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# Diverse patterns of responsiveness to fine temporal features of acoustic signals in a temperate austral forest frog, *Batrachyla leptopus* (Batrachylidae)

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## ABSTRACT

Phonotactic female and vocal male responses of frogs to advertisement calls have been shown to encompass broader ranges than those of variation of natural mate-attracting signals. Anuran aggressive calls contribute to expand the range of sound features significant for communication. Evoked vocal responses (EVRs) of males of *Batrachyla leptopus* to synthetic advertisement calls and variants with different temporal features altered parametrically were studied to assess their correspondence with features of natural signals. Frogs responded to stimuli differing in note rate with vocal patterns that depended on the design of the synthetic sounds: lower call rates were obtained with stimuli composed of notes with linear rise-fall times deviating from the average of this parameter for natural calls. However, opposite results were obtained with stimuli composed of sinusoidally amplitude-modulated notes. Calls of longer duration resembling aggressive calls were emitted in response to low note rate sinusoidal stimuli. Stimuli with note durations above and below the natural average, stimuli having low pulse rates and a continuous tone also elicited longer calls of aggressive type. These patterns relate the vocal responses recorded to recognition of conspecific and heterospecific advertisement and aggressive calls, as well as to novel signal features.

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Aggressive calls; anura; Batrachylidae; evoked vocal responses; temporal selectivity

## Introduction

Animal communication requires a certain amount of matching between the physical structure of signals produced and the detection and processing of the corresponding sensory channel of receiver individuals (Bradbury and Vehrencamp 2011). For the acoustic channel, studies in anurans have provided strong evidence on strict matching between the vocal signals and auditory sensitivity in the spectral domain (e.g. Capranica 1965; Simmons 2013; Yang et al. 2018). In the temporal domain, correspondence between different components of the natural calls and female phonotactic sensitivity has been reported in a number of species (Loftus-Hills and Littlejohn 1971; Straughan 1975; Gerhardt 1978; Schwartz 1987; Klump and Gerhardt 1987; Gerhardt and Doherty

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1988, 1988). Evoked vocal responses (EVRs) of males of different species are selective to stimuli with several temporal parameters within the range of conspecific calls (Capranica 1965; Narins and Capranica 1978; Brzoska et al. 1982; Walkowiak and Brzoska 1982, 1982; Rose and Capranica 1984; Simmons et al. 1993; Allan and Simmons 1994). Neurons in the anuran midbrain are endowed with response patterns that support the behavioural selectivity observed in females and males of different frog species (Narins and Capranica 1980; Rose and Capranica 1983, 1984, 1985; Condon et al. 1991; Hall and Feng 1991; Gooler and Feng 1992; Diekamp and Gerhardt 1995; Penna et al. 1997; Alder and Rose 2000; Penna et al., 2001).

In contrast to the literature cited above, more recent studies have stressed the occurrence of mismatches between signal structure and behavioural preferences. Such perceptual biases operate at sensory and cognitive levels and are determined by environmental or phylogenetic factors (reviewed in Ryan and Cummings 2013). Instances of this kind have been reported for female anurans that prefer frequencies lower than the mean dominant frequency of conspecific calls and relatively long call durations and call rates (reviewed in Gerhardt and Huber 2002; Simmons 2013). Responsiveness to sounds not related to natural signals has been attributed to hidden recognition preferences by neural systems in different anurans (Arak and Enquist 1993). All these factors are relevant to account for recognition spaces of signals that are highly tolerant and broader than signal variation in many tropical anurans (Amézquita et al. 2011; Erdtmann et al. 2011; Vélez et al. 2012).

In addition to advertisement calls, a number of anurans produce aggressive calls during agonistic interactions among males. The structure of these vocalisations is diverse and in some cases their design is similar to the conspecific advertisement call, resulting from graded variation of temporal components relative to this signal (reviewed in: Wells 2007; Wells and Schwartz 2007). This signalling mode may allow males to assess rivals' competitive ability while preserving the attractiveness of signal structure for females (Wells and Schwartz 1984; Wells 1989; Grafe 1995). Male vocal responses to aggressive calls are different from those to advertisement calls, as subjects produce more aggressive calls when exposed to this kind of vocalisation (Wells 2007). These agonistic signals contribute to expand the range of acoustic parameters having communication significance within a given species and may contribute to the relative broadness of the anuran acoustic recognition spaces reported by different authors (Amézquita et al. 2011; Erdtmann et al. 2011; Vélez et al. 2012). Heterospecific aggressive acoustic interactions have been reported to occur among different treefrog ensembles (Schwartz and Wells 1985; Reichert and Gerhardt 2014) widening the extent of signal exchange in natural settings.

The Batrachylidae frog *Batrachyla leptopus* and its congeneric species *B. antartandica* and *B. taeniata* in southern Chile are well suited for studying male responses to different temporal components of sounds of biological significance. These frogs produce advertisement calls composed of short tonal pulses of about 5 ms, repeated in species-specific patterns, but they are spectrally similar, as the dominant frequency of the calls of the three species is about 2 kHz. The calls of *B. taeniata* and *B. antartandica* have a simple temporal structure, with isolated pulses repeated at different rates (40–80 pulses/s and 1–3 pulses/s, respectively, Penna and Veloso 1990; Penna 1997; Penna et al. 1997, 2019), whereas the call of *B. leptopus* has a complex structure relative to the other species, with pulses closely packed in notes repeated at a note rate of 13–17 notes/s (Penna and Veloso 1990; Penna 1997; Penna and Toloza 2014). This frog is found in extensive areas of sympatry with one or the other congener in the

temperate austral forest region; however, at localities where they overlap, chorusing activity typically segregates into monospecific chorusing aggregations. In addition to the advertisement call, *B. leptopus* produces aggressive calls having longer duration and higher number of notes than the first vocalisation. The aggressive call also includes notes with fewer pulses and thus shorter note duration relative to the notes of the advertisement call (Penna 1997, 2005, Figure 1).

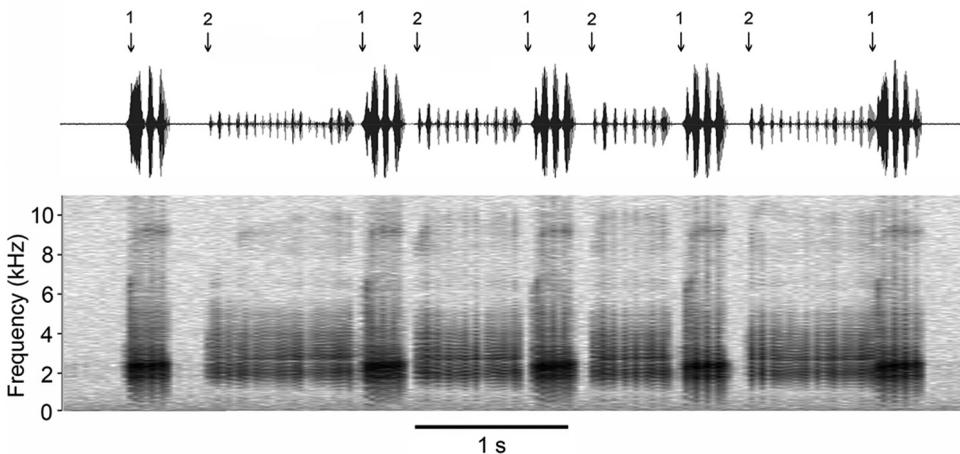
More than two decades ago we conducted initial explorations on the evoked vocal responses of *Batrachyla* frogs to temporal patterns of the signals (Penna 1997). Playback experiments with *B. leptopus* were restricted to a limited set of temporal variables, mainly note rate, and pilot explorations on the effects of note duration and envelope (Penna 1997), but the effects of other temporal variables such as the number of notes and pulse rate, have not been reported.

