

Vocal responses of austral forest frogs to amplitude and degradation patterns of advertisement calls



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ABSTRACT

Degradation phenomena affecting animal acoustic signals may provide cues to assess the distance of emitters. Recognition of degraded signals has been extensively demonstrated in birds, and recently studies have also reported detection of degraded patterns in anurans that call at or above ground level. In the current study we explore the vocal responses of the syntopic burrowing male frogs *Eupsophus emiliopugini* and *E. calcaratus* from the South American temperate forest to synthetic conspecific calls differing in amplitude and emulating degraded and non-degraded signal patterns. The results show a strong dependence of vocal responses on signal amplitude, and a general lack of differential responses to signals with different pulse amplitude modulation depths in *E. emiliopugini* and no effect of relative amplitude of harmonics in *E. calcaratus*. Such limited discrimination of signal degradation patterns from non-degraded signals is likely related to the burrowing habits of these species. Shelters amplify outgoing and incoming conspecific vocalizations, but do not counteract signal degradation to an extent comparable to calling strategies used by other frogs. The limited detection abilities and resultant response permissiveness to degraded calls in these syntopic burrowing species would be advantageous for animals communicating in circumstances in which signal alteration prevails.

1. Introduction

Long-range acoustic communication is crucial for different animal groups in various contexts. The efficiency of this process is favored by broadcast signals that withstand degradation as they propagate, remaining recognizable for potential recipients (Wiley and Richards, 1982; Bradbury and Vehrencamp, 2011). However degradation phenomena affecting these sounds result in signal alterations that can act as significant cues to assess the distance of emitters, namely ranging (Naguib and Wiley, 2001). In a sexual selection context these alterations are helpful for assessing the potential challenge of signalers for male receivers and the effort or risks to reach the sound source for female receivers. Different physical processes affect the structure of propagating signals, causing overall attenuation, frequency dependent attenuation, reverberation and amplitude fluctuations (Naguib and Wiley, 2001).

Studies in birds have tested the abilities of listeners to judge distance of the callers based on degradation patterns of vocalizations, as they provide different cues for ranging (Morton and Derrickson, 1996; Naguib, 1995, 1997a, 1997b; Wiley and Godard, 1996; Phillimore

et al., 1998; Naguib et al., 2000; Nelson, 2000; Mathevon et al., 2008; Radziwon et al., 2011; Pohl et al., 2015). Furthermore in birds different components of the same signal have been shown to experience dissimilar alterations with propagation distance (Naguib et al., 2008; Rek, 2013; Mouterde et al., 2014) and elicit different ranging responses (Sprau et al., 2010). In primates, an increasing number of studies quantifying changes in features of propagating signals have been carried out (e.g. Lameira and Wich, 2008; Maciej et al., 2011; Sabatini et al., 2011), but knowledge on the relative contributions of different degradation processes in shaping behavioral responses of listeners is scant.

Studies in birds and primates support a signal design that maximizes communication range, as optimal relationships between acoustic signal structure and vegetation coverage have been reported to occur in a number of species (Morton, 1975; Ey and Fischer, 2009).

In contrast with findings in birds and primates, studies in anurans have shown predominantly a lack of optimal relationships between signals and vegetation density, perch type and microhabitat (Penna and Solís, 1998; Kime et al., 2000; Bosch and De la Riva 2004; Penna et al., 2006; Röhr and Juncá 2013; Malone et al., 2014). Such lack of

Abbreviations: AM, amplitude modulation; SPL, sound pressure level; H2, stimulus lacking the second harmonic; H3, stimulus lacking the third harmonic

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correspondence suggests that anuran vocalizations are designed primarily to locate mates and competitors within limited breeding areas where relative high densities of vocal interacting emitters occur (Gerhardt and Huber, 2002).

Various studies have documented attenuation and degradation processes affecting anuran signals as they propagate through natural habitats (Ryan and Sullivan, 1989; Ryan et al., 1990; Penna and Solís, 1998; Kime et al., 2000; Castellano et al., 2003; Penna et al., 2006; Kuczynski et al., 2010; Röhr and Juncá, 2013; Schwartz et al., 2016). Recent studies have in addition examined the effect of degradation on responses to sound signals in these vertebrates: Kuczynski et al. (2010) and Schwartz et al. (2016) reported that females of two North American treefrogs *Hyla* exhibit stronger phonotactic responses to non-degraded relative to degraded vocalizations. Similarly, males of the Neotropical frog *Allobates femoralis* (Ringle et al., 2015), and the North American cricket frog *Acris crepitans* (Venator et al., 2017), have been reported to respond with higher vocalization rates to non-degraded than to degraded vocalizations. The species of *Hyla* communicate in a variety of topographical conditions and over different substrates where male acoustic signals are subjected to different attenuation and degradation patterns, improving propagation when they call from structures above ground level (Schwartz et al., 2016). *Allobates* males also call from structures somewhat elevated above ground (Roithmair, 1992). *Acris* calls from the ground or water surface and although males do not occupy elevated calling posts, they call from a variety of substrates that affect propagation signal differently (Venator, 1999). The ability of these species of anurans to move within their territories or to call from positions elevated above ground level provide means to optimize the fidelity of the signals transmitted.

A study on propagation of acoustic signals of anurans from the austral temperate forest (Penna and Solís, 1998) showed that in swamp environments these sounds propagate over an absorbing substrate composed by ferns, grasses and mosses, which affect the transmission of frequencies above about 1 kHz. *Eupsophus emiliopugini* and *E. calcaratus* are two burrowing frogs from the South American temperate forest in Chile and Argentina (Correa et al., 2006) that produce signals differing in their structure: *E. emiliopugini* produces a single or a double-note call having a pulsed structure and the advertisement call of *E. calcaratus* consists of a single note having a harmonic frequency-modulated spectral structure. The call of *E. emiliopugini* has a dominant frequency at about 1100 Hz, encompassed by sidebands generated by the amplitude-modulated nature of the signal (Penna et al., 2005a; Penna and Hamilton-West, 2007) and the call of *E. calcaratus* has two main spectral components corresponding to a second and third harmonic at about 1400 and 2100 Hz, respectively. Any of these two components can be the dominant frequency in this signal (Penna et al., 2005b; Márquez et al., 2005). The call of *E. calcaratus* has higher frequency components and lower amplitude relative to the call of *E. emiliopugini*, and the acoustic active space for the signals of *E. calcaratus* is restricted relative to *E. emiliopugini* (Penna et al., 2013; Penna and Moreno-Gómez, 2014). The signals of both species experience similar attenuation patterns but are affected differently by degradation processes as they propagate in their natural habitat: the call of *E. calcaratus* experiences spectral degradation, with a linear decrease in the amplitude of the second relative to the first harmonic, whereas the call of *E. emiliopugini* shows temporal degradation as a linear decrease in amplitude modulation (AM) depth of its pulsed structure (Penna and Moreno-Gómez, 2015). These two species breed in the very same microenvironment – even occupying the same burrows at different times of the year-. *E. calcaratus* is vocally active from mid winter to mid spring and *E. emiliopugini* from mid spring to early summer and the calling activity of the two species overlaps during mid spring in late October and early November. The refugia from which these burrowing frogs call contribute to the efficiency of sound communication as their resonant nature amplifies incoming vocalizations of neighbors (Penna and Solís, 1996, 1999; Penna, 2004; Penna and Márquez, 2007) and

vocalizations broadcast by residents (Muñoz and Penna, 2016).

Burrowing frogs maintain their locations unaltered inside their shelters and do not occupy calling posts above ground level that reduce signal degradation. In these circumstances it is likely advantageous to maintain choral activity by responding to incoming calls of detectable amplitude in spite of alterations in the fine temporal or spectral structure affecting broadcast signals. Accordingly, it would be expected that burrowing *Eupsophus* frogs are less sensitive to differences between degraded and non-degraded signals relative to surface-calling anuran species for which these capabilities have been formerly tested.

In a broader context, no studies have compared the behavioral responses to acoustic signals having different degradation patterns among animal species coexisting in nature. Comparisons of ranging abilities between different species of birds have been limited to laboratory settings (Phillmore et al., 1998; Radziwon et al., 2011). The calls of the two anurans from the temperate austral forest differ in the degradation processes affecting these sounds: temporal and spectral (Penna and Moreno-Gómez, 2015), providing a unique opportunity to compare detection of degraded signals by species communicating in a shared microenvironment and under common environmental constraints. These species have been shown to behave differently when confronting natural environmental noises (Penna et al., 2005b; Penna and Hamilton-West, 2007) and the evaluation of their capabilities to detect degradation patterns would contribute to a comprehensive assessment of their sound communication strategies.

