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Diverse patterns of temporal selectivity in the evoked vocal responses of a frog from the temperate austral forest, *Batrachyla taeniata* (Batrachylidae)

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ABSTRACT

Evoked vocal responses of male frogs *Batrachyla taeniata* to synthetic advertisement calls and variants having different temporal features altered parametrically were studied to identify patterns of evoked vocal responses (EVRs) that conform with static and dynamic modes of variation and with corresponding selective processes affected by different temporal components of the acoustic signals. Frogs responded with higher call rates and longer call durations to stimuli of 25–100 pulses/s, resembling conspecific calls. This response mode was not related to spectral differences among stimuli, as frogs responded similarly to a series of stimuli built with noise instead of tones. Frogs responded with lower call rates and shorter call durations to a non-pulsed 500-ms tone having the duration of the complete call, a decrement related to the dissimilar spectral composition of the tone, restricted to a single frequency, as frogs responded strongly to a non-pulsed 500-ms stimulus built with noise instead of a 2.1-kHz sinusoidal. Frogs responded with lower call rates and shorter call durations to synthetic calls composed by 3 or less pulses. The EVRs for pulse rate stimuli series are consistent with a stabilizing selectivity pattern, whereas EVRs for pulse duration and call duration stimuli series conform with directional selectivity patterns.

Introduction

A general requirement for animal communication is the effective detection and processing of signals produced by emitter individuals by the respective sensory channel of receiver individuals (Bradbury and Vehrencamp (2011). The search for a strict matching between both domains oriented initial studies in anuran sound communication, as pioneering studies in *Lythobates catesbeianus* showed that in these frogs auditory sensitivity is tuned to the spectral ranges in which most of the energy of conspecific natural calls is concentrated, providing a sensory basis for signal recognition (e.g. Capranica 1965; Simmons 2013) and recent studies also support such correspondence between signals and auditory sensitivity (e.g. Yang et al. 2018). In the temporal domain,

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components of the natural calls on a fine time scale such as waveform periodicity (Gerhardt 1978), pulse rate (Loftus-Hills and Littlejohn 1971; Straughan 1975; Schwartz 1987; Gerhardt and Doherty 1988), number of pulses (Klump and Gerhardt 1987), and pulse rise time (Gerhardt and Doherty 1988) are essential cues governing female phonotactic responses. Males of different species have been shown to give selective evoked vocal responses (EVRs) to stimuli having temporal parameters within the range of conspecific calls. In particular, selective EVRs occur for waveform periodicity (Capranica 1965; Simmons et al. 1993; Allan and Simmons 1994), pulse rate (Brzoska et al. 1982; Walkowiak and Brzoska 1982; Rose and Capranica 1984), pulse duration (Narins and Capranica 1978), and number of pulses (Walkowiak and Brzoska 1982) typical of natural conspecific vocalizations. Midbrain neurons having response patterns supporting the behavioural selectivities observed have been reported in different anuran 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. 1997a, 2001; Alder and Rose 2000).

In contrast with the literature cited earlier, subsequent studies have stressed the occurrence of mismatches between characteristics of the signals and behavioural preferences. As such, in the spectral domain, female anurans prefer frequencies lower than the mean dominant frequency of conspecific calls and in the temporal domain preferences for relatively long call durations and call rates have been reported (reviewed in Gerhardt and Huber 2002; Simmons 2013). The occurrence of mismatches between emitters and receivers has been related to constraints imposed by environmental factors (Endler 1992; Zhao et al. 2016) or sensory systems (Ryan and Rand 1990; Arak and Enquist 1995).

Diverse components of anuran acoustic signals have been classified based on their low or high intra-individual variation as static or dynamic, respectively, and have been proposed to be subjected to stabilizing and directional selection processes, respectively (Gerhardt 1991). As such, static variables like dominant frequency and pulse rate are presumably important for species recognition, and dynamic variables like call rate and call duration are indicative of motivation or quality of the emitter (Gerhardt and Huber 2002).

The Batrachylidae frogs *Batrachyla antartandica, B. leptopus* and *B. taeniata* in Southern Chile are well suited for studying selectivity of males for 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 distinct rates (40–80 pulses/s and 1–3 pulses/s, respectively, Penna and Veloso 1990; Penna 1997; Penna et al. 1997b). *B. leptopus* has a call with 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 Velásquez 2011). These frogs are found in sympatry in the temperate austral forest region; however, at localities where they overlap, chorusing activity typically segregates in monospecific chorusing aggregations.

More than two decades ago, we conducted our initial explorations of the evoked vocal responses of *Batrachyla* frogs to signal temporal patterns revealing the existence

of divergent behavioural patterns among the three species (Penna 1997). Playback experiments with *B. taeniata* were restricted to a limited set of temporal variables, mainly pulse rate (Penna 1997; Solís and Penna 1997) and preliminary explorations on the effects of pulse duration and pulse rise time (Penna 1997). The effect of other temporal variables as number of pulses and pulse rise time had not been reported. Furthermore, possible effects of inherent spectral differences between stimuli of different temporal structure remained unexplored in the data reported at that time.

The relatively simple temporal structure of the vocalizations of frogs *Batrachyla* facilitates explorations of male behavioural responses to various parameters altered systematically in different ways, to identify cues implied in signal recognition in this group of anurans. A set of unpublished data obtained during our early research with *B. taeniata* are relevant to identify patterns of EVRs that conform with static and dynamic modes of variation and with corresponding selective processes affecting different temporal components of the acoustic signals. Specifically, we expect that male frogs respond to static variables like pulse rate and to dynamic variables like call duration (Gerhardt 1991) with stabilizing and directional selectivity patterns, respectively. By employing series of stimuli in which the same temporal parameters are varied in different modes we expect to identify cues relevant for the response patterns observed. The results of the current study also provide insights to interpret more recent studies on strategies used by males of *B. taeniata* to confront biotic (Penna and Velásquez 2011) and abiotic (Penna and Zúñiga 2014) acoustic interference.

Materials and methods

Study site and subjects

This field study was conducted during March and April 1994–1995 at a natural breeding site in the locality of Tinquilco, Chile (39° 07′S, 71°46′W) on the eastern shore of Tinquilco lake. Males called from small crevices or underneath rotten logs and fallen leaves, in a forest edge where *Drimys winteri* was the predominant tree. Ten males of *B. taeniata* were used as experimental subjects. Seven of these individuals were captured after conducting the experiments and their snout-vent lengths and weights averaged 31.9 mm (range 28.3–33.5 mm) and 2.8 g (range 1.8–3.7 g), respectively. The three frogs that were not captured completed the 51-min stimulation regime (see later).