Unpublished field experiments conducted during our early research with *B. leptopus* are relevant to identify patterns of EVRs that conform to recognition of conspecific advertisement and aggressive calls, unveiling relatively broad ranges of responses to temporal parameters that may also comprise heterospecific calls as well as features not related to natural signals. The results of the current study also provide insights to interpret more recent studies on strategies used by males of *B. leptopus* to confront acoustic interferences of biotic origin (Penna and Toloza 2014).

## Materials and methods

### Study site

This field study was conducted during March and April 1994–1995 at a natural breeding site in the locality of Cucao, Chile (43° 40'S, 74°00' W, 20 m elevation) on the northern



**Figure 1.** Oscillogram and spectrogram of the calls of two interacting males of *Batrachyla leptopus* positioned at an estimated distance of 20 cm from each other at the study site. One individual (#1) emits advertisement calls and the other (#2) aggressive calls. Arrows and numbers indicate the onset of their respective vocalisations. Air temperature: 10°C, substrate temperature: 12°C (sampling rate: 44.1 kHz, frequency resolution: 20 Hz).

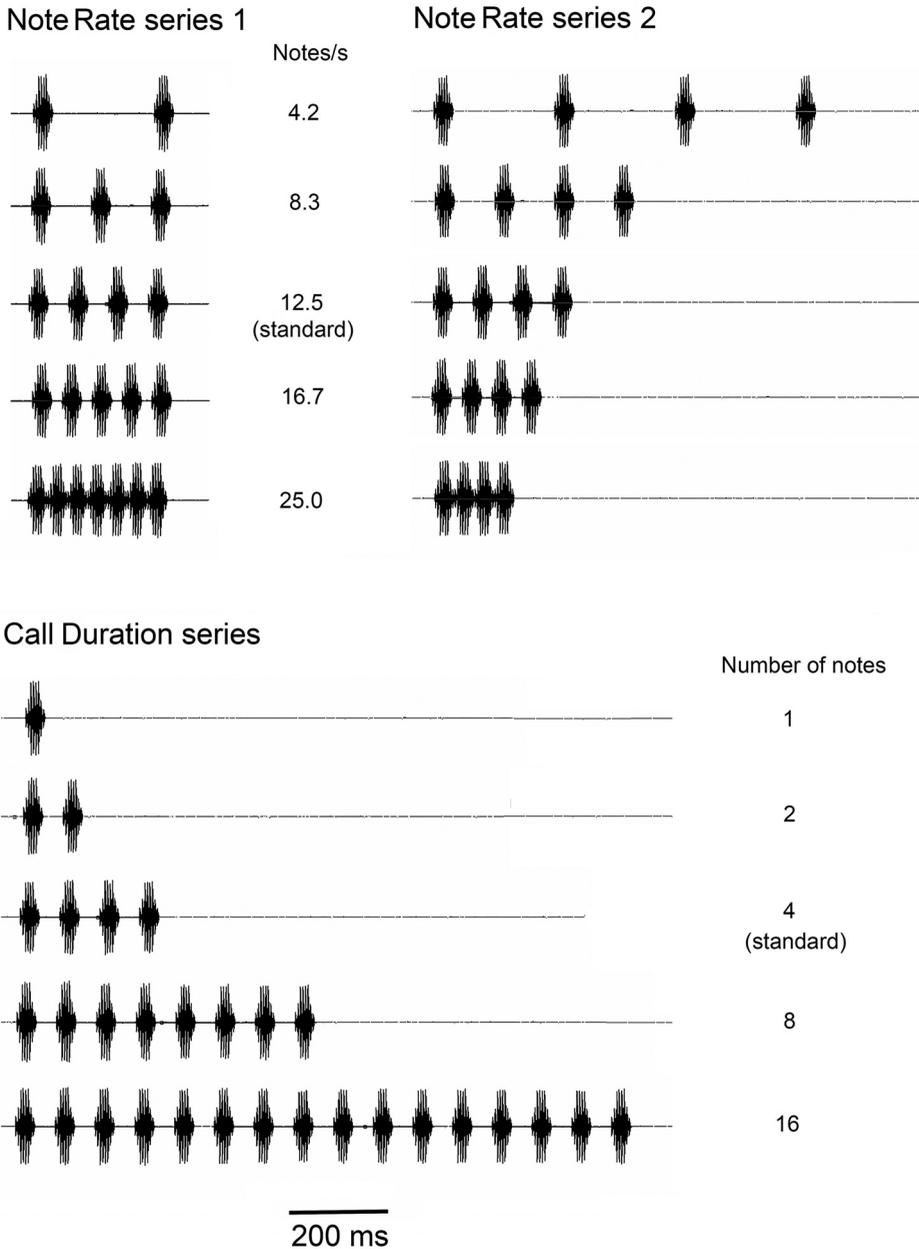
shore of Cucao Lake. Males called from small crevices, hidden among mosses (*Rhacomitrium*), grasses (*Scirpus*) or ferns (*Blechnum*) along the borders of small streams. The frogs were not captured after recording, as it was exceedingly difficult to locate their exact position amid the dense vegetal substrate at the study site.

### Stimuli

Synthetic stimuli were built with a waveform synthesiser (Quatech WSB-100) and recorded on metal cassette tape (TDK MA) with a Sony TK-444 ES II cassette recorder (frequency response 20–19,000 Hz). A ‘standard’ synthetic call was modelled after the species advertisement call recorded in the same study site in previous years at air temperatures of 7.8–12.1°C (Penna 1997). The temporal and spectral parameters used were close to the averages of natural calls at these temperatures and have proved to be effective for eliciting EVRs of males of *B. leptopus* in previous work conducted at the study site (Penna 1997). The standard stimulus consisted of four notes of 40 ms duration, composed of eight pulses of 5 ms duration (rise time: 1 ms; fall time: 4 ms). The first and last pulses within a note had 25% and the second and penultimate pulses had 50% of the maximum amplitude of the four centre pulses. The interval between notes was 40 ms (note rate: 12.5 notes/s) and the call duration was 280 ms. Fifteen call repetitions were presented with an inter-call period of 1.5 s. Series of stimuli were designed to present subjects with sounds deviating from the advertisement call pattern in various temporal components. A 2.1 kHz sinusoidal carrier was used for this stimulus and for the different series of stimuli described below.