We examined the recognition of degraded patterns quantifying the evoked vocal responses of males of the two *Eupsophus* species to synthetic conspecific calls presented at different SPLs and having patterns of structural degradation mimicking those affecting propagating signals in nature (Penna and Moreno-Gómez, 2015), and to synthetic sounds having characteristics beyond the range of variation of degraded signals. Synthetic stimuli have been shown to evoke vocal responses effectively in anuran males in general (Gerhardt and Huber, 2002) and in males of these species in particular (Penna et al., 2005a, 2005b; Penna and Hamilton-West, 2007; Penna and Quispe, 2007). An evaluation of the effect of signals' SPL and temporal and spectral degradation contributes a comparison with anuran species that have been recently shown to recognize degraded features of vocalizations, to determine the extent of such capability among these vertebrates.

2. Methods

2.1. Study site

The experiments were conducted on November 17–24, 2012 for *E. emiliopugini* and on October 11–12, 2013 and October 9–10, 2014 for *E. calcaratus*, at the locality of La Picada (41° 06' S, 72° 30' W, altitude 820 m above sea level), within the Vicente Pérez Rosales National Park in southern Chile. The study site was a bog of volcanic substrate, where males of *E. emiliopugini* and *E. calcaratus* call from inside small burrows along the borders of small streams or pools among vegetation composed mainly of mosses (*Racomitrium*), sedges (*Scirpus*), ferns (*Blechnum*) and prostrate shrubs (*Myrteola*). This vegetation acts as an attenuating substrate for broadcast frog calls (Penna and Solís, 1998). Previous studies on the vocal behavior of both species have been carried out at this site (e.g. Penna and Moreno-Gómez, 2015).

2.2. Stimuli synthesis

Synthetic imitations of non-degraded and degraded calls of both species were generated. A non-degraded synthetic stimulus of *E. emiliopugini* was designed after the values of the parameters of calls recorded at 25 cm from the openings of the burrows where this species call from at the study site (Penna and Moreno-Gómez, 2015). Using Adobe Audition 3.0, 7- ms pulses having rise and fall times of 2 and 5 ms, respectively, and a 1000 Hz sinusoidal carrier were generated. An

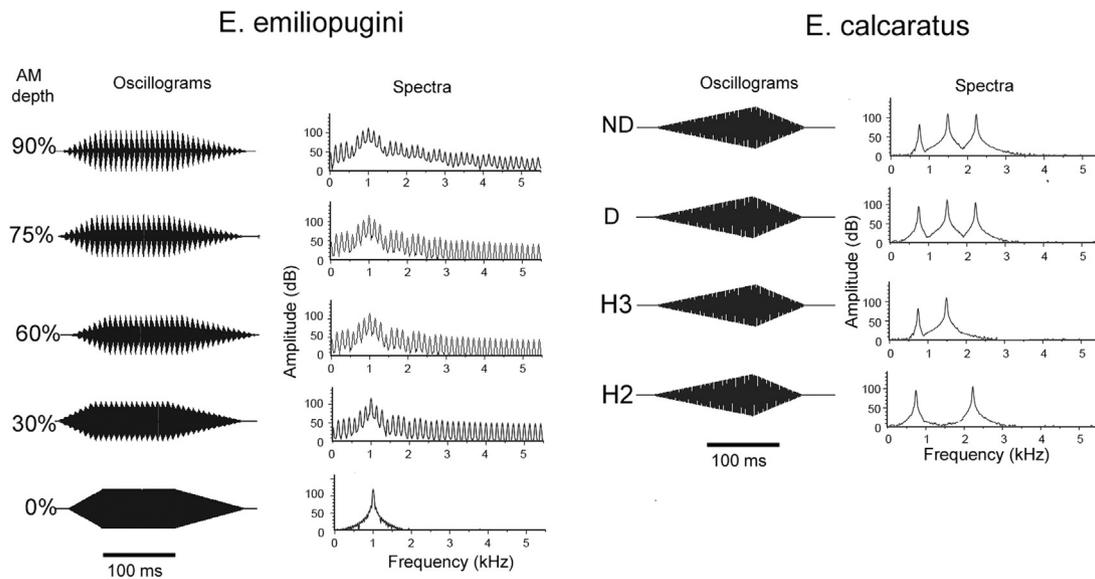


Fig. 1. Stimuli used in the evoked vocal responses experiments. Oscillograms and spectra on the right and left, respectively. Stimuli emulating different degrees of degradation having various amplitude modulation (AM) depths were used for *E. emiliopugini*. A non-degraded stimulus (ND), degraded (D) stimulus and stimuli lacking the third (H3) and second (H2) harmonic were used for *E. calcaratus*.

envelope having an AM depth of 90% was applied to each pulse. A succession of 36 pulses was created and an overall envelope having rise and fall times of 50 and 100 ms, respectively and a plateau of 100 ms was applied to the succession of pulses to obtain a 250-ms synthetic call. Synthetic stimuli variants having pulse AM depths of 75 and 60% were generated because these values correspond to about average and minimum values of vocalizations recorded at 8 m from calling males, respectively (Penna and Moreno-Gómez, 2015). In addition, two stimuli variants having AM depths below the range found in nature (30 and 0%) were also created (Fig. 1). The 0% AM depth synthetic stimulus consisted of a pure tone containing no pulses and having the same overall envelope as the other stimuli variants. The utilization of stimuli variants having AM depths beyond the range found in natural vocalizations is justified because in other anuran species females have been shown to be highly tolerant to degraded temporal structure of calls (Kuczynski et al., 2010), and by using a restricted range of variants, recognition abilities may go undetected. Bouts of synthetic stimuli were constructed with 20 repetitions of the same variant, leaving an inter-stimulus repetition period of 1.5 s which yielded a total duration of 30 s for a bout of stimuli. This periodicity was a realistic one based on data from duetting interactions and playbacks with natural and synthetic calls (Penna et al., 2005a; Penna and Hamilton-West, 2007). A total five bouts of synthetic stimuli were generated, each corresponding to one of the stimulus variants synthesized.

A synthetic non-degraded stimulus of *E. calcaratus* was generated using the R (R Core Team, 2015) library *seewave* (Sueur et al., 2008) by adding three sinusoids having relative amplitudes typical of natural calls recorded at 25 cm from the burrow openings where this species call from (Penna and Moreno-Gómez, 2015). The stimulus had a duration of 250 ms with linear rise and fall ramps of 170 and 80 ms, respectively, following the typical envelope of natural calls. This amplitude envelope was generated with Audacity 2.0.2. Three harmonics of 700, 1400 and 2100 Hz were added for this stimulus. The amplitude of the first and third harmonics were 30 and 4 dB below the second harmonic, respectively. A degraded stimulus variant had the same temporal characteristics, but the relative amplitude of these harmonics was 18 and 9 dB below the second harmonic, respectively, at about average values measured in vocalizations recorded at 4 m from calling males (Penna and Moreno-Gómez, 2015). In addition, two stimuli variants having structures not found in nature, containing only two harmonics were synthesized. For the stimulus variant lacking the

third harmonic (H3), the amplitude of the first harmonic was 18 dB below the second harmonic, following the structure of the degraded call. For the stimulus variant lacking the second harmonic (H2), the amplitude of the first harmonic was 9 dB below the third harmonic, following the structure of the degraded stimulus variant. Bouts of 15 repetitions of each of these four stimuli variants were generated, with an inter-stimulus period of 2.0 s, which yielded a total duration of 30 s for a bout of stimuli. The presentation periodicity was a realistic one based on data from duetting interactions and playbacks with synthetic calls of this frog (Penna and Quispe, 2007).

2.3. Experimental protocol

Playback experiments were conducted at night between 2200 and 0500 h at the study site. For *E. emiliopugini*, air and substrate temperature, measured after each recording with a thermometer (Digi-Sense 8528-20) to the nearest 0.1 °C, were (mean \pm SD) 5.43 \pm 2.11 °C and 9.83 \pm 2.58 °C, respectively, and the relative humidity measured with a psychrometer (Extech RH 390) 92.18 \pm 4.02%. The nearest neighbors were spaced at a distance of 2.97 \pm 2.57 m of the 14 experimental subjects of this species. The root-mean-square (RMS) sound pressure level (SPL) of the calls of the nearest neighbors at the position of the experimental subjects was 66.1 \pm 13.6 dB SPL. For *E. calcaratus*, air and substrate temperature, measured after each recording, were 2.39 \pm 1.42 °C and 7.20 \pm 1.00 °C, respectively, and the relative humidity was 92.17 \pm 3.37%. The nearest neighbors were spaced at a distance of 1.19 \pm 0.68 m of the 14 experimental subjects of this species. The SPL of the calls of the nearest neighbors at the position of the experimental subjects was not measured for this species.

