. antartandica* (see Table S4). No significant differences occurred for call amplitude in any experiment with the two species.

The order of presentation of the noises in the Noise-structure Experiment affected the responses, as the Friedman ANOVAs yielded significant differences for wind, creek, and band-pass noise exposures in sequence A in both species, and in contrast, sequence B yielded in both species significant differences for band-pass noise exposure only (see Tables S1 and S3). It is likely that in sequence B, the initial exposure to band-pass noise, which has its energy concentrated within the spectral range of the frog calls, somehow hinders the responsiveness to subsequent exposures having less energy contents in this spectral domain.

The invariance in vocal activity during exposure to noises alone in *B. leptopus* and *B. antartandica* resembles that observed in a previous

study with another frog of the temperate austral forest, *Eupsophus emiliopugini* (Penna & Hamilton-West, 2007) and is in sharp contrast with results obtained in previous studies with *E. calcaratus* (Penna et al., 2005) and *B. taeniata* (Penna & Zúñiga, 2014). This last species increases significantly its calling activity during exposures to all the continuous abiotic and band-pass noises used in the present study. Diverse reactions to confront acoustic interference have also been reported among anuran species exposed experimentally to anthropogenic noises in habitats different from the temperate austral forest (Cunnington & Fahrig, 2010; Kaiser et al., 2011; Sun & Narins, 2005; Vargas-Salinas et al., 2014). Different reactions to road noise have been related to the spectral contents of the signals: Species having relatively low dominant frequencies, within the frequency range of anthropogenic noise, experience reductions in their vocal activity, and species producing high-frequency calls keep their vocal output unaltered (Cunnington & Fahrig, 2010; Vargas-Salinas et al., 2014). In contrast with these studies, the differences in responsiveness observed in *B. taeniata* from that observed in the other two species are

not related to the spectra of the calls, which are very similar among the three species.

Diverse modes of confronting interference from heterospecific signals have also been reported in tropical katydids (Symes et al., 2016), but the adaptive value and origins of these differences in confronting such biotic acoustic intrusion have not been addressed in these insects.

The lack of vocal responsiveness to continuous noise observed in this study in *B. antartandica* is concordant with the tendency of males to keep silent in the presence of calls of the congeneric species *B. taeniata* and *B. leptopus* (Penna & Meier, 2011). The lack of vocal responsiveness to continuous noise observed in this study in *B. leptopus* contrasts with the tendency of males of this species to vocalize in the presence of calls of the congeneric species *B. taeniata* and *B. antartandica* (Penna & Toloza, 2014).

The lack of vocal activation observed in *B. antartandica* in the current study during exposures to natural abiotic noises of different structure and a band-pass noise contrasts with increases in call output observed during exposure to a 3-min duration broad-band low-pass synthetic noise in an earlier study with this species (Penna & Meier, 2011). The noise used in that study differed from the band-pass noise used in the current study in having high energy contents below 500 Hz and also was not accompanied by synthetic calls in the mid-time of the exposure, so the results are not strictly comparable.

However, the dissimilarities between both studies with *B. antartandica* suggest that the responsiveness to prolonged sound interference could not strictly be a species-specific feature, but rather depend on previous acoustic experience of animals. For instance, a case of long-lasting effect of exposure to biotic signals studied mainly in birds is the dear enemy phenomenon by which territory owners behave less aggressively toward nearby neighbors as compared to unfamiliar conspecifics (Temeles, 1994). This phenomenon has also been reported to occur in frogs, and results from habituation (Bee & Gerhardt, 2001; Humfeld, Marshall, & Bee, 2009). A process concomitant with habituation but having a contrasting nature is sensitization, by means of which responses are enhanced due to repetitive stimulation. For instance, birds *Taenopygia guttata* subjected to prolonged traffic noise exposure experience spectral vocal changes that persist during two months after the cessation of the exposure (Potvin & MacDougall-Shackelton, 2015). Effects of prolonged experience with biotic signals on the activity of the auditory system have been reported in birds *Sturnus vulgaris* and frogs *Hyla cinerea* exposed during days to conspecific call pattern (Gall & Wilczynski, 2014; Sockman, Gentner, & Ball, 2002). In these species, an enhancement of early gene expression occurs in diverse centers of the auditory system, and in the case of the frog species, the auditory thresholds are also lowered (Gall & Wilczynski, 2015). These examples indicate that mechanisms of habituation or sensitization could underlie the changes in responsiveness observed to exposures of anthropogenic and biotic sounds. For the species considered in the current study, the acoustic experience during previous days depends on atmospheric prevailing conditions, highly dissimilar between stormy and calm weather at the

study sites. Such potential involvement of natural noise of abiotic origin on long-term changes in vocal responsiveness remains to be explored.