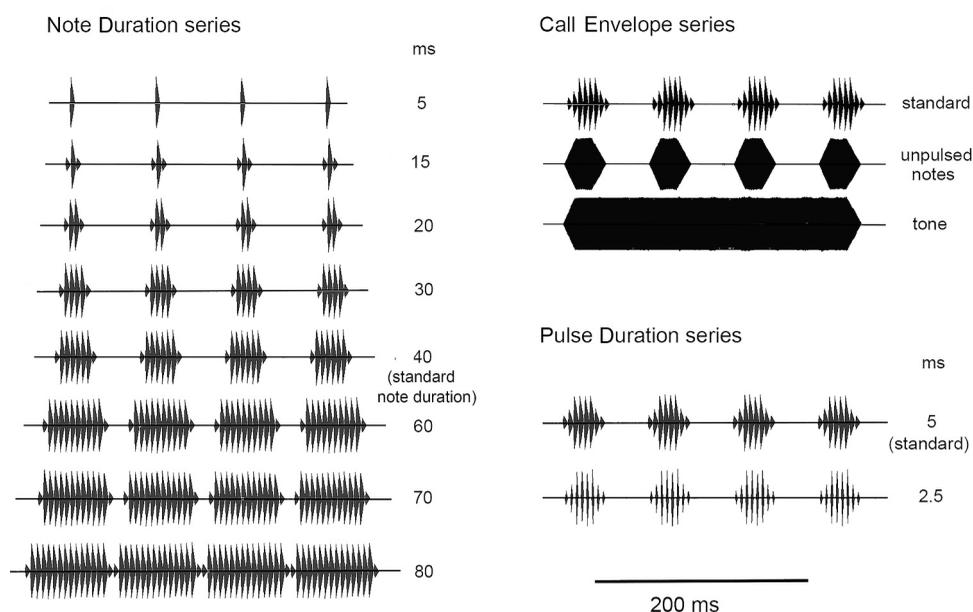
To assess the effect of note rate on EVRs, we constructed two series of synthetic stimuli with different note rates ranging from 4.2 to 25 notes/s. Note Rate series 1 had a constant call duration and Note Rate series 2 had a constant number of notes (Figure 2). A Call Duration series was composed of stimuli containing different number of notes per call (1 to 16 notes, Figure 2). The spectral structure of these stimuli was similar, with side bands around the dominant frequency, as shown in the graphs in Figure S1. The Note Duration series consisted of stimuli with different numbers of 5-ms pulses per note. A standard Note Duration stimulus was composed of four 40-ms notes built with eight pulses, the first and last of which had 25% of the maximum amplitude of the centre pulses. The rest of the stimuli of this series had a similar design, but the notes were composed of different numbers of pulses (1–16 pulses, 5–80 ms note duration, respectively, Figure 3). A Call Envelope series included a stimulus consisting of four unpulsed notes of 40 ms and a tone of 280 ms duration (Figure 3). A Pulse Duration series consisted of a stimulus composed of 2.5-ms and a stimulus composed of 5-ms pulses (Figure 3). The spectral structure of the stimuli of the Note Duration series differed, as stimuli of longer note duration had more prominent side bands relative to shorter note duration sounds. Stimuli of the Call Envelope series differed in their spectral structure, as the two stimuli lacking 5 ms pulses had spectra centred at the dominant frequency, lacking the side band structure of the standard stimulus. The two stimuli of the Pulse Duration series had similar spectral structures with prominent side bands (Figure S2).

In addition to the six series of stimuli having notes with linear rise-fall ramps, three series of stimuli were built composed of notes with a sinusoidal amplitude modulation. A sinusoidal pulse amplitude modulated (SPAM) series consisted of stimuli composed of



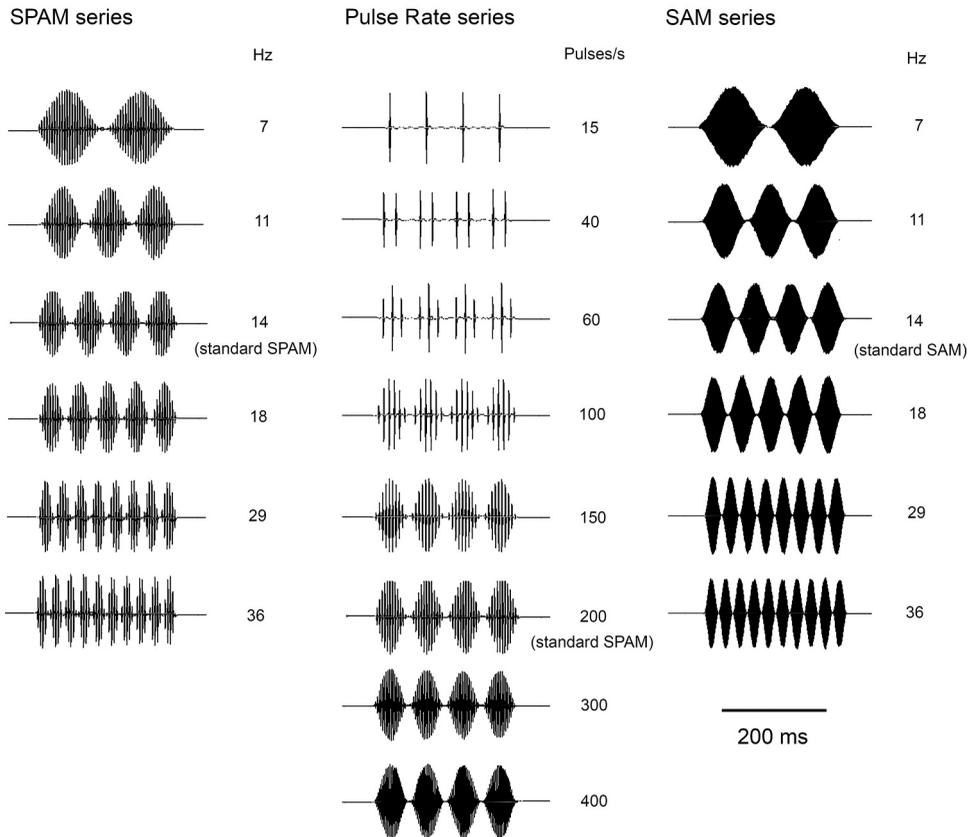
**Figure 2.** Schematic diagrams of Note Rate series 1, Note Rate series 2 and Call Duration series. Time scale is the same for all stimuli.