The SPL values chosen for the presentation of bouts of stimuli were within the range of amplitudes of natural propagating signals measured formerly at different distances for the two species (Penna and Moreno-Gómez, 2015). For *E. emiliopugini* bouts of stimuli having 90, 75 and 60% AM depths were presented at 48, 60, 72, 84 dB SPL, to evaluate a potential interaction between call degradation features found in nature and SPL (see Section 2.5). The bouts of stimuli having AM depths not found in nature (0 and 30%) were presented at 72 dB SPL to allow comparisons of responses to the different stimuli variants at this SPL. For *E. calcaratus* non-degraded and degraded bouts of stimuli were broadcast at 46, 52, 58 and 64 dB SPL. The SPLs used for the two species are within ranges measured for propagating vocalizations in the

field at 0.25–8.0 m for *E. emiliopugini* and 0.25–4.0 m for *E. calcaratus* (Penna and Moreno-Gómez, 2015) and above the auditory thresholds measured in laboratory conditions (Penna et al., 2013; Penna and Moreno-Gómez, 2014). For *E. calcaratus*, the bouts of stimuli having spectral structures not found in nature were presented at 64 dB SPL to allow comparisons of responses to the different stimuli variants at this SPL. The choice of using 64 dB SPL in *E. calcaratus* and 72 dB SPL in *E. emiliopugini* for these comparisons was because these values are within the range of amplitudes of the calls at 1 m from the sound source (Penna and Moreno-Gómez, 2015), a distance at which nearest neighbors are typically positioned relative to focal subjects in chorusing assemblages (Penna and Solís, 1998; Penna et al., 2013).

The bouts of stimuli were broadcast to the subjects of both species in a random sequence, using a latin-square design to avoid potential presentation order effects. Bouts were presented leaving 60- and 45-s silent intervals between successive bouts for *E. emiliopugini* and *E. calcaratus*, respectively. The shorter inter-bout interval used for *E. calcaratus* was advisable due to the severe and unstable weather conditions at the study site during early spring, when this species breeds. The vocal responsiveness of males of this species to prolonged stimulation is also less persistent than in *E. emiliopugini*. For the first bout of stimuli presented to a subject, the preceding interval corresponded to the last 60 and 45 s of the initial basal recording period in *E. emiliopugini* and *E. calcaratus*, respectively. In total, 14 and 10 different bouts of stimuli were presented to each individual of *E. emiliopugini* and *E. calcaratus*, yielding a total experimental time per subject of 1200 and 705 s, respectively (see Fig. 2).

Stimuli were broadcast with an iPod nano (Apple inc) connected to a custom-made impedance-matched operational amplifier, attenuators (Hewlett-Packard 355C and D), a power amplifier (Alpine 3540) and a 10-cm diameter loudspeaker, positioned 0.4–0.6 m in front of the experimental subject. For the experiments with *E. calcaratus*, a 5-band equalizer was plugged between the iPod nano and the custom-made impedance operational amplifier, to equalize the amplitude of the three harmonics contained in the stimulus prior to each experiment as explained in the following subsection. Evoked vocal responses were recorded with a directional microphone (Sennheiser ME 66), the tip of which was placed 0.2–0.4 m in front of the subject. The calls were recorded on the left channel of a digital recorder (Tascam DR 100) and the acoustic stimulus was recorded on the right channel of this recorder via a connecting cable.

Before starting recordings for both species, the amplitude of the non-degraded stimuli at the position of the experimental subjects was adjusted with the attenuator to 72 dB SPL for *E. emiliopugini* and 64 dB

SPL for *E. calcaratus* by placing the microphone of a sound-level meter (Brüel & Kjaer 2238, linear weighting scale) just above the frog position (typically 3–5 cm), making efforts to avoid disturbing the animal. In addition for *E. calcaratus* the amplitude of the three harmonics was adjusted broadcasting continuous tones of the frequencies of the three harmonics and using the equalizer to adjust them to have the same SPL at the position of the subject. These exposures were as short as possible, lasting a few seconds to minimize effects on the subsequent vocal activity of the experimental subjects, and we waited a few minutes until the basal calling activity was resumed before starting the recording.

To avoid interferences during the playback experiments, nearby neighbors were silenced by capturing or disturbing them with gentle vibrations of the substrate. The basal calling activity of the experimental subject was recorded during an interval of two minutes at least, after which the conspecific non-degraded stimulus was presented and if the frog responded producing at least three calls to a bout of stimuli, the playback experiment proceeded thereafter. Similar recording procedures have been used in previous playback studies with these species and are practicable to proceed with the subsequent experimental session, minimizing effects of prolonged exposure on the responsiveness of the experimental subjects (Penna et al., 2005a; Penna and Hamilton-West, 2007). The basal vocal activity of each subject was recorded again for two minutes after playback presentations. The subjects were not captured to avoid altering the burrows where they called from, and therefore relationships of spectral call parameters and body measures were not explored.

2.4. Acoustic analysis

The measures of the evoked vocal responses used for both species obtained with Raven Pro 1.4 were call rate (calls/min), call duration (ms) and call latency (ms). These measures were computed for calls produced by the experimental subjects in response to bouts of 20 repetitions of synthetic stimuli of *E. emiliopugini* and to bouts of 15 repetitions of synthetic stimuli of *E. calcaratus*. Responses to stimuli corresponded to calls emitted by experimental subjects recorded from the onset of the first stimulus repetition of a bout until 1.5 s and 2.0 s after the onset of the last stimulus repetition of the same bout for *E. emiliopugini* and *E. calcaratus*, respectively, which in both cases totaled 30 s. The mean of call duration was obtained for the responses of each individual to each bout of stimuli and also for each period during which no stimulus was presented. Call rate was obtained by dividing the number of calls by the number of seconds of the corresponding period. Call latency was measured within a bout as the time between the onset

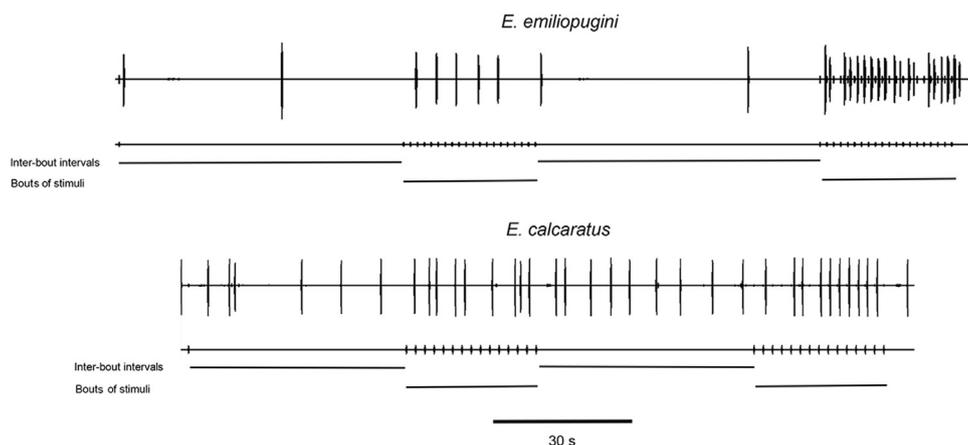


Fig. 2. Recordings of the vocal activity of a male of *E. emiliopugini* and a male of *E. calcaratus* during exposure to two successive bouts of stimuli. Upper traces: evoked vocal responses, lower traces: bouts of stimuli. The first and second bouts of stimuli presented to the male of *E. emiliopugini* had an amplitude modulation (AM) depth of 75% and sound pressure levels of 60 and 84 dB SPL, respectively. The first and second bouts of stimuli presented to the male of *E. calcaratus* corresponded to the degraded stimulus at 52 dB SPL and to the non-degraded stimulus at 58 dB SPL, respectively. Horizontal thin lines indicate two inter-bout intervals and two bouts of stimuli presented to each individual. The horizontal gross line corresponds to the time scale for both recordings.

of a stimulus and a call produced during the subsequent inter-stimulus repetition period (i.e. 1.5 s and 2.0 s in *E. emiliopugini* and *E. calcaratus*, respectively). The call attributes measured are significant for calling competition in different anurans (Gerhardt and Huber, 2002), and also in one of the species of the current study (Penna et al., 2005a).