Stimuli

Synthetic stimuli were built with a waveform synthesizer (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 at air temperatures averaging 13.4°C (range 11.5–14.7°C). 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. taeniata* in a previous study at the study site (Penna 1997). The Standard stimulus consisted of 25 pulses of 5 ms duration (rise time: 1 ms; fall time: 4 ms) repeated with an inter-pulse period (time between two successive pulse onsets) of 20 ms, corresponding to a pulse rate of 50 pulses/s. The call duration was 500 ms, and 15 call repetitions were presented at an inter-

call period of 1.5 s. Series of stimuli were designed to present subjects with sounds deviating from the pattern of the advertisement calls in various temporal components. A 2.1 kHz sinusoidal carrier was used for this stimulus and for the different series of tonal stimuli described later.

To assess the effect of pulse repetition rate on EVRs, we constructed three series of synthetic stimuli with different pulse rates, ranging from 12.5 to 200 pulses/s for Pulse Rate series 1 and from 6.25 to 200 pulses/s for Pulse Rate series 2 and 3. Pulse Rate series 1 had a constant number of pulses, with pulse rates ranging from 12.5 to 200 pulses/s, Pulse Rate series 2 had a constant call duration with pulse rates ranging from 6.25 to 200 pulses/s. For these two series of stimuli, the inter-call period (time between the onset of two successive stimuli repetitions) was 1.5 s, except for the 12.5 pulses/s of Pulse Rate series 1, which had a duration of 2 s and an inter-call period of 3 s. Eight call repetitions of this stimulus were presented instead of the 15 repetitions used for all the other stimulus variants of this series (and for all the series of stimuli used in this study) to preserve a time of presentation of stimuli repetitions similar to the other stimuli variants in this series (22.5 s). Pulse Rate series 3 had the same number of pulses as Pulse Rate series 1 ($N = 25$), but in addition, stimuli in this series had a constant duty cycle, that is, the inter-call period was always three times the duration of the stimulus and therefore the total time of presentation of the 15 stimuli repetitions differed for this series (Figure 1). The Pulse Duration series consisted of stimuli composed of 25 pulses at a repetition rate of 50 pulses/s, encompassing a pulse duration range of 2.5–20 ms. A stimulus consisting of a 500 ms-tone was also included in this series. An Inverse Pulse stimulus composed of 25 pulses having a rise time of 4 ms and a fall time of 1 ms was also presented. A Rise Time series consisted of stimuli composed of 25 pulses having a duration of 20 ms a fall time of 5 ms and a repetition rate of 50 pulses/s, encompassing a pulse rise-time range of 1–15 ms. A Fall Time
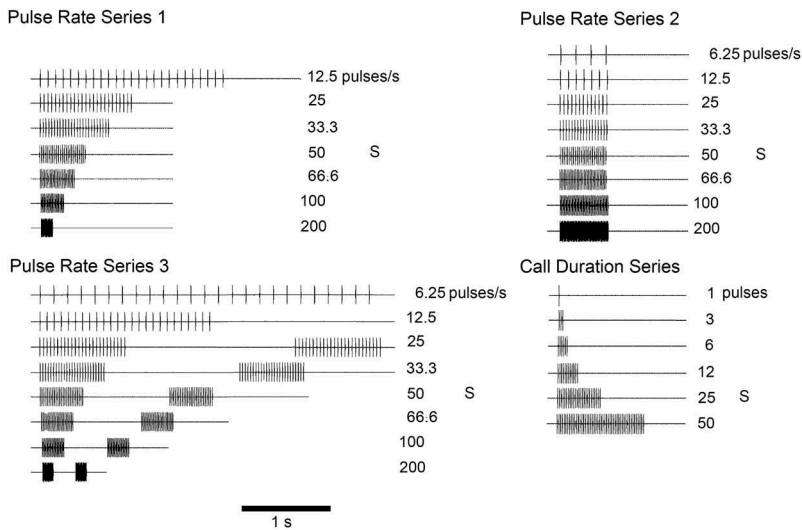

Figure 1. Schematic diagrams of the synthetic stimuli of Pulse Rate series 1, 2 and 3 and Call Duration series. On the left side of each stimulus, pulse rates are indicated for Pulse Rate series 1, 2 and 3 and number of pulses for call duration series. Time scale is the same for all stimuli. For Pulse Rate series 3, inter-stimulus periods are shown for the six last stimuli. Abbreviations: S: Standard stimulus.

series consisted of stimuli composed of 25 pulses having a duration of 20 ms, a rise time of 1 ms and a repetition rate of 50 pulses/s, encompassing a pulse fall-time range of 1–15 ms (Figure 2). Finally, a Call Duration series encompassing a range of 1–50 pulses per call was
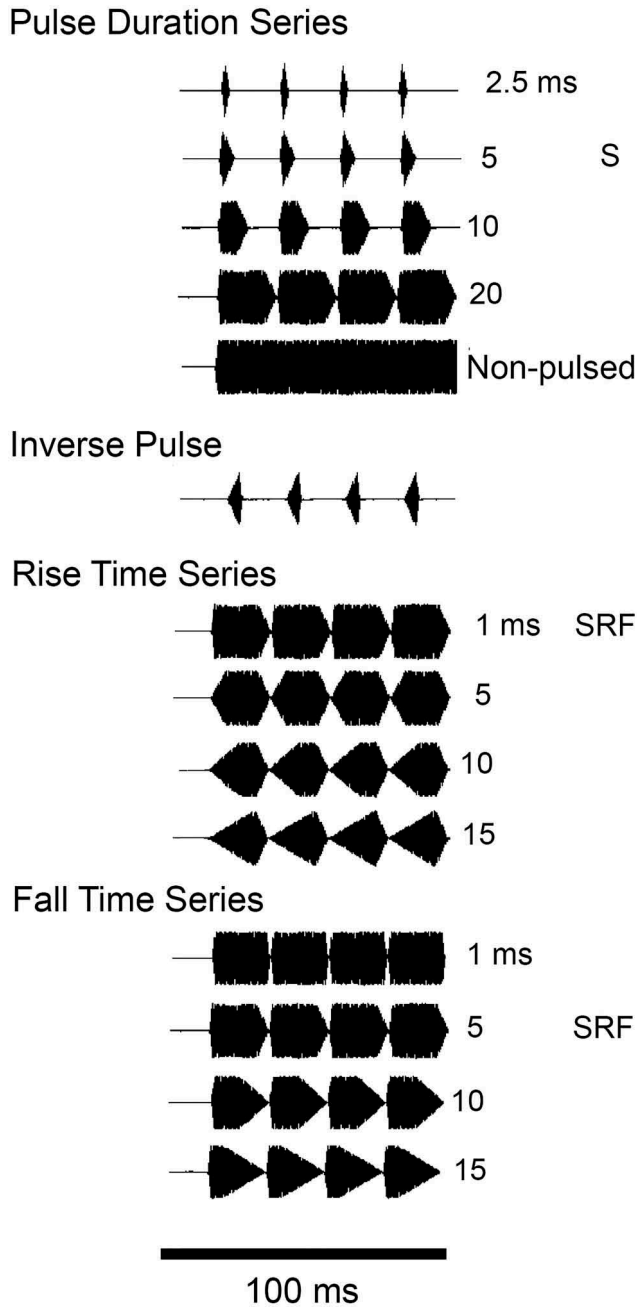