2.5 ms pulses with a constant pulse rate of 200 pulses/s which were amplitude modulated at rates of 7–36 Hz. The stimuli of these series had a constant duration of 280 ms and therefore a number of notes that increased with note rate. The standard SPAM stimulus had a 14 Hz amplitude modulation and contained four notes. A series of sinusoidal amplitude-modulated (SAM) stimuli lacking a pulsed structure was also built following



**Figure 3.** Schematic diagrams of Note Duration series, Call Envelope series and Pulse Duration series. Time scale is the same for all stimuli.

the same note rate design as the SPAM series, and the standard SAM stimulus was amplitude modulated at a rate of 14 Hz. Finally, stimuli for a Pulse Rate series were built with a 14-Hz sinusoidal amplitude modulation containing pulses of 2.5 ms duration, repeated at rates encompassing a range of 15–400 pulses/s (and thus a different number of pulses per note). The standard stimulus for this series was the same as for the SPAM series, with a pulse rate of 200 pulses/s (Figure 4). The spectral structure of the SPAM series presented prominent, similar side bands for the six stimuli comprising this series. In contrast, the spectra of the SAM stimuli were centred at the dominant frequency, lacking side bands. The spectra of the Pulse Rate series differed among the stimuli, as the prominence of the side bands increased with pulse rate (Figure S3). All the stimuli of the different series were equalised at the same peak sound pressure level (SPL), but the relationship between that value and the effective or root-mean-square (RMS) value differed among series. In Note Rate series 1 and 2, this difference decreased from 15 to 10 dB between the stimuli having the lowest (4.2 notes/s) and highest (25 notes/s) note rate, respectively. In the Note Duration series, the difference between the peak and RMS value decreased from 19 to 8 dB between the stimuli having the shortest (5 ms) and longest (80 ms) note duration. In the Call Duration series, the difference between the peak and the RMS value was constant at 12 dB. In the Pulse Duration series, the differences between the peak and RMS value were 12 and 15 dB for the standard and 2.5 ms stimulus, respectively. In the Call Envelope series, the differences between the peak and RMS values were 12, 8 and 4 dB for the standard, unpulsed notes and tone stimulus, respectively. In the SPAM and SAM series with sinusoidal amplitude modulation at different rates (7–36 Hz), the differences between peak and RMS values within



**Figure 4.** Schematic diagrams of Sinusoidal Pulse Amplitude Modulation (SPAM) series, Pulse Rate series and Sinusoidal Amplitude Modulation (SAM) series. Time scale is the same for all stimuli.

each series were constant at 13 and 7 dB, respectively. In the Pulse Rate series, the differences between the peak and RMS values decreased from 21 to 10 dB between the stimuli having the lowest (15 pulses/s) and highest (400 pulses/s) pulse rates.

### **Experimental set-up and protocol**

Synthetic stimuli were played back with a cassette recorder (Sony TC-D5M, frequency response 20–19,000 Hz), fed into an impedance-matched operational amplifier, attenuators (Hewlett-Packard 355 C and D, frequency response 0–100,000 Hz), a power amplifier (Alpine 3540, frequency response 10–50,000 Hz) and a loudspeaker (JBL T-50, frequency response 40–24,000 Hz). The loudspeaker was positioned 0.8–1.2 m in front of the experimental subject. EVRs were recorded with a directional microphone (AKG CK8 or CK9, frequency response 30–18,000 Hz), the tip of which was placed 0.1–0.3 m in front of the calling frog. Calls were recorded on the left channel of a second cassette recorder (Sony TC-D5M). The stimuli delivered were recorded via a connecting cable from the line output of playback cassette recorder to the right line input of this second recorder.

Experiments were conducted between 2100 and 0400 hr. Air and substrate temperatures monitored with a digital thermometer (Digi-Sense 8528–20) during recordings were between 8.0–11.8°C and 10.8–14.2°C, respectively. Spontaneous basal vocal activity of the subjects before beginning playbacks was recorded for an average time of 308 s (range = 110–790 s). Thereafter, the synthetic stimuli were presented and the animal's EVR recorded. Special care was taken to suppress vocal activities of neighbouring frogs so that the EVR of individual frogs could be recorded without interference. This was achieved by gently tapping the substrate near the perching sites of the neighbours. Nine series of stimuli were presented, and within each series the stimuli were presented in a random order, in which a particular stimulus type was followed by a different one, using a different sequence for each frog. The stimuli series were presented in a fixed order as follows: (1) Note Rate series 1: 4.2, 8.3, 12.5 (standard 1), 16.7 and 25.0 notes/s; (2) Note Rate series 2: 4.2, 8.3, 16.7 and 25.0 notes/s; (3) Note Duration series: 5, 15, 20, 30, 40 (standard note duration), 60, 70 and 80 ms; (4) Call Duration series: 1, 2, 8 and 16 notes; (5) Call Envelope series: unpulsed notes and continuous tone; (6) Pulse Duration series: 2.5 and 5 ms (standard); (7) SPAM series: 7, 11, 14 (standard SPAM), 18, 29 and 36 Hz; (8) Pulse Rate series: 15, 20, 40, 100, 150, 300 and 400 pulses/s; (9) SAM series: 7, 11, 14 (standard SAM), 18, 29 and 36 Hz. Within each series, 15 repetitions of each stimulus were delivered and intervals of 30 s elapsed between the presentation of stimulus repetitions having the same temporal structure and the following repetitions of a different design. An interval of 3 min elapsed between the end of the presentation of the first six series, for which note amplitude was modulated with linear rise-fall ramps and the three last series, built with sinusoidal amplitude modulations. The presentation of the six first series of stimuli lasted 23 min and the last three 17 min, that is, a total of about 43 min.

After completing the presentation of these nine series of stimuli, a series of 15 repetitions of standard stimulus delivered at increasing SPLs in 6- or 12-dB steps were presented to nine of the eleven experimental subjects, encompassing a total range of 34–103 dB peak SPL (equivalent to 22–91 dB SPL RMS). This series is referred to as the SPL series. The number of bouts of 15 stimulus repetitions was different for the subjects (range: 8–11), depending mostly on the stability of environmental conditions allowing the maintenance of an already prolonged stimulation needed for the presentation of the preceding nine series of stimuli of different temporal structure. An order of increasing amplitude was employed for stimulus presentation to minimise possible effects of high-amplitude exposures on subsequent vocal activity of the subjects. The absolute SPL values of bouts of stimuli repetitions presented at increasing levels were not the same for all the individuals tested, as the level at which the standard stimulus was delivered at the position of the experimental subject during the presentation of series with different temporal structure was not set before beginning the experiment, but measured after completing the experimental session for each individual, to minimise disturbances to the subject. After the presentation of all the series of stimuli to an experimental subject, the peak SPL of the standard stimulus was measured setting the attenuators at values at which the series of stimuli of different temporal structure had been presented, with the microphone of a sound level meter (Bruel & Kjaer 2230) positioned at the location of the calling frog pointing towards the loudspeaker, using a linear frequency weighting scale. This standard stimulus peak SPL was maintained as uniform as possible among all

individuals tested, by varying the placement of the loudspeaker according to the topography of the site. The amplitude of the stimulus at the position of the subjects turned out to be within a range of 86–94 dB peak SPL.

### **Data analysis**

The EVR of a frog was measured as call rate and call duration produced during the presentation of a bout of 15 repetitions of a stimulus. Calls produced between the onset of the first stimulus repetition of a bout and 1.5 s after the onset of the 15<sup>th</sup> stimulus repetition were computed as EVRs. Recordings were digitised with a Macintosh computer (Power PC 7100) fitted with 104 MB RAM expansions, using Signalyze 3.12 software.

EVR measures within a stimulus series were analysed with generalised linear mixed effects models (GLMMs) or linear mixed effects models (LMMs), in which GLMMs and LMMs were used for call rate and call duration, respectively. A Poisson family with a log link was used to fit the models for call rate. Individual intercepts were included as random effects in order to control for data dependence. Stimulus type and temperature were included as fixed effects, and p-values were obtained using a parametric bootstrap procedure with 1000 simulations procedure implemented in R (version 4.0.2, R Core Team 2020) library ‘afex’ (Singmann et al. 2020). Call durations of EVRs were log-transformed in order to normalise data, the only exceptions being for the NR2 and PD stimulus series. When the effect of stimulus type was significant, *a posteriori* paired contrasts between standard stimuli and stimulus variants were performed using the ‘emmeans’ library (Lenth 2020).