2.5. Statistical analysis

The effects of acoustic stimulations on evoked vocal responses were evaluated using linear mixed-effects models (LMMs), to account for data dependence resulting from testing multiple stimuli on the same experimental subjects. Individual intercepts were included as a random effect, however individual random slopes were not included due to issues associated to model convergence. We performed four types of analyses, and in all these we fitted models having different fixed effects structures. Because substrate and air temperature may have effect on call characteristics (e.g. Gerhardt and Huber, 2002; Ziegler et al., 2016), some models also incorporated these factors. For each call characteristic within each analysis type, models were compared using model selection based on Akaike's Information Criteria corrected for small sample sizes. We followed the recommendations of Anderson (2008) to evaluate the models. In the first analysis, we evaluated if the basal vocal activity, measured in terms of call rate and call duration changed between the beginning (initial vocal activity) and the end (final vocal activity) of the experimental session (Table 1, models: MI-1 to MI-4). In the second analysis, we evaluated the existence of differences in vocal activity in terms of call rate between each bout of stimuli and the inter-bout preceding interval (Table 1, models: MII-1 to MII-4). Call duration and call latency were not considered in this analysis to avoid extensive data presentation, and call rate was the variable that exhibited the most conspicuous changes. In the third analysis, we evaluated the effects of different temporal or spectral degradation patterns found in nature and SPL on the vocal activity measured in terms of call rate, call duration and call latency (Table 1, models: MIII-1 to MIII-10). Finally, in the fourth analysis we evaluated

Table 1

Summary of fixed effects included in models fitted for the four analyses applied to the vocal activity of *E. emiliopugini* and *E. calcaratus*. Abbreviations: Ts: substrate temperature, Ta: air temperature.

Analysis	Model	Fixed effects included
Effect of experimental session on basal vocal activity	MI-1	Intercept + Experimental session + Ts + Ta
	MI-2	Intercept + Experimental session
	MI-3	Intercept + Ts + Ta
	MI-4	Intercept
Effect of stimulus type on evoked vocal activity	MII-1	Intercept + Stimulus + Ts + Ta
	MII-2	Intercept + Stimulus
	MII-3	Intercept + Ts + Ta
	MII-4	Intercept
Combined effect of stimulus type and SPL on evoked vocal activity	MIII-1	Intercept + Stimulus + SPL + Stimulus:SPL + Ts + Ta
	MIII-2	Intercept + Stimulus + SPL + Stimulus:SPL
Effect of non-natural stimuli on evoked vocal activity	MIV-1	Intercept + Stimulus + Ts + Ta
	MIV-2	Intercept + Stimulus
	MIV-3	Intercept + Ts + Ta
	MIV-4	Intercept
	MIII-3	Intercept + Stimulus + SPL + Ts + Ta
	MIII-4	Intercept + Stimulus + SPL
	MIII-5	Intercept + Stimulus + Ts + Ta
	MIII-6	Intercept + Stimulus
MIII-7	Intercept + SPL + Ts + Ta	
MIII-8	Intercept + SPL	
MIII-9	Intercept + Ts + Ta	
MIII-10	Intercept	

the effects of constant- SPL stimuli having temporal or spectral degradation features found in nature and beyond the natural degradation patterns. Effects of these stimuli on vocal activity were measured in terms of call rate, call duration and call latency. This last analysis intended to search for potential tolerance to exceedingly altered call structure (Table 1, models: MIV-1 to MIV-4). If needed, dependent variables were log (or log + 1 for variables containing values equal to zero) or square-root transformed in order to improve normality and model fitting to the data. Models were fitted with the R (version 3.2.1) library "lme4" (Bates et al., 2015) and model selection was performed using the library AICcmodavg (Mazerolle, 2016). A summary of the fixed effects included in the models is provided in Table 1.

3. Results

3.1. Basal vocal activity

The basal vocal activity was recorded previous to the beginning of the experimental session during an interval of two minutes at least. The 14 *E. emiliopugini* males and the 14 *E. calcaratus* males called at call rates (mean \pm SD) of 2.73 ± 1.80 calls/min and 9.20 ± 3.99 calls/min, respectively. Call duration was 233 ± 44 ms and 291 ± 45 ms, respectively. The mean dominant frequency of the calls of *E. emiliopugini* measured during this interval was 1065 Hz (range: 861–1378 Hz). The means of the three main spectral components of the call of *E. calcaratus*, the first, second and third harmonic were 659 Hz (range: 455–810 Hz), 1318 Hz (range: 912–1617 Hz) and 1977 Hz (range: 1367–2423 Hz), respectively, and the mean amplitude of the second harmonic was 30.1 dB (range: 8.2–43.0 dB) above the first harmonic. The relative amplitudes of the second and third harmonics had a wide range of variation, but in most cases the amplitude of the second was above the third harmonic, having a mean of 2.3 dB (range: –21.5–23.1 dB). Negative values resulted when the second harmonic had a lower amplitude than the third harmonic. A similar signal variation has been reported in a previous study with this species (Penna, 2004).

In *E. emiliopugini*, the model selection procedure to evaluate the effect of recording period on the basal call rate measured before and after the experimental session showed that the top-ranked model included the intercept and the temperatures, and had a probability of 0.697. The model-set having a cumulative probability > 0.950 comprised three models, one of which included the recording period in addition to the temperatures, but this had a relatively low probability (0.231). For call duration, the top-ranked model included the intercept, the recording period and the temperatures and had a probability of 0.746. The model-set having a cumulative probability > 0.950, comprised two models that included temperatures, and one included the recording period. Results are shown in detail in Table S1 and Fig. S1.

In *E. calcaratus*, the top-ranked model for the analysis of call rate included the intercept and the recording period, having a probability of 0.424. The model-set having a cumulative probability > 0.950, comprised the four models, among which the two models including the recording period had the highest probabilities. For call duration, the top-ranked model included only the intercept, having a probability of 0.545. The model-set having a cumulative probability > 0.950 comprised three models, among which the model including the recording period had the lowest probability (0.157). Results are shown in detail in Table S2 and Fig. S1.

3.2. Evoked vocal responses to bouts of synthetic stimuli

3.2.1. *Eupsophus emiliopugini*

Males responded to the bout of 20 repetitions of the non-degraded stimulus (90% AM depth) presented at the highest amplitude (84 dB SPL) with a call rate of 28.55 ± 18.44 calls/min, a call duration of 323 ± 87 ms and a call latency of 739 ± 136 ms.

Table 2

Model selection to evaluate the effect of stimulus type, sound pressure level and their interaction on the vocal activity of *E. emiliopugini*. Abbreviations: Ts: substrate temperature, Ta: air temperature, K: number of estimated parameters, AICc: Akaike's Information Criteria corrected for small sample sizes. Delta AICc: difference between the best model and the other models, AICc Wt: weight of the evidence of the model (probability of the model), Cum. Wt: cumulative weight of the ranked models (cumulative probability), LL: log likelihood of the model.

Variable	Model	Fixed effects included	K	AICc	Delta AICc	AICc Wt	Cum. Wt	LL
Call rate	MIII-8	Intercept + SPL	6	596.842	0.000	0.451	0.451	-292.160
	MIII-7	Intercept + SPL + Ts + Ta	8	597.039	0.197	0.409	0.859	-290.067
	MIII-4	Intercept + Stimulus + SPL	8	600.417	3.575	0.075	0.935	-291.756
	MIII-3	Intercept + Stimulus + SPL + Ts + Ta	10	600.726	3.883	0.065	1.000	-289.662
	MIII-2	Intercept + Stimulus + SPL + Stimulus:SPL	14	611.746	14.904	0.000	1.000	-290.500
	MIII-1	Intercept + Stimulus + SPL + Stimulus:SPL + Ts + Ta	16	612.417	15.574	0.000	1.000	-288.407
	MIII-10	Intercept	3	670.840	73.998	0.000	1.000	-332.347
	MIII-9	Intercept + Ts + Ta	5	670.877	74.035	0.000	1.000	-330.253
	MIII-6	Intercept + Stimulus	5	674.584	77.742	0.000	1.000	-332.107
	MIII-5	Intercept + Stimulus + Ts + Ta	7	674.727	77.885	0.000	1.000	-330.013
Call duration	MIII-1	Intercept + Stimulus + SPL + Stimulus:SPL + Ts + Ta	16	-181.203	0.000	0.525	0.525	108.491
	MIII-7	Intercept + SPL + Ts + Ta	8	-179.877	1.326	0.271	0.796	98.412
	MIII-3	Intercept + Stimulus + SPL + Ts + Ta	10	-179.242	1.961	0.197	0.993	100.354
	MIII-2	Intercept + Stimulus + SPL + Stimulus:SPL	14	-171.498	9.705	0.004	0.997	101.188
	MIII-8	Intercept + SPL	6	-169.741	11.462	0.002	0.999	91.143
	MIII-4	Intercept + Stimulus + SPL	8	-169.073	12.131	0.001	1.000	93.010
	MIII-9	Intercept + Ts + Ta	5	-157.556	23.648	0.000	1.000	83.971
	MIII-5	Intercept + Stimulus + Ts + Ta	7	-156.447	24.756	0.000	1.000	85.590
	MIII-10	Intercept	3	-147.021	34.182	0.000	1.000	76.587
	MIII-6	Intercept + Stimulus	5	-145.886	35.318	0.000	1.000	78.137
Call latency	MIII-7	Intercept + SPL + Ts + Ta	8	-5.692	0.000	0.404	0.404	11.320
	MIII-9	Intercept + Ts + Ta	5	-4.863	0.829	0.267	0.671	7.625
	MIII-3	Intercept + Stimulus + SPL + Ts + Ta	10	-3.407	2.285	0.129	0.800	12.437
	MIII-5	Intercept + Stimulus + Ts + Ta	7	-2.701	2.992	0.091	0.890	8.716
	MIII-8	Intercept + SPL	6	-1.439	4.253	0.048	0.939	6.992
	MIII-10	Intercept	3	-0.632	5.060	0.032	0.971	3.392
	MIII-4	Intercept + Stimulus + SPL	8	0.768	6.460	0.016	0.987	8.090
	MIII-6	Intercept + Stimulus	5	1.446	7.138	0.011	0.998	4.470
	MIII-1	Intercept + Stimulus + SPL + Stimulus:SPL + Ts + Ta	16	5.376	11.069	0.002	1.000	15.201
	MIII-2	Intercept + Stimulus + SPL + Stimulus:SPL	14	9.287	14.980	0.000	1.000	10.795