Figure 2. Schematic diagrams of pulse duration, pulse rise time, pulse fall time series and the inverse pulse. Time scale is the same for all stimuli. For each stimulus, the four initial pulses are shown. Abbreviations: S: Standard stimulus, SRF: Standard rise-fall time stimulus.

presented. Stimuli in this series were composed of pulses having 5 ms duration repeated at a rate of 50 pulses/s (Figure 1). A standard call was delivered as part of the following: Pulse Rate series 1 (Standard stimulus 1), Pulse Duration series (Standard stimulus 2) and Call Duration series (Standard stimulus 3). The presentation of this stimulus during the presentation of three different series of stimuli presented sequentially along the experimental sequence allowed to monitor possible changes in frogs' responsiveness over time due to fatigue, habituation or sensitization.

In addition all these series of stimuli, which were built using a 2.1 kHz sinusoidal as a carrier, two series of stimuli built with white noise instead of a pure tone and having the same temporal structure as Pulse Rate series 2 and Pulse Duration series were presented. These series are referred to as follows: Pulse Rate series 2 Noise and Pulse Duration series Noise. These series are meant to control for spectral differences inherent to sounds built with sinusoidal carriers having dissimilar temporal envelopes (e.g. Penna et al. 2001).

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 h. Air and substrate temperatures monitored with a digital thermometer (Digi-Sense 8528–20) during recordings were between 6.5–14.8°C and 8.6–16.5°C, respectively. Spontaneous basal vocal activity of the subjects before beginning playbacks was recorded for an average time of 209.7 s (range = 134–407 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. Ten 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 and using a different sequence for each frog. The stimuli series were presented in a fixed order as follows: (1) Pulse Rate series 1: 12.5, 25, 33.3, 50 (Standard 1), 66.7, 100 and 200 pulses/s; (2) Pulse Rate series 2: 6.25, 12.5, 25, 33.3, 66.7, 100 and 200 pulses/s; (3) Pulse Duration series: 2.5, 5 (Standard 2), 10, 20 ms (Standard Rise–Fall Time) and a 500-ms tone; (4) Inverse Pulse stimulus (4 ms rise time, 1 ms fall time) (5) Rise Time series: 1 (Standard Rise–Fall Time) 5, 10, 15 ms; (6) Fall Time series: 1, 5, 10 and 15 ms; (7) Call Duration series: 1, 3, 6, 12, 25 and 50 pulses (Standard 3); (8) Pulse Rate series 3: 6.25, 12.5, 25, 33.3, 66.7, 100 and 200 pulses/s. After the presentation of all these

series of tonal stimuli, the two series of stimuli constructed with white noise as a carrier were presented, namely (9) Pulse Rate series 2 Noise and (10) Pulse Duration series Noise. These two series were presented to rule out effects of inherent spectral differences between stimuli having a sinusoidal carrier and different temporal structure. Fifteen repetitions of each stimulus were delivered and intervals of 30 s elapsed between the presentation of successive bouts of stimuli repetitions. The times of presentation of the different series of stimuli were as follows: (min:s) Pulse Rate series 1: 6:09, Pulse Rate series 2: 6:08, Pulse Duration series: 4:23, Inverse Pulse stimulus: 0:53, Rise Time series: 3:30, Fall Time series: 2:38, Call Duration series: 5:15, Pulse Rate series 3: 10:45, Pulse Rate series 2 Noise: 7:00, Pulse Duration Noise: 3:30. All the 10 individuals considered for the study completed this stimulation regime, which lasted for 51 min.

At the end of an experiment, the peak sound pressure level (SPL) of the stimulus was measured with a sound level meter (Bruel & Kjaer 2230), using a linear weighting scale, and with the microphone positioned at the location of the calling frog pointing towards the loudspeaker. The SPL of the stimulus was maintained as uniform as possible for all individuals tested by varying the placement of the loudspeaker according to the topography of the site. SPLs of the stimuli at the position of the subjects turned out to be within a range of 86–93 dB peak SPL. In addition, SPLs of neighbours at the position of the frog tested were measured after the experiment.

Data analysis

The EVR of a frog was measured as call rate and duration of calls 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 15th stimulus repetition were computed as EVRs. Recordings were digitized with a Macintosh computer (Power PC 7100) fitted with 104 MB RAM expansions, using the Signalyze 3.12 software.