The effect of SPL on call duration and call rate was evaluated by linear regression analyses performed for each subject. This analysis was performed for nine individuals, as two individuals exposed to less than eight different SPLs were excluded.

## **Results**

### **Basal calling activity**

The eleven individuals called regularly during the period of basal call recording, producing an average of 42.1 calls/min (range: 35.5–52.1 calls/min) during bouts of calling activity. Call duration averaged 270 ms (range: 149–412 ms); the dominant frequency was 2332 Hz (range: 2129–2583 Hz). The average values are close to the parameter values employed to design the standard call used in this study.

### **Evoked vocal responses**

Males of *B. leptopus* typically started responding shortly after the beginning of a bout of 15 repetitions of the standard stimulus, and vocalised mostly during intervals between stimulus repetitions, alternating their emissions with the synthetic calls. All the experimental subjects gave EVRs to the standard stimulus presented at different times of the experimental schedule. Temperature had no effect on call rate or call duration in responses to any of the nine series of stimuli of different temporal structure analysed (Table 1).

**Table 1.** Results of linear mixed models (LMMs) and generalised linear mixed models (GLMMs) performed for call duration and call rate, respectively, in which responses to stimuli with different temporal variables were evaluated. Temperature substrate was also incorporated in the analyses. Significant factors are in bold.

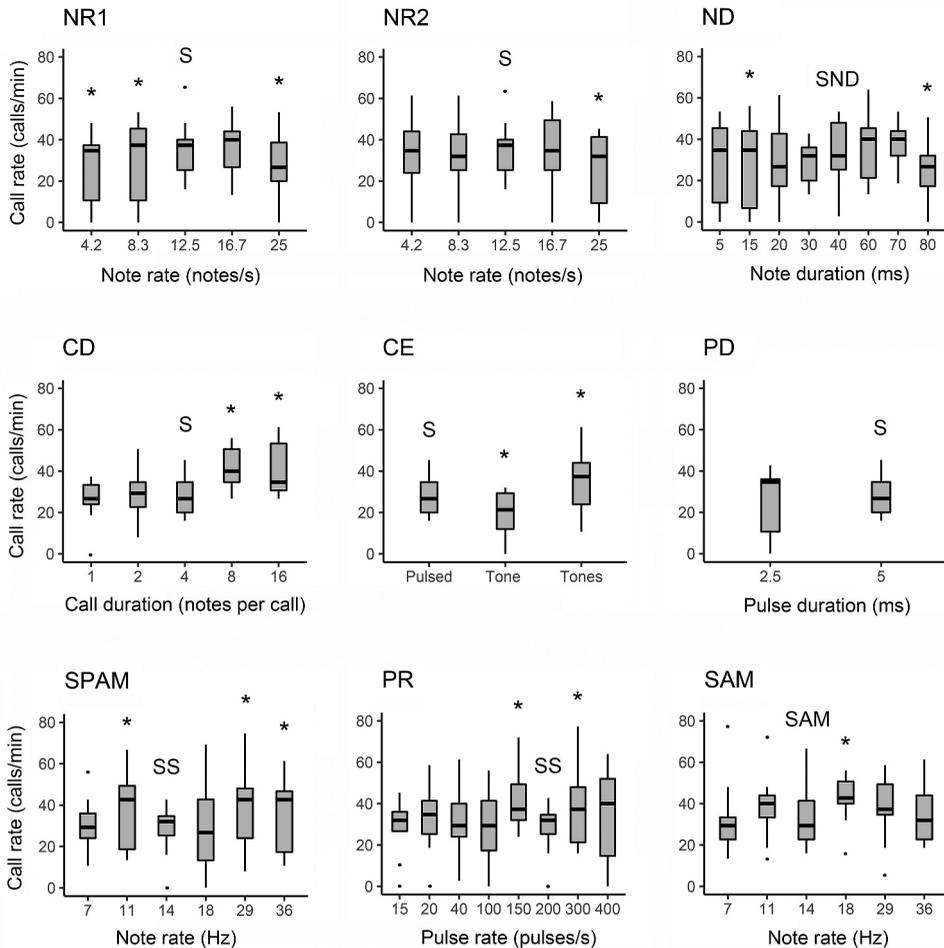
Response variable	Stimuli series	Factor	df	$\chi^2$	p-val
Call rate	Note Rate 1	Stimulus	4	29.62	<b>&lt;0.001</b>
		Temperature	1	0.00	0.996
	Note Rate 2	Stimulus	4	19.45	<b>&lt;0.001</b>
		Temperature	1	2.68	0.149
	Note Duration	Stimulus	7	48.61	<b>&lt;0.001</b>
		Temperature	1	0.76	0.433
	Call Duration	Stimulus	4	79.42	<b>&lt;0.001</b>
		Temperature	1	2.88	0.141
	Call Envelope	Stimulus	2	58.16	<b>&lt;0.001</b>
		Temperature	1	0.63	0.466
	Pulse Duration	Stimulus	1	2.45	0.125
		Temperature	1	0.24	0.673
	SPAM	Stimulus	5	22.42	<b>0.002</b>
		Temperature	1	1.87	0.238
	Pulse Rate	Stimulus	7	51.90	<b>&lt;0.001</b>
		Temperature	1	0.00	0.964
	SAM	Stimulus	5	21.47	<b>0.002</b>
		Temperature	1	1.80	0.245
Call duration	Note Rate 1	Stimulus	4	1.76	0.803
		Temperature	1	2.13	0.193
	Note Rate 2	Stimulus	4	5.54	0.303
		Temperature	1	4.67	0.062
	Note Duration	Stimulus	7	23.93	<b>0.003</b>
		Temperature	1	2.17	0.206
	Call Duration	Stimulus	4	2.49	0.703
		Temperature	1	3.23	0.108
	Call Envelope	Stimulus	2	12.62	<b>0.003</b>
		Temperature	1	2.06	0.184
	Pulse Duration	Stimulus	1	0.91	0.431
		Temperature	1	1.94	0.230
	SPAM	Stimulus	5	28.66	<b>&lt;0.001</b>
		Temperature	1	2.38	0.18
	Pulse Rate	Stimulus	7	25.5	<b>&lt;0.001</b>
		Temperature	1	0.72	0.440
	SAM	Stimulus	5	21.3	<b>&lt;0.001</b>
		Temperature	1	0.33	0.596

### Note Rate series 1

Frogs normally responded strongly to stimuli having intermediate note rates and responded with lower call rates to stimuli having extreme values of this parameter. The analysis showed that call rate differed significantly among stimulus types ( $X^2_{(4)} = 29.62$ ,  $p < 0.001$ ). *A posteriori* pairwise contrasts indicated that call rate to the standard stimulus (12.5 notes/s) was higher relative to the stimuli of 4.2, 8.3 and 25 notes/s (Figure 5, Table S1). Call duration did not differ significantly among stimulus types ( $X^2_{(4)} = 1.76$ ,  $p = 0.803$ ; Figure 6, Table S2).