Males of *E. emiliopugini* altered their vocal activity when exposed to bouts of stimuli relative to the inter-bout preceding intervals, indicating that in general, stimulation effectively elicited vocal changes in experimental subjects. We evaluated the effect of stimulation on call rate performing separate analyses and the corresponding model selection procedures to assess the effect of each type of stimulus. Among the 14 top-ranked models obtained, 12 models included the intercept and stimulus type, having probabilities ranging from 0.418 to 0.930. An exception corresponded to the 90% modulation depth stimulus presented at 48 dB SPL, for which the top-ranked model included only the intercept, having a probability of 0.405. The other exception corresponded to the 60% modulation depth stimulus presented at 48 dB SPL, for which the top-ranked model included the intercept, stimulus type and temperatures, having a probability of 0.837 (Table S3, Fig. S2). A recording of the vocal activity of one subject exposed to two successive bouts of stimuli and the corresponding preceding inter-bout intervals is shown in Fig. 2.

The analysis of the combined effect of stimulus type and SPL showed that, for call rate the top-ranked model included the intercept and the SPL, having a probability of 0.451. The model-set having a cumulative probability > 0.950 comprised four models, all of which included SPL. In this model-set, two out of four models included the effect of stimulus type, but both had relatively low probabilities (< 0.075). For call duration the top-ranked model had a probability of 0.525 and included the intercept, stimulus type, SPL, the interaction between stimulus type and SPL, and the temperatures. The model-set having a cumulative probability > 0.950, comprised three models, all of which included SPL, and stimulus type was included in two of these models. For call latency the top-ranked model included the intercept, SPL and the temperatures, having a probability of 0.404. The model-set having a cumulative probability > 0.950 comprised six models, three of which included SPL and two included stimulus type, suggesting that these

fixed effects may not have a clear influence on call latency. Overall, these results indicate that SPL has a clear effect on call rate and call duration, but stimulus type does not. Call latency in contrast is not clearly affected by any of these factors (Table 2, Fig. 3).

The analysis of responses to bouts of stimuli having degradation patterns found in nature and also patterns beyond the natural degradation range presented at the constant amplitude of 72 dB SPL showed no clear effects on call rate, call duration and call latency as none of the top-ranked model included the stimulus type. The model-sets having a cumulative probability > 0.950 included the effect of stimulus type in the analyses of call rate and call duration, but with relatively low probabilities (< 0.088) (Table 3, Fig. 4).

3.2.2. *E. calcaratus*

Males responded to the bout of 15 repetitions of the non-degraded call presented at the highest amplitude (64 dB SPL) with a call rate of 16.29 ± 7.48 calls/min, a call duration of 286 ± 54 ms, and a call latency of 905 ± 241 ms.

Males of *E. calcaratus* in general altered their vocal activity when exposed to bouts of stimuli relative to the inter-bout preceding intervals. Separate analyses and model selection procedures to evaluate the effect of each type of stimuli were applied to call rate. Among the 10 top-ranked models, 8 models included the intercept and stimulus type. The probability of these models ranged from 0.500 to 0.955. The model corresponding to the non-degraded stimulus presented at 46 dB SPL included the intercept only, having a probability of 0.463. The model corresponding to the stimulus lacking the third harmonic presented at 64 dB SPL included the intercept, stimulus type and the temperatures, having a probability of 0.765 (Table S4, Fig. S3). A recording of the vocal activity of one subject to two successive bouts of stimuli and the corresponding preceding silent intervals is shown in Fig. 2.

The analysis that evaluated the combined effects of stimulus type

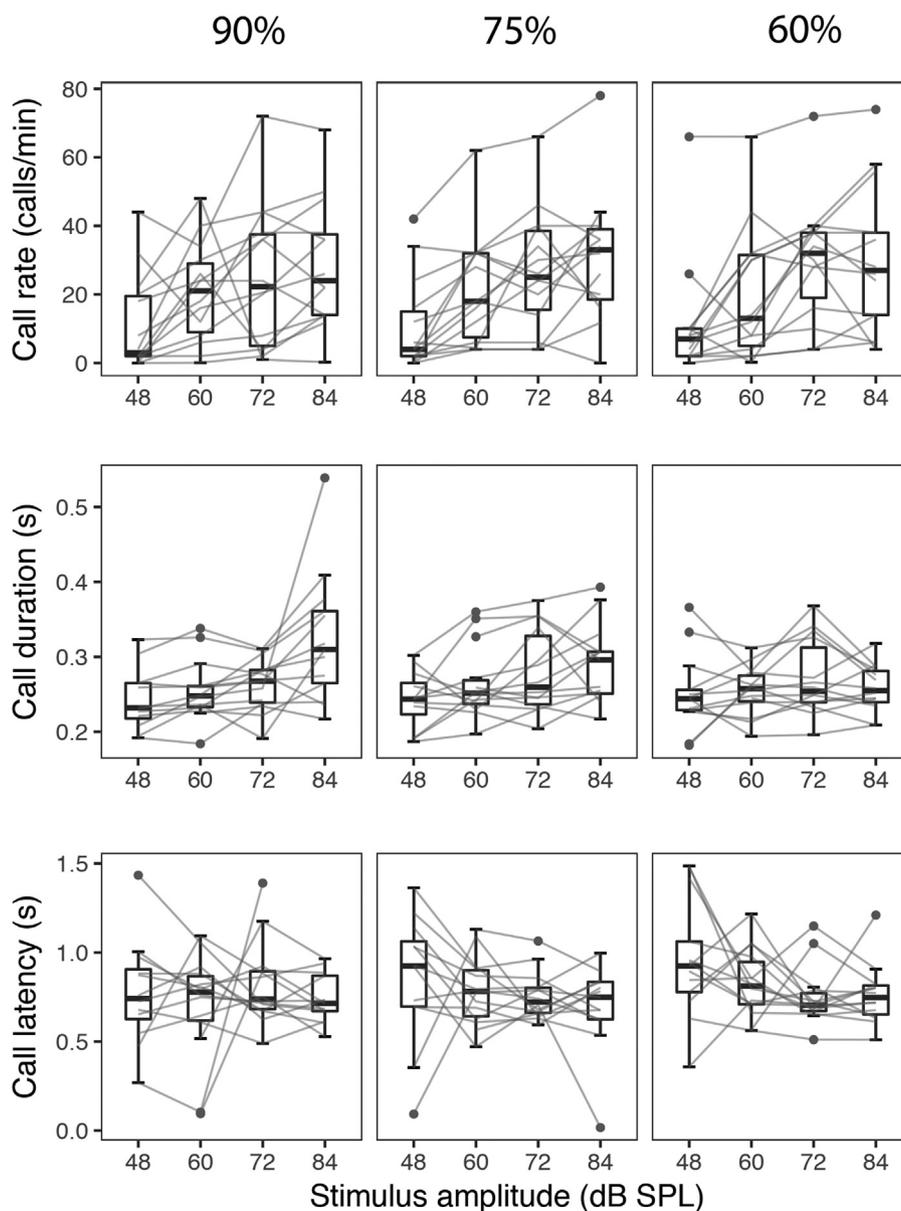


Fig. 3. Evoked vocal responses of 14 males of *E. emiliopugini* to stimuli of different amplitude modulation depths (90, 75 and 60%, as indicated on top of the graphs), presented at different amplitudes. Boxplots depict quartiles and ranges, and gray lines indicate individual measures for the three variables analyzed. Dots correspond to outliers.