Differences between EVR measures within a stimuli series were analysed with generalized 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. For call rate, a Poisson family with a log link was used to fit the models, a method appropriate to analyse count data. Individual intercepts were included as random effects to control for data dependence. Stimuli type and temperature were included as fixed effects, and p-values were obtained using type-3 tests under a parametric bootstrap with 1000 simulations procedure. Type-3 analysis allows the evaluation of the effect of one factor while controlling for the effect of the other factors included in the models; therefore, this procedure allowed to evaluate differences among stimuli types while controlling for temperature. Bootstrapping routines allow more robust estimations of the significance of the effects included in the models. When the effect of temperature was not significant, the models were refitted excluding this factor and the significance of stimuli type was reevaluated following the same methods mentioned earlier. This procedure was performed to minimize constraints associated to sample size and the number of factors included in the models, which may affect statistical power (Crawley 2013). When the effect of stimuli type was significant, Tukey *a posteriori* pairwise comparisons were performed. Comparisons considered in the

analyses corresponded to those between stimuli variants and standard stimuli as follows: EVRs to Pulse Rate series 1 and 2 were compared to responses to the Standard stimulus included in Pulse Rate series 1 (Standard stimulus 1). EVRs to Pulse Duration series were compared to responses to the Standard Pulse Duration stimulus included in this series (Standard stimulus 2). EVRs to the Rise and Fall Time series were compared to responses to the 20-ms duration stimulus of Pulse Duration series (Standard Rise-Fall time stimulus), EVRs to Call Duration series were compared to responses to the Standard stimulus included in this series (Standard stimulus 3) and EVRs to Pulse Rate series 3 were also compared to the Standard stimulus included in Call Duration series (Standard stimulus 3). EVRs to Pulse Rate series 2 Noise and Pulse Duration Noise series were compared to the Standard Noise stimulus included in Pulse Rate series 2 Noise. EVRs to Standard stimuli 1, 2 and 3 presented at different times throughout the experiment were compared with each other by means of Tukey *a posteriori* pairwise comparisons.

Model fitting and significance were obtained using the R (version 3.5.1, R Core Team 2018) library 'afex' (Singmann et al. 2018) and *a posteriori* tests were performed using the library 'emmeans' (Lenth 2018). Call duration of EVRs to the Pulse Duration Series and to the Rise Time Series were log transformed to normalize data. To evaluate call rate of EVRs to Pulse Rate Series 3, responses to the stimulus of 12.5 pulses/s was removed from the analyses of the variable call rate, because individuals showed almost no response to this stimulus type, and therefore the model fitting failed when the analysis included the responses to this particular stimulus.

Results

Basal calling activity

The 10 individuals called regularly during periods of basal call recording averaging 210 s (range = 134–407 s), producing during bouts of calling activity an average of 42.7 calls/min (range: 33.1–50.8 calls/min), call duration averaged 503.0 ms (range = 359–736 ms) and dominant frequency was 2029 Hz (range: 1697–2358 Hz). The average values are close to the parameters employed to design the standard call used in this study.

Evoked vocal responses

Males of *B. taeniata* typically started responding shortly after the beginning of a bout of 15 repetitions of the standard stimulus, and vocalized mostly during intervals between stimuli repetitions, alternating their emissions with the synthetic calls, overlaps between the two sounds occurring very seldom. All the experimental subjects gave EVRs to the Standard stimulus presented at different times of the experimental schedule. Each repetition of the Standard stimulus typically evoked a single call, but in some cases two calls were produced during the period elapsing between the onsets of two consecutive stimulus repetitions.

The EVRs to Standard stimulus 1 had a call rate of 33.9 calls/min (range: 18.7–61.3 calls/min), a call duration of 549 ms (range: 318–673 ms), and these values were similar to those

of EVRs to the Standard stimuli 2 and 3 presented at different times throughout the experimental schedule. Call rate was not affected by temperature ($X^2_{(1)} = 0.10$, $p = 0.78$), and therefore this environmental variable was removed from the model, and the analysis showed that call rate did not show significant differences among Standard stimuli ($X^2_{(2)} = 4.04$, $p = 0.140$). Similarly, call duration was not affected by temperature ($X^2_{(1)} = 3.39$, $p = 0.14$); therefore, it was removed from the model, and the analysis showed that call duration did not show significant differences among Standard stimuli ($X^2_{(2)} = 0.75$, $p = 0.73$).

Temperature had a restricted effect on EVRs to the different series of stimuli, as it only affected call rate in responses to Pulse Rate series 1 ($X^2_{(1)} = 11.30$, $p = 0.01$), and call duration in responses to Pulse Rate series 1 ($X^2_{(1)} = 9.94$, $p = 0.008$) and Pulse Duration series ($X^2_{(1)} = 5.93$, $p = 0.04$). As such, temperature was retained in the model for these three analyses of EVRs measures but for the rest of the analyses in which temperature had no effect (17 out of 20 analyses, $p > 0.05$), the environmental variable was removed from the models.

Pulse Rate series 1

Frogs normally responded strongly to stimuli having intermediate pulse rates and responded with lower call rates to stimuli having extreme values of this parameter. The analysis showed that call rate differed significantly among stimuli types ($X^2_{(6)} = 352.68$, $p = 0.001$). Significant *a posteriori* Tukey pairwise comparisons were found between the standard stimulus and the stimuli of 12.5, 100 and 200 pulses/s (Table 1, Figure 3).

The analysis of call duration showed that this response measure did not differ significantly among stimuli types ($X^2_{(6)} = 2.01$, $p = 0.940$; Table 2, Figure 4).

Table 1. Results of generalized linear mixed effects models (GLMMs) and a posteriori Tukey pairwise comparisons of call rates between standard stimulus and variants for series of stimuli in which different temporal variables were modified. *: significant differences for GLMMs and Tukey tests ($p < 0.05$), NS: non-significant differences for GLMMs and Tukey tests, -: Comparison for 12.5 pulses/s not carried out for Pulse Rate series 3 because of low responsiveness (see text) . GLMMs for the Inverse Pulse series, Rise Time series and Fall Time series of stimuli did not yield significant differences.