In recent years, concerns about and studies on the effect of anthropogenic noise have increased considerably (reviewed in Barber et al., 2010; Luther & Gentry, 2013; Roca et al., 2016). However, the effects of natural abiotic noise interferences, which have had a ubiquitous and long-term presence in the history of sound-communicating animals, deserve more study. Such research would provide cues to understand the consequences of extant acoustic environmental alterations of human origin. The Editor's guidance is greatly appreciated.

ACKNOWLEDGEMENTS

This study was supported by FONDECYT Grant 1140014. The procedures used in this study comply with the laws of animal welfare in Chile (Protocol CBA# 061 FMUCH). Two anonymous reviewers contributed valuable comments that shaped the final version of the manuscript.

REFERENCES

- Amézquita, A., Flechas, S. V., Lima, A. P., Gasser, H., & Hödl, W. (2011). Acoustic interference and recognition space within a complex assemblage of dendrobatid frogs. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 17058–17063.
- Barber, J. R., Crooks, K. R., & Fristrup, K. M. (2010). The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology and Evolution*, 25, 180–189.
- Bee, M., & Gerhardt, H. C. (2001). Habituation as a mechanism of reduced aggression between neighboring territorial male bullfrogs (*Rana catesbeiana*). *Journal of Comparative Psychology*, 115, 68–82.
- Bradbury, J. W., & Vehrencamp, S. L. (1998). *Principles of animal communication*. Sunderland, MA: Sinauer Associates.
- Brumm, H. (2006). Signaling through acoustic windows: Nightingales avoid interspecific competition by short-term adjustment of song timing. *Journal of Comparative Physiology A*, 192, 1279–1285.
- Brumm, H., & Slabbekoorn, H. (2005). Acoustic communication in noise. *Advances in the Study of Behavior*, 35, 151–209.
- Cunnington, G. M., & Fahrig, L. (2010). Plasticity in the vocalizations of anurans in response to traffic noise. *Acta Oecologica*, 36, 463–470.
- Douglas, H. D. III, & Conner, W. E. (1999). Is there a sound reception window in coastal environments. Evidence from shorebird communication systems. *Naturwissenschaften*, 86, 228–230.
- Dubois, A., & Martens, J. (1984). A case of possible vocal convergence between frogs and a bird in Himalayan torrents. *Journal of Ornithology*, 125, 455–463.
- Dunlop, R. A. (2016). The effect of vessel noise on humpback whale, *Megaptera novaeangliae*, communication behavior. *Animal Behavior*, 111, 13–21.
- Ellinger, N., & Hödl, W. (2003). Habitat acoustics of a neotropical lowland rainforest. *Bioacoustics*, 13, 297–321.
- Feng, A. S., Narins, P. M., Xu, C. H., Lin, W. Y., Yu, Z. L., Qiu, Q., ... Shen, J. X. (2006). Ultrasonic communication in frogs. *Nature*, 440, 333–336.
- Gall, M. D., & Wilczynski, W. (2014). Prior experience with conspecific signals enhances auditory midbrain responsiveness to conspecific vocalizations. *Journal of Experimental Biology*, 217, 1977–1982.
- Gall, M. D., & Wilczynski, W. (2015). Hearing conspecific vocal signals alters peripheral auditory sensitivity. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 282, 20150749.