Table 3

Model selection to evaluate the effect of stimulus type having characteristics not found in nature on the vocal activity of *E. emiliopugini*. Abbreviations as in Table 2.

Variable	Model	Fixed effects included	K	AICc	Delta AICc	AICc Wt	Cum. Wt	LL
Call rate	MIV-4	Intercept	3	242.832	0.000	0.626	0.626	-118.234
	MIV-3	Intercept + Ts + Ta	5	244.523	1.690	0.269	0.894	-116.793
	MIV-2	Intercept + Stimulus	7	246.933	4.101	0.080	0.975	-115.563
	MIV-1	Intercept + Stimulus + Ts + Ta	9	249.243	6.411	0.025	1.000	-114.122
Call duration	MIV-3	Intercept + Ts + Ta	5	-109.801	0.000	0.890	0.890	60.377
	MIV-1	Intercept + Stimulus + Ts + Ta	9	-105.172	4.629	0.088	0.978	63.111
	MIV-4	Intercept	3	-102.102	7.699	0.019	0.997	54.235
	MIV-2	Intercept + Stimulus	7	-98.213	11.588	0.003	1.000	57.024
Call latency	MIV-4	Intercept	3	-40.443	0.000	0.777	0.777	23.406
	MIV-3	Intercept + Ts + Ta	5	-37.417	3.026	0.171	0.948	24.185
	MIV-2	Intercept + Stimulus	7	-34.735	5.708	0.045	0.993	25.285
	MIV-1	Intercept + Stimulus + Ts + Ta	9	-31.086	9.357	0.007	1.000	26.068

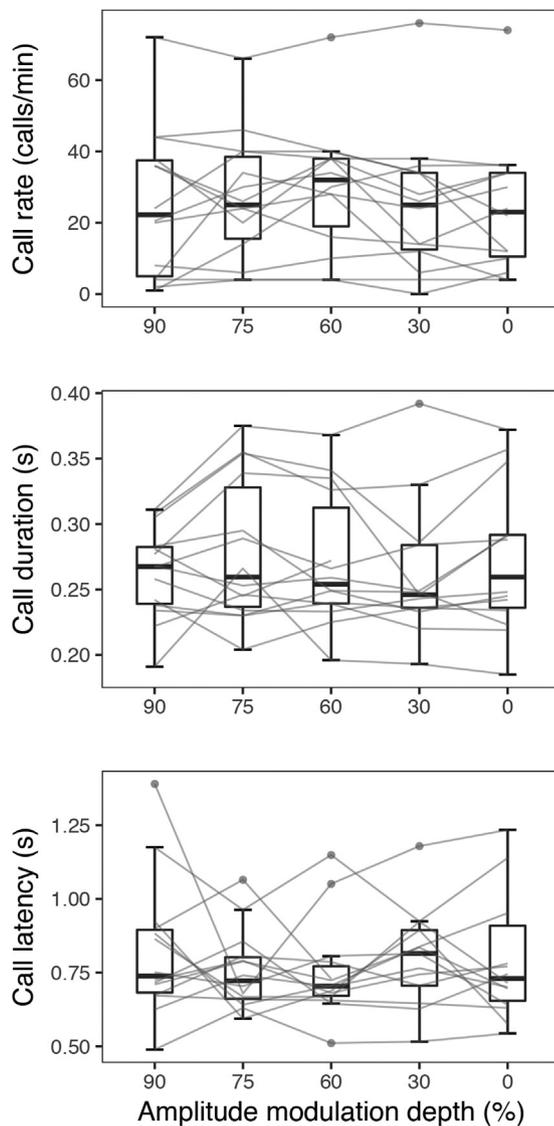


Fig. 4. Evoked vocal responses of 14 males of *E. emiliopugini* to stimuli of different amplitude modulation depths (%) presented at a constant amplitude (72 dB SPL). Symbols as in Fig. 3.

and SPL showed that for call rate, the top-ranked model included the intercept, SPL and the temperatures and had a probability of 0.460. The model-set having a cumulative probability > 0.950 comprised four models, all of which included SPL. Stimulus type was included in two of these models but had relative low probabilities (< 0.142). For call duration the top-ranked model had a probability of 0.341 and included the intercept and SPL. The model-set having a cumulative probability > 0.950 comprised five models, all of which included SPL. Three of these models included the effect of stimulus type but had low relative probabilities (< 0.109). For call latency the top-ranked model included only the intercept and had a probability of 0.503. The ranked model-set having a cumulative probability > 0.950 , comprised five models, one of which included SPL and had a low probability (0.053). Two of these models included stimulus type and also had low probabilities (< 0.172). Overall, results of this analysis indicate that SPL has a significant effect on call rate and call duration, but the effect of stimulus type may not be important. Stimulus type and SPL apparently do not affect call latency (Table 4, Fig. 5).

The analysis of responses to bouts of stimuli having spectral degradation patterns found in nature and also patterns beyond the natural degradation range and presented at the constant amplitude of

64 dB SPL did not indicate a clear effect of stimulus type on call rate, call duration and call latency, as none of the top-ranked models included stimulus type. However, the ranked model-sets having a cumulative probability > 0.950 include the effect of stimulus type, so the effect of this factor cannot be totally dismissed (Table 5, Fig. 6).

4. Discussion

Results of this study show that the vocal responses of males of *E. emiliopugini* and *E. calcaratus* depend strongly on stimulus SPL. Call rate, the vocal response measure most sensitive to manipulations of acoustic stimuli in these species (Penna et al., 2005a, 2005b; Penna and Hamilton-West, 2007) depends exclusively on this property. In contrast, the responses to stimuli resembling calls of non-degraded and degraded nature and also to stimuli having spectral and temporal characteristics beyond the range of variation of degraded signals are in general not affected.

In *E. emiliopugini*, vocal responses to stimuli differing in SPL and AM depth are affected by the first factor, where call rate and duration tend to increase with SPL. Nevertheless, for call duration, the top-ranked model included the interaction between AM depth and SPL suggesting that an effect on this variable cannot be totally dismissed. Lower AM depths show a tendency to evoke calls having shorter durations at high SPLs and longer durations at low SPLs. In this species, responses to stimuli at a constant SPL and encompassing AM depths beyond the natural range of variation are not related to this temporal factor.

In *E. calcaratus*, vocal responses to stimuli differing in SPL and harmonic structure are affected by the first factor in terms of call rate and call duration. In this species, responses to stimuli at a constant SPL and encompassing harmonic structures beyond the natural range of variation are not affected by this spectral factor.

The lack of differences in responses to stimuli of diverse harmonic structure in *E. calcaratus* for detection of degraded vocalization is consistent with the large inter-individual variation in harmonic structure in this species, as shown by the harmonic structure range of calls recorded from the experimental subjects (see sub-section 3.2.2.). Furthermore, burrow resonances affect the relative amplitudes of the harmonics of the calls of *E. calcaratus* by decreasing the amplitude of the third relative to the second harmonic (Penna, 2004), an effect similar to spectral degradation affecting propagated calls of this species.

The restricted dependence of vocal responses of males of *E. emiliopugini* on temporal degraded patterns of stimuli contrasts with results of a study with females of the North American treefrog *Hyla versicolor* showing a clear dependence of phonotactic responses on call AM depth (Kuczynski et al., 2010). A recent study in *H. chrysocelis* has also shown preferences for signals having non-degraded temporal features (Schwartz et al., 2016). Results of the current study are also in contrast with recent studies in male Neotropical frogs *Allobates femoralis* (Ringle et al., 2015) and North American frogs *Acris crepitans* (Venator et al., 2017), showing recognition of temporal degraded patterns of conspecific calls.

The restricted dependence of vocal responses of burrowing frogs *Eupsophus* on call degraded patterns could be related to the resources for increasing the propagation range of acoustic signals in these species. The shelters in which breeding males dwell have resonance properties that enhance the amplitude of incoming (Penna and Solís, 1996, 1999; Penna, 2004) and outgoing (Muñoz and Penna, 2016) conspecific calls. However these improvements in amplitude of signals reaching recipients are not accompanied by reduction of degradation processes as occur in animals calling from exposed positions elevated from ground level (Ringle et al., 2015; Schwartz et al., 2016). In these circumstances, it would be advantageous for *Eupsophus* frogs to keep responding to neighbors' calls affected by degradation processes.