| Stimulus series	GLMMs	Standard stimulus			Temporal variants				
Pulse Rate 1 (Pulses/s)	*			12.5	25	33.3	66.7	100	200
		50		*	NS	NS	NS	*	*
Pulse Rate 2 (Pulses/s)	*		6.25	12.5	25	33.3	66.7	100	200
		50	*	*	NS	NS	NS	NS	*
Pulse Rate 3 (Pulses/s)	*		6.25	12.5	25	33.3	66.7	100	200
		50	*	–	*	*	NS	NS	*
Pulse Duration (ms)	*		2.5	10	20	500			
		5	*	*	NS	*			
Inverse Pulse (Pulse type)	NS								
Rise Time (ms)	NS								
Fall Time (ms)	NS								
Call Duration (Number of pulses)	*		1	3	6	12	50		
		25	*	*	NS	*	NS		
Pulse Rate 2 Noise (Pulses/s)	*		6.25	12.5	25	33.3	66.7	100	200
		50	*	*	*	NS	NS	NS	*
Pulse Duration Noise (ms)	*		2.5	10	20	500			
		5	NS	*	NS	NS			
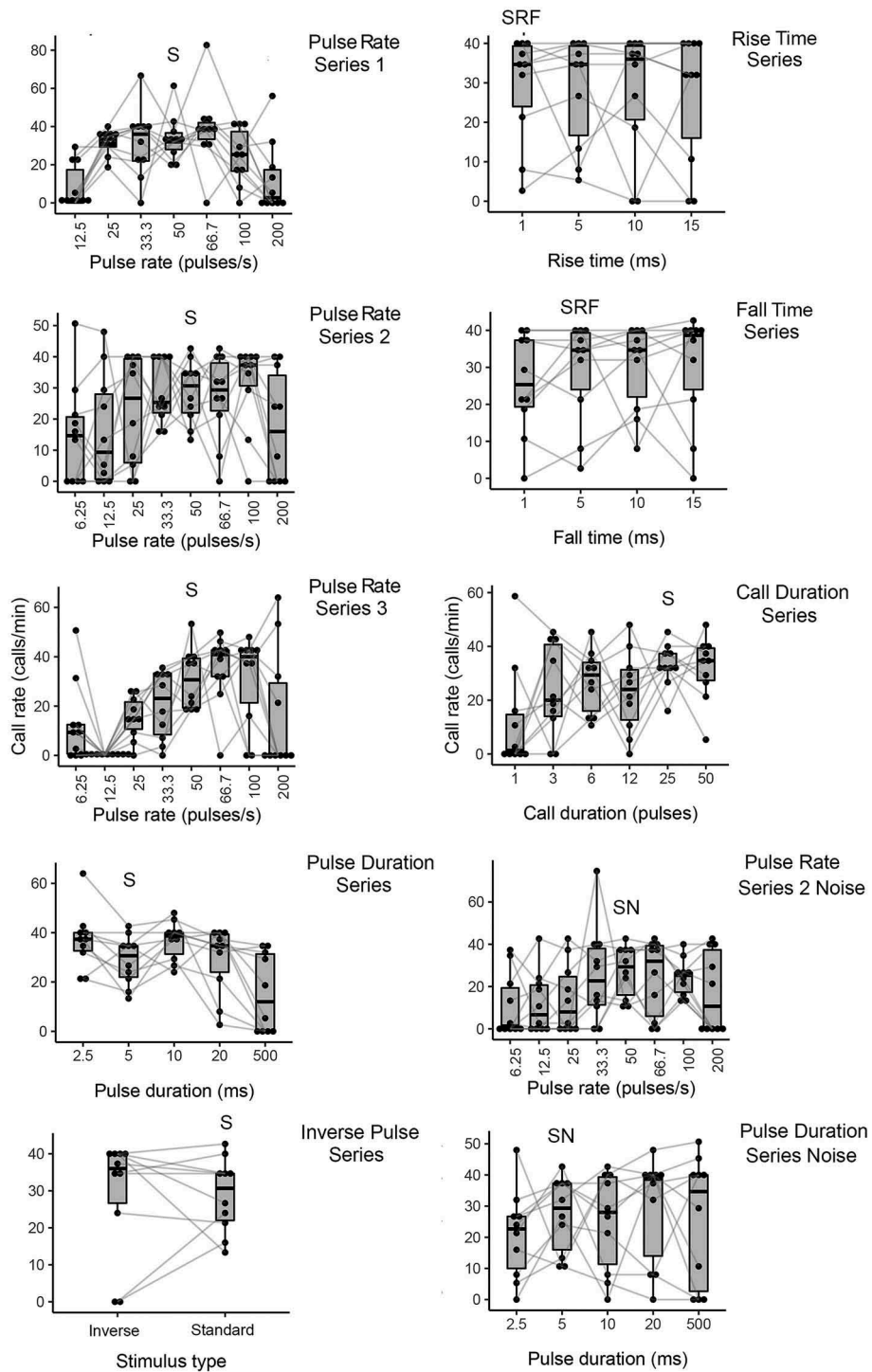
Figure 3. Call rates of males of *B. taeniata* in response to playbacks of series of stimuli in which different temporal components of synthetic calls were modified. Boxes correspond to first and third quartiles and horizontal lines inside boxes to second quartiles (medians). Vertical lines above and below the boxes correspond to ranges. Black circles and thin lines between boxes represent data of individual subjects. Abbreviations: S: Standard stimulus, SRF: Standard rise-fall time stimulus, SN: Standard noise stimulus.

Table 2. Results of linear mixed effects models (LMMs) and *a posteriori* Tukey pairwise comparisons of call durations between standard stimulus and variants for series of stimuli in which different temporal variables were modified. Symbols as in Table 1. LMMs for Pulse Rate series 1, Inverse Pulse series, Rise Time series and Fall Time series of stimuli did not yield significant differences.

Stimulus series	LMMs	Standard stimulus	Temporal variants						
Pulse Rate 1 (Pulses/s)	NS								
Pulse Rate 2 (Pulses/s)	*		6.25	12.5	25	33.3	66.7	100	200
		50	*	*	NS	NS	NS	NS	NS
Pulse Rate 3 (Pulses/s)	*		6.25	12.5	25	33.3	66.7	100	200
		50	*	NS	NS	NS	NS	NS	NS
Pulse Duration (ms)	*		2.5	10	20	500			
		5	NS	NS	NS	*			
Inverse Pulse (Pulse type)	NS								
Rise Time (ms)	NS								
Fall Time (ms)	NS								
Call Duration (Number of pulses)	*		1	3	6	12	50		
		25	*	NS	NS	NS	NS		
Pulse Rate 2 Noise (Pulses/s)	*		6.25	12.5	25	33.3	66.7	100	200
		50	NS	NS	NS	NS	NS	NS	NS
Pulse Duration Noise (ms)	*		2.5	10	20	500			
		5	NS	*	NS	NS			

Pulse Rate series 2

Frogs responded to this series in a similar fashion as to the preceding series, giving stronger responses to intermediate values of stimulus pulse rate. The analysis showed that call rate differed significantly among stimuli types ($X^2_{(7)} = 130.09$, $p = 0.001$). Significant *a posteriori* Tukey pairwise comparisons were found between the standard stimulus and the stimuli of 6.25, 12.5 and 200 pulses/s (Table 1, Figure 3)

The analysis of call duration showed that this response measure differed significantly among stimuli types ($X^2_{(7)} = 49.05$, $p = 0.001$). Significant *a posteriori* Tukey pairwise comparisons were found between the standard stimulus and the stimuli of 6.25 and 12.5 pulses/s (Table 2, Figure 4).