- García-Rutledge, E. J., & Narins, P. M. (2001). Shared acoustic resources in an old world frog community. *Herpetologica*, 57, 104–116.
- Goutte, S., Dubois, A., Howard, S. D., Márquez, R., Rowley, J. J. L., Dehling, J. M., ... Legendre, F. (2016). Environmental constraints and call evolution in torrent-dwelling frogs. *Evolution*, 70, 811–826.
- Greenfield, M. D. (1988). Interspecific acoustic interactions among katydid *Neoconocephalus*: Inhibition-induced shifts in diel periodicity. *Animal Behavior*, 36, 684–695.
- Hart, P. J., Hall, R., Ray, W., Beck, A., & Zook, J. (2015). Cicadas impact bird communication in a noisy tropical rainforest. *Behavioral Ecology*, 26, 839–842.
- Hoskin, C. J., & Higgie, M. (2010). Speciation via species interactions: The divergence of mating traits within species. *Ecology Letters*, 13, 409–420.
- Humfeld, S. C., Marshall, V. T., & Bee, M. A. (2009). Context-dependent plasticity of aggressive calling in a dynamic social environment. *Animal Behavior*, 78, 915–924.
- Kaiser, K., & Hammers, J. L. (2009). The effect of anthropogenic noise on male advertisement call rate in the neotropical treefrog, *Dendrosophus triangulum*. *Behaviour*, 146, 1053–1069.
- Kaiser, K., Scofield, D. G., Alloush, M., Jones, R. M., Marczak, S., Martineau, K., ... Narins, P. M. (2011). When sounds collide: The effect of anthropogenic noise on a breeding assemblage of frogs in Belize, Central America. *Behaviour*, 148, 215–232.
- Lampe, U., Reinhold, K., & Schmoll, T. (2014). How grasshoppers respond to road noise: Developmental plasticity and population differentiation in acoustic signaling. *Functional Ecology*, 28, 660–668.
- Latimer, W., & Broughton, W. B. (1984). Acoustic interference in bush crickets: a factor in the evolution of singing insects? *Journal of Natural History*, 18, 599–616.
- Lengagne, T. (2008). Traffic noise affects communication behaviour in a breeding anuran, *Hyla arborea*. *Biological Conservation*, 141, 2023–2031.
- Lenske, A. K., & La, V. T. (2014). White-throated sparrows alter songs differentially in response to chorusing anurans and other background noise. *Behavioural Processes*, 105, 28–35.
- Littlejohn, M. J., & Martin, A. A. (1969). Acoustic interactions between two species of Leptodactylid frogs. *Animal Behavior*, 17, 785–791.
- Love, E. K., & Bee, M. A. (2011). An experimental test of noise-dependent voice amplitude regulation in Cope's grey treefrog, *Hyla chrysoscelis*. *Animal Behavior*, 80, 509–515.
- Luther, D. A. (2008). Signaller: Receiver coordination and the timing of communication in Amazonian birds. *Biology Letters*, 4, 651–654.
- Luther, D. (2009). The influence of the acoustic community on songs of birds in a neotropical rain forest. *Behavioral Ecology*, 20, 864–871.
- Luther, D. A., & Derryberry, E. P. (2012). Birdsongs keep pace with city life: Changes in song over time in an urban songbird affects communication. *Animal Behavior*, 83, 1059–1066.
- Luther, D., & Gentry, K. (2013). Sources of background noise and their influence on vertebrate acoustic communication. *Behaviour*, 150, 1045–1068.
- Okamoto, K. W., & Grether, G. F. (2013). The evolution of species recognition in competitive and mating contexts: The relative efficacy of alternative mechanisms of character displacement. *Ecology Letters*, 16, 670–678.
- Ophir, A. G., Schrader, S. B., & Gillioli, J. F. (2010). Energetic cost of calling: General constraints and species-specific differences. *Journal of Evolutionary Biology*, 23, 1564–1569.
- Penna, M. (1997). Selectivity of evoked vocal responses in the time domain by frogs *Batrachyla* (Leptodactylidae). *Journal of Herpetology*, 31, 30–45.
- Penna, M., Feng, A. S., & Narins, P. M. (1997). Temporal selectivity of evoked vocal responses of *Batrachyla antartandica* (Amphibia, Leptodactylidae). *Animal Behavior*, 54, 833–848.
- Penna, M., & Hamilton-West, C. (2007). Susceptibility of evoked vocal responses to noise exposure in a frog of the temperate austral forest. *Animal Behavior*, 74, 45–56.
- Penna, M., & Meier, A. (2011). Interferences on vocal behaviour of a frog from the southern temperate forest, *Batrachyla antartandica*. *Ethology*, 117, 1147–1157.