### Note Rate series 2

Frogs responded to this series in a less selective mode than to the preceding series, giving weaker responses to higher values of stimulus note rate. The analysis showed that call rate differed significantly among stimulus types ( $X^2_{(4)} = 19.45$ ,  $p < 0.001$ ). *A posteriori* pairwise contrasts indicated that call rate to the standard stimulus (12.5 notes/s) was

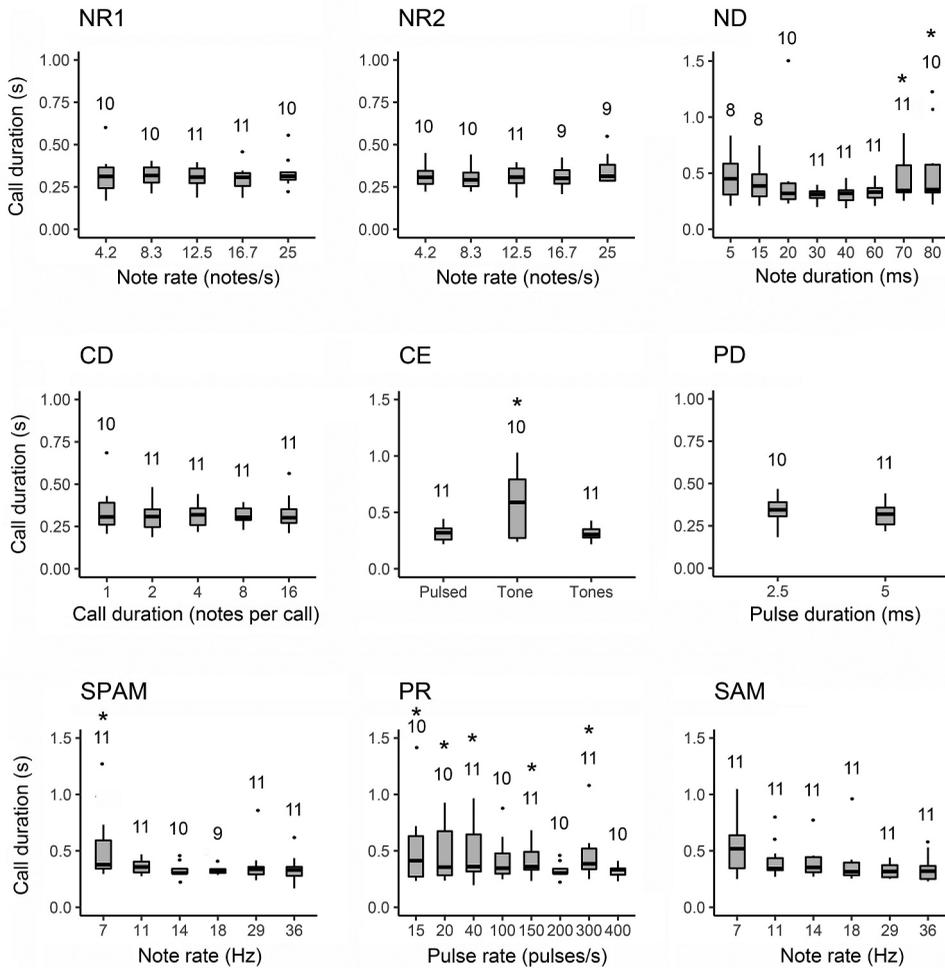


**Figure 5.** Call rate of males of *B. leptopus* in response to playbacks of series of stimuli in which different temporal components of synthetic calls were modified. Boxes correspond to first and third quartiles and horizontal lines inside boxes to second quartiles (medians). Vertical lines above and below the boxes correspond to 1.5 interquartile ranges, and dots correspond to outliers. Abbreviations: S: Standard stimulus, SND: Standard note duration stimulus, SS: Standard sinusoidal pulse amplitude-modulated stimulus, SAM: Standard sinusoidal amplitude-modulated stimulus. Asterisks indicate stimuli variants for which responses differ significantly from those to the corresponding standard stimulus.

higher than to the stimulus of 25 notes/s (Figure 5, Table S1). Call duration did not differ significantly among stimulus types ( $X^2_{(4)} = 5.54$ ,  $p = 0.303$ ) (Figure 6, Table S2).

### Note Duration series

Frogs showed a tendency to respond with lower call rates to stimuli having extreme note durations. The analysis showed that call rate differed significantly among stimulus types ( $X^2_{(7)} = 48.61$ ,  $p < 0.001$ ). Significant *a posteriori* pairwise contrasts showed that the call rates in response to the stimuli composed of notes of 15 and 80 ms pulses were lower than to the standard stimulus (40 ms) (Figure 5, Table S1). Call duration differed significantly



**Figure 6.** Call duration of males of *B. leptopus* in response to playbacks of series of stimuli in which different temporal components of synthetic calls were modified. Symbols and abbreviations as in Figure 5. Numbers above the boxes indicate the numbers of animals that emitted calls during the presentation of the different stimuli.

among stimulus types ( $X^2_{(7)} = 23.93$ ,  $p = 0.003$ ). *A posteriori* pairwise contrasts showed that call duration in response to the stimuli composed of notes of 70 and 80 ms was longer than to the standard stimulus (40 ms) (Figure 6, Table S2).

**Call Duration series**

Frogs showed a tendency to respond with higher call rates to stimuli having longer call durations. The analysis showed significant differences in call rate among responses to stimulus types ( $X^2_{(4)} = 79.42$ ,  $p < 0.001$ ). *A posteriori* pairwise contrasts showed that call rate in response to the stimuli composed of 8 and 16 notes was higher than in response to the standard stimulus (4 notes) (Figure 5, Table S1). Call duration did not differ significantly among stimulus types ( $X^2_{(4)} = 2.49$ ,  $p = 0.703$ ) (Figure 6, Table S2).

### **Call Envelope series**

Frogs responded with different call rates to this series of stimuli ( $X^2_{(2)} = 58.16$ ,  $p < 0.001$ ). A *posteriori* pairwise contrasts showed that call rate in response to the stimuli of unpulsed notes and continuous tone were higher and lower relative to the standard stimulus, respectively (Figure 5, Table S1). Call duration also showed significant differences ( $X^2_{(2)} = 12.62$ ,  $p = 0.003$ ). A *posteriori* pairwise contrasts showed that call duration in response to the continuous tone was significantly longer than in response to the standard stimulus (Figure 6, Table S2).

### **Pulse Duration series**

Frogs' responses to the stimulus composed of pulses of 2.5 ms duration were similar relative to the standard stimulus (5 ms) in terms of call rate ( $X^2_{(1)} = 2.45$ ,  $p = 0.125$ ) and call duration ( $X^2_{(1)} = 0.91$ ,  $p = 0.431$ ). (Figures 5 and 6, Tables S1 and S2).