Pulse Rate series 3

Frogs responded to this series in a similar way as for the two preceding series. The analysis showed that call rate differed significantly among stimuli types ($X^2_{(6)} = 209.06$, $p = 0.001$). Significant *a posteriori* Tukey pairwise comparisons were found between the standard stimulus and the stimuli of 6.25, 25, 33.3 and 200 pulses/s. The comparison between the standard stimulus and the 12.5 pulses/s stimulus could not be carried out due to model fitting issues (Table 1, Figure 3).

The analysis of call duration showed that this response measure differed significantly among stimuli types ($X^2_{(7)} = 29.67$, $p = 0.002$). A significant *a posteriori* Tukey pairwise comparison was found between the standard stimulus and the stimulus of 6.25 pulses/s only (Table 2, Figure 4).

Pulse Duration series

Frogs responded actively to stimuli having pulse duration across the 2.5–20 ms range, but responses to the non-pulsed tone stimulus were considerably lower. The analysis
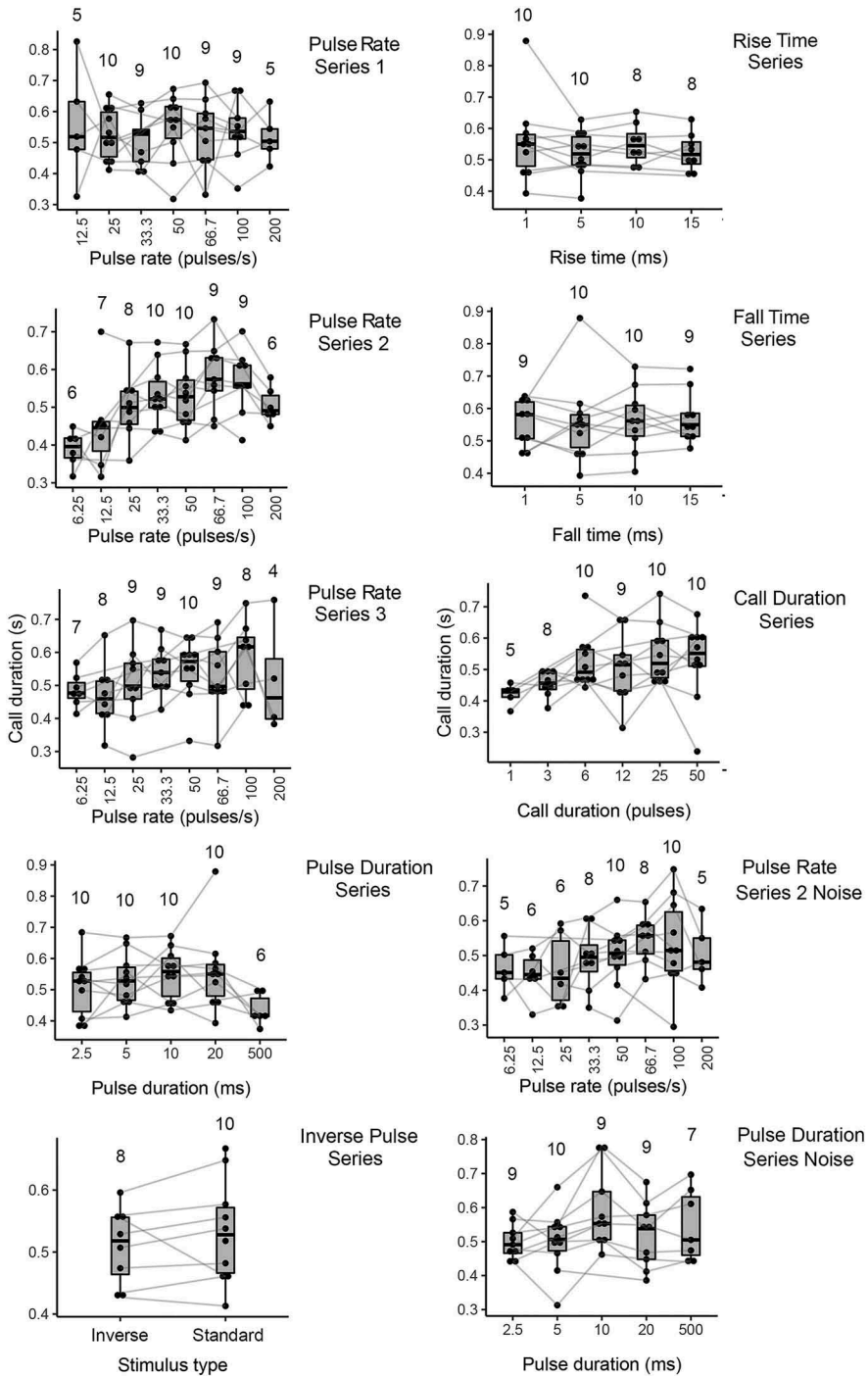
Figure 4. Call duration of males of *B. taeniata* in response to playbacks of series of stimuli in which different temporal components of synthetic calls were modified. Symbols as in Figure 3. Numbers above the boxes indicate the numbers of animals that emitted calls during the presentation of the different stimuli.

showed that call rate differed significantly among stimuli types ($X^2_{(4)}$ = 114.60, p = 0.001). Significant *a posteriori* Tukey pairwise comparisons were found between the standard stimulus and the stimuli of 2.5 and 20 ms pulses, which evoked higher call rates, and the non-pulsed stimulus, which evoked lower call rates (Table 1, Figure 3).

The analysis of call duration showed that this response measure differed significantly among stimuli types ($X^2_{(4)}$ = 17.63, p = 0.02). A significant *a posteriori* Tukey pairwise comparison was found between the standard stimulus and the non-pulsed stimulus only (Table 2, Figure 4).

Inverse Pulse series

The analysis showed that call rate did not differ significantly among stimuli types. Call rate showed no significant differences among stimuli types ($X^2_{(1)}$ = 0.01, p = 0.93; Table 1, Figure 3).