- Penna, M., Pottstock, H., & Velásquez, N. (2005). Effect of natural and synthetic noise on evoked vocal responses in a frog of the temperate austral forest. *Animal Behavior*, 70, 639–651.
- Penna, M., & Toloza, J. (2014). Vocal responsiveness to interfering sounds by a frog from the southern temperate forest, *Batrachyla leptopus*. *Ethology*, 121, 26–37.
- Penna, M., & Velásquez, N. (2011). Heterospecific vocal interactions in a frog from the southern temperate forest, *Batrachyla taeniata*. *Ethology*, 117, 63–71.
- Penna, M., & Veloso, A. (1990). Vocal diversity in frogs of the South American temperate forest. *Journal of Herpetology*, 24, 23–33.
- Penna, M., & Zúñiga, D. (2014). Strong responsiveness to noise interference in an anuran from the southern temperate forest. *Behavioral Ecology and Sociobiology*, 68, 85–97.
- Popp, J. W., Ficken, R. W., & Reinartz, J. A. (1985). Short-term temporal avoidance of interspecific acoustic interference among forest birds. *The Auk*, 102, 744–748.
- Potvin, D., & MacDougall-Shackelton, S. A. (2015). Experimental chronic noise exposure affects adult song in zebra finches. *Animal Behavior*, 107, 201–207.
- Roca, I. T., Desrochers, L., Giacomazzo, M., Bertolo, A., Bolduc, P., Deschesnes, R., ... Proulx, R. (2016). Shifting song frequencies in response to anthropogenic noise: A meta-analysis on birds and anurans. *Behavioral Ecology*, 27, 1269–1274.
- Römer, H., Bailey, W., & Dadour, I. (1989). Insect hearing in the field. III. Masking by noise. *Journal of Comparative Physiology A*, 164, 609–620.
- Schatral, A., & Yeoh, P. B. (1990). Spatial distribution calling and interspecific acoustic interactions in two species of the Australian tettigoniid genus *Tympanophora* (Orthoptera, Tettigoniidae). *Journal of Zoology London*, 221, 375–390.
- Schmidt, A. K. D., Römer, H., & Riede, K. (2013). Spectral niche segregation and community organization in a tropical cricket assemblage. *Behavioral Ecology*, 24, 470–480.
- Siegel, S., & Castellan, N. J. Jr (1988). *Nonparametric statistics for the behavioral sciences*. New York, NY: McGraw-Hill.
- Sockman, K. W., Gentner, T. Q., & Ball, G. F. (2002). Recent experience modulates forebrain gene-expression in response to mate-choice cues in European starlings. *Proceedings of the Royal Society of London B: Biological Sciences*, 269, 2479–2485.
- Solís, R., & Penna, M. (1997). Testosterone levels and evoked vocal responses in a natural population of the frog *Batrachyla taeniata*. *Hormones and Behavior*, 31, 101–109.
- Stanley, C. Q., Walter, M. H., Venkatraman, M. X., & Wilkinson, G. S. (2016). Insect noise avoidance in the dawn chorus of Neotropical birds. *Animal Behavior*, 112, 255–265.
- Sun, J. W. C., & Narins, P. M. (2005). Anthropogenic sounds differentially affect amphibian call rate. *Biological Conservation*, 121, 419–427.
- Symes, L., Page, R. A., & ter Hofstede, H. M. (2016). Effects of acoustic environment on male calling activity and timing in Neotropical forest katydids. *Behavioral Ecology and Sociobiology*, 10, 1485–1495.
- Temeles, E. J. (1994). The role of neighbors in territorial systems: When are they 'dear enemies'? *Animal Behavior*, 47, 339–350.
- Vargas-Salinas, F., & Amezcua, A. (2013). Stream noise, hybridization, and uncoupled evolution of call traits in two lineages of poison frogs: *Oophaga histrionica* and *Oophaga lehmanni*. *PLoS One*, 8, e77545.
- Vargas-Salinas, F., Cunnington, G. M., Amézquita, A., & Fahrig, L. (2014). Does traffic noise alter calling time in frogs and toads? A case study of anurans in Eastern Ontario, Canada. *Urban Ecosystems*, 17, 945–953.

- Wong, S., Parada, H., & Narins, P. M. (2009). Heterospecific acoustic interference: Effects on calling in the frog *Oophaga pumilio* in Nicaragua. *Biotropica*, 41, 74–80.
- Zelick, R. D., & Narins, P. M. (1983). Intensity discrimination and the precision of call timing in two species of Neotropical treefrogs. *Journal of Comparative Physiology A*, 153, 403–412.

How to cite this article: Penna M, Cisternas J, Toloza J. Restricted responsiveness to noise interference in two anurans from the southern temperate forest. *Ethology*. 2017;123: 748–760. <https://doi.org/10.1111/eth.12644>

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.