In contrast with recent studies on detection of temporal degraded patterns (Kuczynski et al., 2010; Ringle et al., 2015; Schwartz et al., 2016; Venator et al., 2017), no studies on detection of degraded

Table 4

Model selection to evaluate the effect of stimulus type, sound pressure level and their interaction on the vocal activity of *E. calcaratus*. Abbreviations as in Table 2.

Variable	Model	Fixed effects included	K	AICc	Delta AICc	AICcWt	Cum.Wt	LL
Call rate	MIII-7	Intercept + SPL + Ts + Ta	8	278.591	0.000	0.460	0.460	-130.597
	MIII-8	Intercept + SPL	6	279.495	0.904	0.293	0.753	-133.348
	MIII-3	Intercept + Stimulus + SPL + Ts + Ta	9	280.948	2.357	0.142	0.894	-130.592
	MIII-4	Intercept + Stimulus + SPL	7	281.763	3.171	0.094	0.988	-133.343
	MIII-1	Intercept + Stimulus + SPL + Stimulus:SPL + Ts + Ta	12	287.084	8.492	0.007	0.995	-129.966
	MIII-2	Intercept + Stimulus + SPL + Stimulus:SPL	10	287.612	9.021	0.005	1.000	-132.717
	MIII-9	Intercept + Ts + Ta	5	301.113	22.522	0.000	1.000	-145.274
	MIII-10	Intercept	3	302.272	23.680	0.000	1.000	-148.025
	MIII-5	Intercept + Stimulus + Ts + Ta	6	303.340	24.749	0.000	1.000	-145.270
	MIII-6	Intercept + Stimulus	4	304.416	25.825	0.000	1.000	-148.021
Call duration	MIII-8	Intercept + SPL	6	-237.114	0.000	0.341	0.341	124.961
	MIII-7	Intercept + SPL + Ts + Ta	8	-237.029	0.085	0.326	0.667	127.220
	MIII-4	Intercept + Stimulus + SPL	7	-234.837	2.278	0.109	0.776	124.962
	MIII-3	Intercept + Stimulus + SPL + Ts + Ta	9	-234.661	2.453	0.100	0.876	127.221
	MIII-2	Intercept + Stimulus + SPL + Stimulus:SPL	10	-233.922	3.192	0.069	0.945	128.061
	MIII-1	Intercept + Stimulus + SPL + Stimulus:SPL + Ts + Ta	12	-233.464	3.650	0.055	1.000	130.324
	MIII-9	Intercept + Ts + Ta	5	-216.468	20.646	0.000	1.000	113.520
	MIII-10	Intercept	3	-216.263	20.851	0.000	1.000	111.244
	MIII-5	Intercept + Stimulus + Ts + Ta	6	-214.245	22.869	0.000	1.000	113.527
	MIII-6	Intercept + Stimulus	4	-214.123	22.991	0.000	1.000	111.250
Call latency	MIII-10	Intercept	3	-87.408	0.000	0.503	0.503	46.815
	MIII-6	Intercept + Stimulus	4	-85.266	2.142	0.172	0.676	46.820
	MIII-9	Intercept + Ts + Ta	5	-85.185	2.223	0.166	0.842	47.876
	MIII-5	Intercept + Stimulus + Ts + Ta	6	-82.961	4.447	0.054	0.896	47.880
	MIII-8	Intercept + SPL	6	-82.901	4.508	0.053	0.949	47.850
	MIII-4	Intercept + Stimulus + SPL	7	-80.633	6.775	0.017	0.966	47.855
	MIII-7	Intercept + SPL + Ts + Ta	8	-80.424	6.985	0.015	0.981	48.911
	MIII-2	Intercept + Stimulus + SPL + Stimulus:SPL	10	-79.828	7.581	0.011	0.993	51.003
	MIII-3	Intercept + Stimulus + SPL + Ts + Ta	9	-78.067	9.342	0.005	0.997	48.916
	MIII-1	Intercept + Stimulus + SPL + Stimulus:SPL + Ts + Ta	12	-76.975	10.433	0.003	1.000	52.063

patterns in the spectral domain by anurans have been conducted. Females of the North American treefrog *Hyla cinerea* are sensitive to relative amplitude of call spectral peaks (Gerhardt, 1976, 1981), but their abilities to detect spectral degradation patterns occurring in nature have not been explored.

The responsiveness of *E. calcaratus* to calls having degraded spectral patterns is consistent with a former study in which males of this species responded similarly to stimuli composed by the second and third harmonics or just by the second harmonic (Penna and Quispe, 2007). Also in the closely related *E. roseus*, males show no phonotactic preferences for spectral patterns of advertisement calls, in contrast with females, which prefer calls containing harmonics with similar amplitudes (Moreno-Gómez et al., 2015), a behavior concordant with the auditory sensitivity of females of this species (Moreno-Gómez et al., 2013). According to this sexual difference in behavioral responses, spectral degradation patterns could be significant for *Eupsophus* females. Because the auditory sensitivity of males of *E. roseus* has not been studied, it is not possible to relate the behavioral differences observed to sensory capabilities of both sexes. However, degradation may be expected to have greater impact on female than on male responses in *Eupsophus*, since males call from inside their burrows at stable distances from their neighbors. Females instead arrive from the exterior, approaching sound sources at different distances, attracted by resident callers inside their burrows.

It is also particularly interesting that the two species of *Eupsophus* confront noise with opposing vocal strategies: *E. calcaratus* increases its vocal output (Penna et al., 2005b), while *E. emiliopugini* diminishes its call rate in the presence of prolonged noise (Penna and Hamilton-West, 2007). Noise is known to affect the perception of distance in humans; under noise, sound sources are judged to be closer than in quiet backgrounds (Mershon et al., 1989). Discrimination of degraded patterns of vocalizations by birds is also impaired to some extent by background noise (Pohl et al., 2015). It could be expected that males of

E. calcaratus as they increase their vocalization rate in the presence of noise are less sensitive to degradation patterns since apparently they are able to communicate in the presence of high noise levels under which detection of degraded patterns of vocalizations is compromised. In contrast, males of *E. emiliopugini*, which suppress their vocal rate in the presence of noise would be expected to be more sensitive to degradation patterns as they communicate preferentially during quiet background conditions. Nevertheless the very restricted discrimination between degraded and non-degraded patterns in *E. emiliopugini* and the lack of discrimination in *E. calcaratus* suggests that the continuity of vocal responsiveness is advantageous to maintain the choral activity and the subsequent female attraction in both taxa. Also, since males of a congeneric species respond phonotactically to conspecific calls (Moreno-Gómez et al., 2015), it is likely that the chorusing activity promotes recruitment of additional vocal participants.

Auditory systems in different animal groups are endowed with a relative tolerance, having perceptual scopes broader than the range of variation of conspecific signals. Such relative tolerance would favor signal detection and processing of degraded signals occurring in natural environments (Luther and Wiley, 2009; Amézquita et al., 2011; Erdtmann et al., 2011; Vélez et al., 2012). In addition, studies reporting clustering trends in vocalizations among coexisting anuran (Chek et al., 2003; Amézquita et al., 2011) and bird species (Planqué and Slabbekoorn, 2008; Malavasi and Farina, 2013; Tobias et al., 2014a, 2014b) also suggest that perceptual permissiveness rather than segregation underlies communication in these communities.

A neurophysiological substrate for detection of degraded patterns of vocalizations has been reported for the North American frog *Rana pipiens*. Midbrain neurons in this species decrease their discharge synchrony in response to pulsed stimuli having increased reverberation times, which emulate the effects of temporal degradation on propagating calls (Ratnam et al., 2004; Feng and Schul, 2007). Neurons capable of detecting naturally degraded calls have been recently reported in