### **SPAM series**

Frogs responded with different call rates to this series of stimuli ( $X^2_{(5)} = 22.42$ ,  $p = 0.002$ ). A *posteriori* pairwise contrasts showed that call rate in response to the stimuli of 11, 29 and 36 Hz was higher than to the standard stimulus (14 Hz) (Figure 5, Table S1). Call duration differed significantly among stimulus types ( $X^2_{(5)} = 28.66$ ,  $p < 0.001$ ). A *posteriori* pairwise contrasts showed that call duration in response to the stimulus of 7 Hz was longer than to the standard stimulus (14 Hz) (Figure 6, Table S2).

### **Pulse Rate series**

Frogs responded with different call rates to this series of stimuli ( $X^2_{(7)} = 51.90$ ,  $p < 0.001$ ). A *posteriori* pairwise contrasts showed that call rate in response to the stimuli of 150 and 300 Hz was higher than to the standard stimulus (200 Hz) (Figure 5, Table S1). Call duration differed significantly among stimulus types ( $X^2_{(7)} = 25.50$ ,  $p < 0.001$ ). A *posteriori* pairwise contrasts showed that call duration in response to the stimuli of 15, 20, 40, 150 and 300 Hz were longer than to the standard stimulus (200 Hz) (Figure 6, Table S2).

### **SAM series**

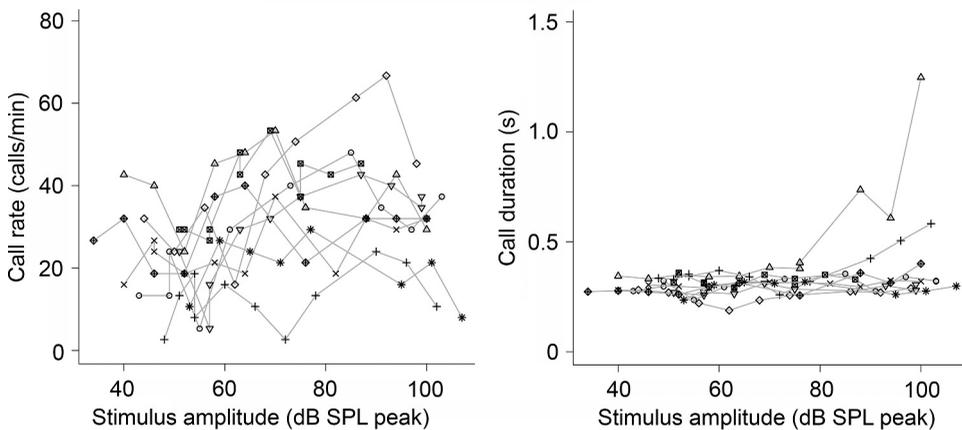
Frogs responded with different call rates to this series of stimuli ( $X^2_{(5)} = 21.47$ ,  $p = 0.002$ ). A *posteriori* pairwise contrasts showed that call rate in response to the stimulus of 18 Hz was higher than to the standard stimulus (14 Hz) (Figure 5, Table S1). Call duration differed significantly among stimulus types ( $X^2_{(5)} = 21.30$ ,  $p < 0.001$ ), but a *posteriori* pairwise contrasts showed no significant differences between any stimulus type and the standard stimulus (14 Hz) (Figure 6, Table S2).

### **SPL series**

The nine subjects tested with this series responded steadily to standard stimulus of increasing amplitude. There were significant relationships between SPL and call rate ( $N = 4$ ) and between SPL and call duration ( $N = 4$ ; not the same individuals as for call rate,  $p < 0.05$ , Table 2, Figure 7). However, the values reached for these acoustic variables in response to stimuli of high SPLs were lower than the maxima values obtained in responses to the different series of stimuli of different temporal structure. This difference

**Table 2.** Results of linear regressions for call duration and call rate variations associated to stimuli SPL. The analyses were performed for each individual by separate. Significant regressions are in bold.

Response variable	Individual	df	F	p-val
Call duration	BL94-1	1,9	2.80	0.129
	BL94-2	1,9	12.81	<b>0.006</b>
	BL94-3	1,9	11.30	<b>0.008</b>
	BL94-4	1,9	8.82	<b>0.016</b>
	BL94-5	1,7	0.85	0.387
	BL94-6	1,8	4.20	0.075
	BL94-7	1,9	0.29	0.601
	BL95-1	1,6	<0.01	0.993
	BL95-2	1,8	9.91	<b>0.014</b>
	Call rate	BL94-1	1,9	10.47
BL94-2		1,9	0.46	0.517
BL94-3		1,9	1.75	0.219
BL94-4		1,9	3.99	0.077
BL94-5		1,7	9.28	<b>0.019</b>
BL94-6		1,8	10.51	<b>0.012</b>
BL94-7		1,9	6.71	<b>0.029</b>
BL95-1		1,6	0.72	0.430
BL95-2		1,8	0.67	0.438



**Figure 7.** Call rate and call duration of males of *B. leptopus* in response to playbacks of the standard stimulus at different sound pressure levels. Different symbols identify nine subjects that were exposed to this experimental situation.

was particularly clear for call duration, as the maximum call duration ranged between 324 and 1247 ms for the four individuals in which a significant regression between stimulus SPL and note duration occurred, whereas the maximal values obtained in responses to the series with different temporal structure ranged between 943 and 1413 ms.

**Discussion**

Our results show that EVRs of males of *B. leptopus* depend on different temporal acoustic characteristics, showing dissimilar response patterns to different series of stimuli in terms of call rate and call duration. The animals continued to respond throughout the presentation of

the entire sequence of stimulus series and some of the stimulus variants evoked vocalisations featuring aggressive call patterns.

### **Selectivity for note rate**

Note rate had a substantial effect on EVRs in terms of evoked call rates; the effect was more pronounced for Note Rate series 1 compared to Note Rate series 2, as significant differences in call rate occurred between the standard stimulus (12.5 notes/s) and three and one variants, respectively, within the notes/s range employed (Table 1). It is apparent that frogs tended to respond less to stimuli with high note rate in both series of stimuli, as frogs tended to lower their call rates either if the stimulus has a constant (Note Rate series 1) or shorter (Note Rate series 2) duration, as well as to stimuli having low note rates and constant duration (Note Rate series 1). However, responses to these series of stimuli do not show significant changes in call duration. A qualitative classification of EVRs functions, as employed in a former study on the congeneric species *B. antartandica* (Penna et al. 1997) would indicate that in terms of call rate, responses to Note Rate series 1 show a band-pass or stabilising response pattern that shifts to a low-pass directional response type if the stimulus duration is shortened at high rates.

Such response patterns contrast with those obtained for series in which note rate was varied using different rates of sinusoidal amplitude modulation (SPAM and SAM series). For the SPAM modality, frogs showed a tendency to respond with higher call rates to stimuli having note rates lower and higher than the standard stimulus, a pattern corresponding to a response function inverted relative to that of Note Rate series 1, namely band suppression. In responses to the SAM series, only one stimulus having high note rate relative to the standard stimulus elicited a higher call rate and thus no clear function pattern can be assigned here.

Contrasting response patterns of call duration were also obtained between Note Rate series 1 and 2 versus the sinusoidal amplitude-modulated series, as flat, all-pass functions were obtained in the first case and descending low-pass functions in the second case.