The analysis of call duration showed that this response measure did not differ significantly among stimuli types ($X^2_{(1)}$ = 0.40, p = 0.58; Table 2, Figure 4).

Rise Time and Fall Time series

Frogs responded with similar call rates to all stimuli of the Rise Time and Fall Time Series.

The analyses showed that call rate did not differ significantly among stimuli types in the Rise Time and in the Fall Time series ($X^2_{(3)}$ = 1.09, p = 0.75 and $X^2_{(3)}$ = 5.21, p = 0.17, respectively; Table 1, Figure 3).

The analyses of call duration showed that this response measure did not differ significantly among stimuli types in the Rise Time and in the Fall Time series ($X^2_{(3)}$ = 4.70, p = 0.23 and $X^2_{(3)}$ = 1.05, p = 0.80, respectively; Table 2, Figure 4).

Call Duration series

Frogs responded with lower call rates to stimuli composed of lower number of pulses in this series. The analysis showed that call rate differed significantly among stimuli types ($X^2_{(5)}$ = 125.81, p = 0.001). Significant *a posteriori* Tukey pairwise comparisons were found between the standard stimulus and the stimuli composed by 1, 3 and 12 pulses (Table 1, Figure 3).

The analysis of call duration showed that this response measure differed significantly among stimuli types ($X^2_{(5)}$ = 18.92, p = 0.001). A significant *a posteriori* Tukey pairwise comparison was found between the standard stimulus and the stimulus composed by 1 pulse only (Table 2, Figure 4).

Pulse Rate series 2 Noise

Similarly to Pulse rate 2 series of sinusoidal carrier, frogs gave stronger responses to stimuli having intermediate values of pulse rates, The analysis showed that call rate differed significantly among stimuli types ($X^2_{(7)}$ = 162.52, p = 0.001). Significant *a posteriori* Tukey pairwise comparisons were found between the standard stimulus and the stimuli of 6.25, 12.5, 25 and 200 pulses/s (Table 1, Figure 3).

The analysis of call duration showed that this response measure differed significantly among stimuli types ($X^2_{(7)}$ = 21.59, p = 0.008). No significant *a posteriori* Tukey

pairwise comparisons were found between the standard stimulus and any other stimulus variants (Table 2, Figure 4).

Pulse Duration series Noise

Frogs responded to all stimuli of this series with similar call rates. The analysis showed that call rate differed significantly among stimuli types ($X^2_{(4)}$ = 15.85, p = 0.001). A significant *a posteriori* Tukey pairwise comparison was found between the standard stimulus and the stimuli of 10 ms pulses only (Table 1, Figure 3).

The analysis of call duration showed that this response measure differed significantly among stimuli types ($X^2_{(4)}$ = 16.00, p = 0.003). A significant *a posteriori* Tukey pairwise comparison was found between the standard stimulus and the stimuli of 10 ms pulses only (Table 2, Figure 4).

Discussion

Results of our experiments show that EVRs of males of *B. taeniata* are dependent on the temporal characteristics of the stimuli. Frogs gave weaker responses to stimuli having temporal patterns that differed widely from those of their natural advertisement calls. It is possible that due to the low number of frogs sampled and the limited variation in some stimuli parameters differences that do not reach statistical significance may actually be real.

Selectivity for pulse rate

Pulse rate has substantial effect on EVRs, and the effect is similar in Pulse Rate series 1 relative to Pulse Rate series 2, as significant differences in call rate occurred between the standard (50 pulses/s) stimulus and 3 and 2 variants, respectively, in the 12.5–100 pulses/s range (Table 1). It is apparent that frogs tend to cease responding if the stimulus pulse rate is high and this decrease is observed for stimuli having a shorter (Pulse Rate series 1) or constant (Pulse Rate series 2) duration. At the low end, it is apparent that frogs tend to cease responding if the stimulus has an extended (Pulse Rate series 1) or constant (Pulse Rate series 2) duration. The first outcome is congruent with experiments of EVRs to heterospecific signals that have shown that males of *B. taeniata* tend to reduce their call rate in the presence of calls of *B. antartandica*, characterized by prolonged emissions of pulses at low rates (Penna and Velásquez 2011).

In particular, the responsiveness of the experimental subjects is not affected significantly by the intervals between successive stimuli repetitions, as shown by the similar band-pass response patterns observed in exposures to Pulse Rate series 1 and 3, in which the stimuli duration vary in the same fashion, that is, inversely related to pulse rate. The similar vocal response pattern to the two series occurs even though the inter-stimuli intervals vary in direct and inverse proportions to pulse rate in Pulse Rate series 1 and 3, respectively.

Furthermore, males of *B. taeniata* have been shown to increase their vocal output when exposed to continuous noises (Penna and Zúñiga 2014) and therefore these frogs do not necessarily respond synchronizing their calls with temporally organized stimuli.

The effects of different pulse rates on call duration are relatively restricted as compared to call rate, as no significant differences in this EVR measure occurred for Pulse Rate series 1 and for Pulse Rate series 2 and 3, differences between stimuli having low pulse rate and the Standard stimulus occurred but the analyses did not yield differences for stimuli having high pulse rates.

A factor that needs to be assessed when comparing signals having dissimilar temporal structure are the spectral differences inherent to sounds of various temporal envelopes. In the current study the variation in call rate of responses to the Pulse Rate series 2 series built with noise yielded four significant differences, a result similar to the three significant differences obtained for Pulse Rate series 2 built with sinusoidal carrier. Furthermore, the band-pass shape of the graph obtained for the two series was similar, and thus it may be assumed that spectral differences inherent to stimuli built with a sinusoidal carrier differing in pulse rate are not determinant for the subjects' responsiveness, as stimuli built with white noise, and thus having similar spectra, yielded similar results.

Overall, the experiments employing series of stimuli having different pulse rates show that *B. taeniata* has a band-pass type of selectivity for this parameter, a result bearing similarity with findings in other anuran species for this temporal property (Walkowiak and Brzoska 1982; Rose and Capranica 1984). Coincidentally, electrophysiological studies in different anurans have identified midbrain auditory neurons that respond in a band-pass mode to parametric variation of pulse rate, providing a neural substrate for such a pattern of behavioural selectivity (Rose and Capranica 1983, 1984; Walkowiak 1988; Gooler and Feng 1992; Penna et al. 1997a, 2001). Preliminary neurophysiological evidence (Cañete 2019) indicates that the proportion of band-pass neurons for pulse rate is higher in *B. taeniata* (27%) than the 4.5% reported for the congeneric *B. antartandica* in a former study (Penna et al. 2001), pointing out that a dissimilar neural selectivity underlies interspecific patterns of vocal responses, as this study shows that vocal responses of *B. taeniata* follow a band-pass and those of *B. antartandica* respond in a low-pass pattern to pulse rate (Penna et al. 1997a).