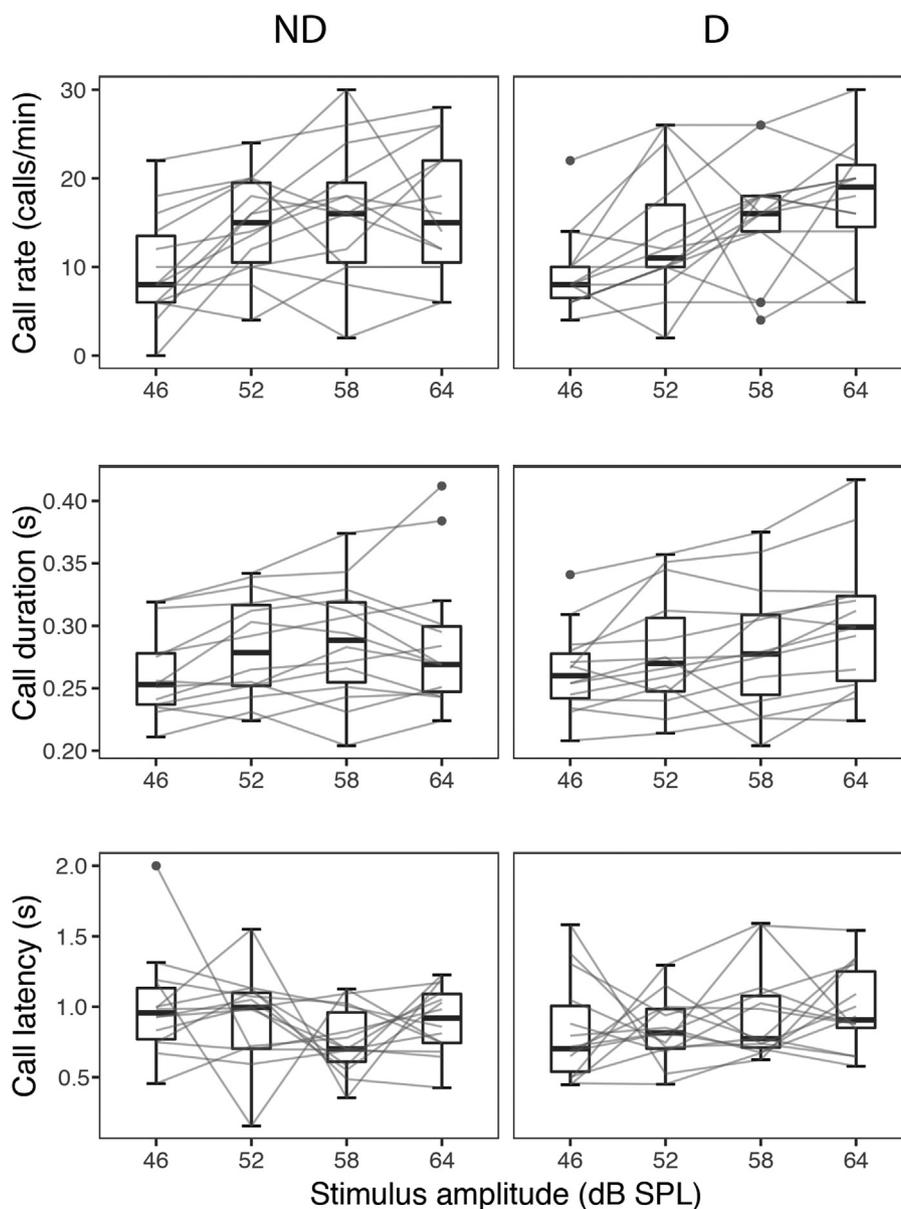


Fig. 5. Evoked vocal responses of 14 males of *E. calcaratus* to stimuli having different spectral structure: non-degraded (ND) and degraded (D) as indicated on top of the graphs, presented at different amplitudes. Symbols as in Fig. 3.

Table 5
Model selection to evaluate the effect of stimulus type having characteristics not found in nature on the vocal activity of *E. calcaratus*. Abbreviations as in Table 2.

Variable	Model	Fixed effects included	K	AICc	Delta AICc	AICc Wt	Cum. Wt	LL
Call rate	MIV-3	Intercept + Ts + Ta	5	135.289	0.000	0.605	0.605	-62.044
	MIV-4	Intercept	3	136.482	1.193	0.333	0.938	-65.010
	MIV-1	Intercept + Stimulus + Ts + Ta	8	140.978	5.689	0.035	0.974	-60.957
	MIV-2	Intercept + Stimulus	6	141.560	6.271	0.026	1.000	-63.923
Call duration	MIV-4	Intercept	3	-102.552	0.000	0.407	0.407	54.507
	MIV-3	Intercept + Ts + Ta	5	-101.804	0.748	0.280	0.686	56.502
	MIV-2	Intercept + Stimulus	6	-101.213	1.339	0.208	0.894	57.464
	MIV-1	Intercept + Stimulus + Ts + Ta	8	-99.854	2.698	0.106	1.000	59.459
Call latency	MIV-4	Intercept	3	4.539	0.000	0.562	0.562	0.961
	MIV-2	Intercept + Stimulus	6	5.576	1.037	0.335	0.897	4.069
	MIV-3	Intercept + Ts + Ta	5	8.659	4.120	0.072	0.969	1.271
	MIV-1	Intercept + Stimulus + Ts + Ta	8	10.307	5.768	0.031	1.000	4.378

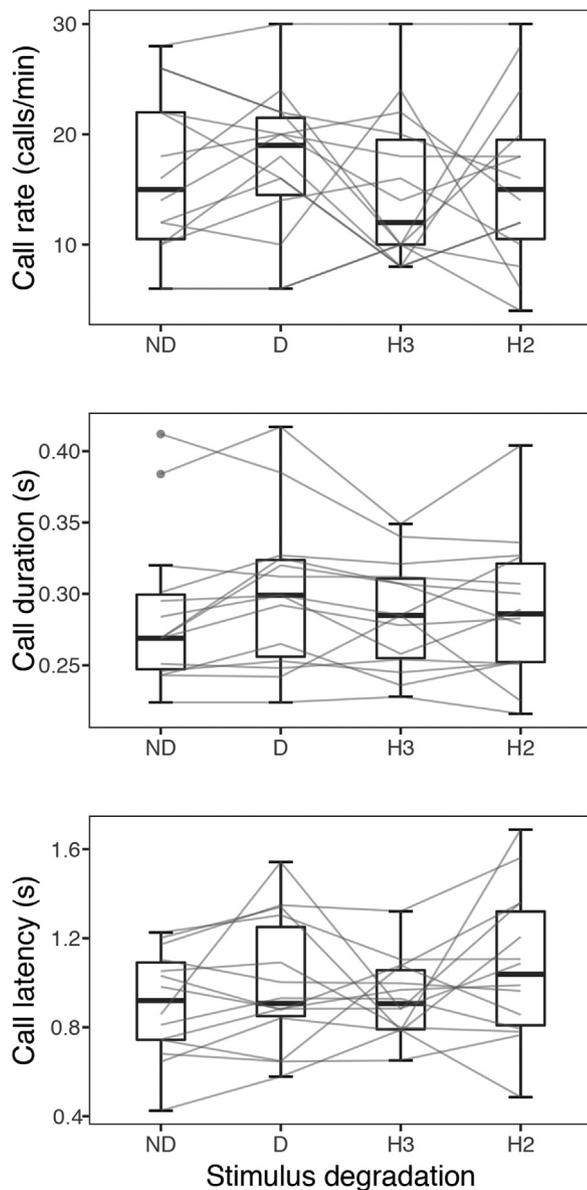


Fig. 6. Evoked vocal responses of 14 males of *E. calcaratus* to stimuli having different spectral structure, presented at a constant amplitude (64 dB SPL). ND: non-degraded, D: degraded, H3: lacking third harmonic, H2: lacking third harmonic. Symbols as in Fig. 3.

birds Mouterde et al., 2017). If this is a neural property having an extensive distribution in anurans, the circumstances that restrict the use of the detection capabilities supported by such neurons is an issue that deserves further research efforts.

The contrast between results of the current study showing a general lack of discrimination of degraded patterns of vocalizations by males of two anuran species and those studied by other researchers, showing recognition of degraded patterns of vocalizations by North American female (Kuczynski et al., 2010; Schwartz et al., 2016), and Neotropical (Ringle et al., 2015) and North American (Venator et al., 2017) male frogs indicate an important variation of this capability in anurans. Different responsiveness in discrimination of familiar structure of vocalizations has also been reported for these vertebrates. Some species have been shown to recognize individuals based on acoustic signals (Lesbarreres and Lode, 2002; Feng et al., 2009; Davis, 1987; Bee and Gerhardt, 2001, 2002) whereas at least another species lacks this capability (Bee, 2003; Gardner and Graves, 2005). Different modalities of social interactions and distribution patterns in breeding aggregations characteristic of different species may underlie the diverse capabilities

of recognition of familiar versus unfamiliar and of degraded versus non-degraded acoustic signals in anurans.

In conclusion, our results showing effects of SPL but a general lack of effects of degradation patterns on vocal responses of two syntopic anuran species communicating with remarkably different signals suggest that responsiveness to a wide range of signal patterns prevails in environments and circumstances in which alterations of broadcast signals are not counteracted. Further comparisons of responses to degraded patterns of vocalizations between other vertebrates living syntopically would determine the extent to which dissimilarities in recognition of propagating signals are significant for the effectiveness of sound communication systems operating in shared environments.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.beproc.2017.05.008>.

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