The contrast between results obtained for Note Rate series 1 and 2, which have constant and linear rise-fall times, and those for sinusoidally modulated stimulus series suggest that note envelope is relevant for signal recognition, as patterns of response selectivity are altered if this temporal feature is modified. The dissimilar modes of responses between series of stimuli in which note rate varied following a different general design may result from interactive effects of different temporal variables on responses, as has been reported to occur for female phonotactic responses in treefrogs (Gerhardt and Doherty 1988; Gerhardt and Huber 2002).

### **Selectivity for note duration and pulse duration**

Note duration affected the EVRs of the subjects, as significant lower call rates relative to the standard stimulus were observed during exposures to extremely short and long notes, namely a band-pass function. An opposite effect on call duration of responses was observed, as longer call durations occurred in the responses to short and long notes, corresponding to a band-suppression function. Stimuli of short note duration have

a temporal structure resembling that of aggressive calls, as this is a characteristic of this natural vocalisation. This result identifies note duration as a relevant cue for aggressive call recognition in this frog, as this temporal feature alters the response pattern. Differential vocal responses to advertisement and aggressive calls have also been reported in other anurans, which would allow modulation of vocal interactions according to the competitive context (e.g. Wells 2007).

In contrast to the apparent adaptive character of responses to stimuli composed of short notes, the long calls elicited by stimuli with long note durations are not susceptible to straightforward interpretations, but can be combined with results obtained in responses to the SPAM, SAM and Call Envelope series, as discussed below. No effects of pulse duration of the stimulus were observed in terms of call rate or call duration of the responses, as the range of variation was restricted to the standard stimulus and a single variant, due to constraints imposed by the stimulus structure.

### **Selectivity for call duration**

Males of *B. leptopus* had a tendency to respond with higher call rates to stimuli having durations longer than the standard call; however, the call duration of the responses was not affected by this stimulus variable. Accordingly, the response function is of the high-pass type for call rate and all-pass for call duration. The stronger responses in terms of call rate to long calls indicate that animals are prompted to respond to a feature characteristic of the aggressive calls of this species, but the increased responsiveness does not affect the aggressiveness of the calls emitted. Similar directional patterns with stronger responses for longer calls have been reported for the congeneric species *B. taeniata* (Penna and Velásquez 2011). Preferences for longer calls have been reported for the phonotactic responses of female anurans of a number of different species and are related to offspring benefits in the North American treefrog *Hyla versicolor* (Welch et al. 1998). By responding with higher call rates to stimuli of longer duration, male anurans likely increase their chances to overcome the higher interference imposed by longer calls of competitors. The lack of effect of call duration of the stimulus on call duration of the evoked responses indicates that this parameter is not relevant for eliciting aggressive patterns of response in this frog.

### **Selectivity for pulse rate**

Males of *B. leptopus* have a tendency to respond with higher call rates to stimuli having pulse rates slightly lower and higher than the standard call, and thus no clear EVR function can be assigned in this case. However, a strong result for this stimulus series is the clearly longer duration of the responses to stimuli having lower pulse rates relative to the standard call, that is, a low-pass EVR function. Stimuli of low pulse rates have a temporal structure resembling that of aggressive calls, as low pulse rates result in notes composed of low numbers of pulses, that is, shorter notes, a characteristic of this natural vocalisation. This result concurs to support the effectiveness of note duration in governing recognition of aggressive calls in this frog. The different male vocal responsiveness to advertisement and aggressive calls allows modulation of vocal interactions according to the competitive context in a number of anurans (reviewed in Wells 2007).

### **Selectivity for call envelope, responsiveness to heterospecific and non-natural signals**

Due to the non-systematic variation trend of stimuli in this series, it is not possible to assign EVR functions here. The stimulus composed of unpulsed notes elicited responses with higher call rates relative to the standard stimulus, but call duration is similar in responses to both stimuli. The response pattern to the tone, characterised by long call durations and low call rates resembles the responses to the longer note stimuli of the Note Duration series, and these stimuli resemble the tone in having a temporal structure that tends to continuity, as the intervals between notes are brief. Other sounds that evoke long-duration calls are the stimuli having low amplitude modulation rates in the SPAM and SAM series, and these stimuli are also similar to continuous signals. As such, males of *B. leptopus* tend to respond aggressively to prolonged sounds that have no apparent relationship with conspecific acoustic signals in their fine temporal structure.

Such responsiveness could be related to the capacity of this species to interact with signals produced by other animals. One possible natural stimulus is the call of the congeneric species *B. taeniata*, with which *B. leptopus* occasionally interacts vocally in nature (Penna and Toloza 2014). The call of this congeneric frog lasts about 500 ms and consists of a homogeneous series of pulses, lacking a note structure, thus somewhat resembling stimuli to which the experimental subjects responded with longer calls. Aggressive calling to heterospecific signals has been observed in treefrogs (Schwartz and Wells 1984; Reichert and Gerhardt 2014). Interspecific acoustic signalling also occurs in rodents (Pasch et al. 2013) and birds (Laiolo 2012), and promotes communal signalling among soniferous animals (Malavasi and Farina 2013; Tobias et al. 2014).

The responsiveness to signals differing from natural conspecific calls can be interpreted in contexts different from heterospecific interactions. Responsiveness to sounds not related to natural signals has been accounted for in different anurans in terms of hidden recognition preferences of neural systems (Arak and Enquist 1993), pre-existing sensory bias (Ryan and Rand 1993) and response generalisation (Ryan et al. 2003). These processes have been implied in evoked advertisement calls of various anurans, and our study in *B. leptopus* would indicate that evoked aggressive calling patterns could also be affected by similar evolutionary mechanisms.

In several of the series of stimuli to which the subjects were exposed, variations in the effective energy and spectra of the sounds inherent in differences of temporal structure occurred, and therefore a caveat to be considered to account for the dissimilar responsiveness to stimuli of a given series is the potential influence of the effective amplitude and spectral structure. These issues are addressed in the Supplemental Discussion.

### **Concluding remarks**

Behavioural responses to components of anuran advertisement calls comply with stabilising or directional selection patterns (Gerhardt 1991), corresponding, respectively, to the band-pass and high-pass EVR functions obtained for some of the series of stimuli in our study. These response modes are relevant for species recognition and for evaluating motivation or quality of emitters, respectively (Gerhardt 1991; Bush et al. 2002). Other functions like the band-suppression and low-pass patterns reported in the current study

likely result from responsiveness to features characteristic of aggressive calls, vocalisations that occur extensively in anurans (Wells 2007; Schwartz, 2007). Additional sources for the diverse response patterns observed may be contributed by responsiveness to heterospecific signals (Schwartz and Wells 1985; Reichert and Gerhardt 2014) and to features not present in natural signals (Arak and Enquist 1993). The various response functions thus generated likely contribute to the relative broadness of acoustic recognition spaces reported for male anurans (Amézquita et al. 2011; Erdtmann et al. 2011; Vélez et al. 2012).

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Juan Panza collaborated in the field experiments and Aníbal Martínez collaborated in the data analysis. Albert S. Feng contributed the design of sinusoidal amplitude-modulated signals. Anonymous reviewers contributed comments that strengthened the manuscript.

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No potential conflict of interest was reported by the author(s).

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## Ethical approval

The procedures used in this study comply with the laws of animal welfare in Chile (Protocol CBA # 061 FMUCH).

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