Selectivity for pulse duration, rise and fall time

Pulse duration affected the EVRs of the subjects, and in particular a lower call rate and call duration occurred during exposure to the non-pulsed stimulus of the Pulse Duration series. In a former study, significant lower calling activity was reported in the presence of a 500 ms tone (Penna 1997), so it is likely that the lack of a pulsed structure, in general constrains the evoked response of this species. A study on interspecific interference showed that males of *B. taeniata* when exposed to a synthetic imitation of the call of *B. leptopus*, a signal composed of notes having durations of 40 ms, reduce the EVRs relative to those elicited by the conspecific call, composed of 5-ms pulses, which suggests that the vocal activity of *B. taeniata* is reduced in the presence of stimuli having relatively long durations (Penna and Velásquez 2011). Similar to the effect of pulse duration on the vocal activity of *B. taeniata*, this temporal variable was found to have a pronounced effect on the EVRs of *B. antartandica*, and the wider range of variation of the parameter, rendered possible by the slow pulse rate of this species showed that pulse durations of 48 and 96 ms yielded significant lower EVRs relative to the standard 5-ms stimulus (Penna 1997; Penna et al. 1997b).

In contrast with the decrease in call rate and call duration obtained with the 500 ms tone stimulus of the Pulse Duration series, synthetized using a 2.1 kHz tone carrier, the 500 ms stimulus of the Pulse Duration series built with white noise did not produce decreases in EVRs to the pure tone relative to the standard stimulus, which indicates that the effect observed is likely due to inherent spectral differences between the stimuli built with a 2.1 kHz tone, as the continuous 500-ms tone has a single-frequency spectrum.

Electrophysiological studies in amphibians (Narins and Capranica 1980; Gooler and Feng 1992; Penna et al. 1997a, 2001) have revealed that different midbrain neurons show selectivities for tone bursts of different durations, which may support recognition of stimuli of dissimilar pulse durations.

The lack of selectivity for rise and fall time of the pulses contrasts with studies that have shown effects of these features on the phonotactic responses of North American treefrogs (Gerhardt and Doherty 1988; Gerhardt and Schul 1999; Gerhardt 2005). The absence of an effect on the EVRs of males of *B. taeniata* could be related to the atypical characteristics of the stimuli in the series used to test the effect of rise and fall time, consisting of pulses having a 20-ms duration, well beyond the typical 5-ms duration of pulses in the natural calls of these frogs.

Selectivity for call duration

Males of *B. taeniata* have a tendency to respond with lower call rates to stimuli having durations shorter than the standard call, and call duration of EVRs is also shorter for the single-pulse stimulus as compared to the Standard stimulus. Such preferential responses to long calls are likely meant to confront larger acoustic interference. Preferences for longer calls have been reported for the phonotactic responses of female anurans of different species and are related to offspring benefits in the North American treefrog *Hyla versicolor* (Gerhardt and Huber 2002). The mode of response of *B. taeniata* males to this stimuli series is supported by electrophysiological studies revealing auditory neurons in anurans that need to integrate a minimum of pulses to respond (Alder and Rose 1998, 2000; Edwards et al. 2002).

Interspecific comparisons and evolutionary implications of selectivity patterns

The selectivity patterns of the EVRs of *B. taeniata* show similarities and contrasts with those documented previously for the congeneric species *B. antartandica*. The band-pass selectivity for pulse rate of *B. taeniata* contrasts with the low-pass selectivity of *B. antartandica*, and the long-pass selectivity of *B. taeniata* for call duration contrasts with the short-pass selectivity of the second species for pulse trains. These dissimilarities are consistent with interspecific differences in processing of acoustic temporal patterns that are likely to operate in the selectivity of EVRs of both species for conspecific relative to heterospecific vocalizations (Penna and Meier 2011; Penna and Velásquez 2011). In nature, the geographic distributions of *Batrachyla* species overlap, but these frogs tend to build up monospecific choruses in separate areas. The patterns of selectivity of their responses to temporal characteristics of signals are likely to promote such spatial segregation among species.

The band-pass selectivity pattern observed for pulse rate in *B. taeniata* is concordant with the low intra-individual variation that this characteristic generally has in anuran calls, as it is generally classified as a static character. On the other hand, the long-pass selectivity for call duration is concordant with the high intra-individual variation of this characteristic, considered to be a dynamic characteristic of acoustic signals (Gerhardt 1991).

Correspondingly, pulse rate is a characteristic likely to be subjected to stabilizing selection pressures, presumably important for species recognition, whereas call duration is likely subjected to directional selection, and probably indicative of motivation or quality of the emitter (Gerhardt 1991; Gerhardt and Huber 2002). The importance of these behavioural preferences has been widely documented for female anurans but the relevance of male selectivity for acoustic signal features has been mostly disregarded. However, recent studies in *Pleurodema thaul*, a frog having an extensive distribution in Chile, have shown that males are selective for spectral and temporal features of the advertisement calls characterizing distant populations of this species, and these EVRs patterns have probably affected evolutionary divergence of the sound communication system, as females of this species do not exert selectivity for the sound features tested with males (Velásquez et al. 2014, 2015). Studies on preferences of females of *B. taeniata* for call patterns have not been conducted due to the rare occurrence of exemplars at the study site and thus comparisons with males' selectivity are not available.

The patterns of temporal selectivity in the EVRs of males of *Batrachyla*, based on pronounced differences in the temporal structure of their signals may also be significant for the divergence of the sound communicating systems of these species. Such divergence comprises different strategies for confronting parametric variation in temporal sound components (Penna 1997; Penna et al. 1997b; this study), interference from heterospecific signals (Penna and Meier 2011; Penna and Velásquez 2011; Penna and Toloza 2014) as well as interference from abiotic noise sources (Penna and Zúñiga 2014; Penna et al. 2017).

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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