Susceptibility of evoked vocal responses to noise exposure in a frog of the temperate austral forest

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Animals that communicate by means of acoustic signals show diverse strategies in the presence of noise interference. Penna et al. (2005, *Animal Behaviour*, **70**, 639−651) found that the leptodactylid frog *Eupsophus calcaratus* from the temperate austral forest increases its vocal output in the presence of natural noises and a band-pass noise overlapping the main spectral components of its advertisement call. We subjected the sympatric species *E. emiliopugini* to similar experimental conditions to assess its response to noise exposure. Male *E. emiliopugini* showed no increase in vocal activity in the presence of moderate noise levels (67 dB RMS SPL, fast weighting) and decreased their vocal output in the presence of band-pass noise of increasing intensity (49−85 dB RMS SPL, fast weighting). However, *E. emiliopugini*, like *E. calcaratus*, increased the amplitude of their vocal responses in these circumstances. The vocal responses of males of *E. emiliopugini* under noise exposure and their contrast with the congeneric species unveil different strategies in confronting interference, whose origins and adaptive significance warrant further study.

Vertebrates that communicate by sound in terrestrial environments use different strategies to overcome noise interference. Various birds and mammals, including man, increase the amplitude of their vocalizations in the presence of noise (e.g. Sinnot et al. 1975; Cynx et al. 1998; Brumm & Todt 2002; Pytte et al. 2003; Brumm 2004), a short-term response known as the Lombard effect. In the long term, frogs, birds and mammals have been reported to produce signals having spectra that stand out from the background noise of their natural environments. In some cases the spectra of the signals are in a mid-frequency 'silent window' encompassed by ranges of elevated background noise at lower and higher frequencies (e.g. Morton 1975; Brenowitz 1982; Wiley & Richards 1982; Brown & Waser 1984; Waser & Brown 1986; de la Torre & Snowdon 2002). In other instances, frogs and birds that dwell in noisy stream environments produce vocalizations containing frequencies well above the noise spectral range (Dubois & Martens 1984; Haddad & Giaretta 1999;

Hödl & Amézquita 2001). In some of these cases the spectra of the signals extend well into the ultrasound range (Feng et al. 2000, 2006; Narins et al. 2004).

Additional strategies used by animals for communicating in noise comprise the increase in the emission rate of vocalizations by quails (Potash 1972) and penguins (Lengagne et al. 1999) and the increase in signal duration by marmosets (Brumm et al. 2004). The different strategies used by animals to communicate amid natural noise have been systematized in a recent review by Brumm & Slabbekoorn (2005).

Several studies have investigated the effect of noise on anuran male call production and female phonotaxis (reviewed in Penna et al. 2005a). In general, noise at high levels inhibits male calling (e.g. Schwartz & Wells 1983a, b) and impairs the ability of females to orient towards the signals (e.g. Ehret & Gerhardt 1980; Wollerman 1999); however, noise at low or moderate levels facilitates both behavioural responses (e.g. Narins 1982; Schwartz & Gerhardt 1998).

In a recent study of the leptodactylid frog *Eupsophus calcaratus*, Penna et al. (2005a) found that males increased their call rate and call duration when exposed to moderate levels of abiotic noises of wind, rain, creek and sea surf and

to a band-pass noise encompassing the main spectral components of the conspecific advertisement call. The vocal responsiveness in the presence of noise indicates that this frog, native to a relatively simple sound environment in the temperate forest of southern Chile, is capable of responding actively to considerable levels of interference.

Eupsophus emiliopugini is also a leptodactylid frog from the temperate forests of southern Chile, where it breeds from late spring to early summer (November–December). Males of this and related species call from inside burrows excavated among mosses and ferns in bogs (Penna & Solís 1996, 1999). The geographical distribution of *E. emiliopugini* overlaps with that of *E. calcaratus*, which breeds earlier in the year (August–October; Penna 2004). Males of *E. emiliopugini* often occupy the same burrows used earlier by the congeneric species and most often produce a single-note, amplitude-modulated call (Penna & Solís 1996, 1998, 1999). However, when spaced at short distances, neighbours engage in duets during which double-note calls are given. Occasionally, longer calls of up to 10 notes can be heard, apparently produced during short-range encounters between males occupying closely spaced burrows. These longer calls probably convey an aggressive message to the opponent. In breeding areas, females are rarely seen and their call preferences remain unexplored. Males of *E. emiliopugini* respond readily when presented with playbacks of a natural advertisement call (Penna et al. 2005b), and their call rate depends directly on the level of the stimulus.

In the present study, we endeavoured to subject males of *E. emiliopugini* to experimental conditions similar to those in the previous study with *E. calcaratus* (Penna et al. 2005a) to compare the responses of these frogs when confronting noise intrusion. Males of *E. emiliopugini* were induced to call in response to a synthetic imitation of the conspecific advertisement call presented with different types of noise. First, we tested the responsiveness of frogs to various natural abiotic noises and a synthetic band-pass noise encompassing the frequency range of the main spectral components of the advertisement call to explore their effects on frog's evoked vocal responses (EVRs). In a second experiment, the susceptibility of the EVRs to noise intensity was evaluated with band-pass noise.

Sun & Narins (2005) reported different responses to anthropogenic noise in a calling assemblage of tropical anurans; most taxa decreased their vocal activity, but one species augmented its vocal output in these circumstances. To the best of our knowledge, no experimental studies comparing the effect of natural noises on related vertebrate taxa have been conducted, and thus this study is aimed at contributing evidence on the use of different strategies in the presence of interference in natural settings.

METHODS

Study Site

The study was conducted during October 2002 and 2003 in La Picada (41°05′S, 72°30′W, 800 m above sea level), within the Vicente Pérez Rosales National Park in southern Chile. The study site was a bog in which males of *E. emiliopugini* called from burrows hidden among mosses (*Rhacomytrium*), grasses (*Scyrpus* and *Myrteola*) or ferns (*Blechnum*) along the borders of small streams. Bioacoustical studies with *E. emiliopugini* and other frog species have been conducted at this site for several years.

Noise Recording

Natural noises of wind, rain and creeks were recorded in this locality and noise from the sea surf was recorded in the locality of Cucao (43°40′S, 74°00′W) in the National Park of Chiloé with the microphone of a sound level meter (Brüel & Kjaer 2230) fitted with a windscreen (UA 0237) and connected with an extension cable (UA 0028). Details of the recording procedures and sound pressure levels (SPLs) measured for the different noise types are provided in Penna et al. (2005a). Surf noise was included in the experimental design, because although frogs at the study site are not exposed to this sound, populations of *E. emiliopugini* in coastal localities as Cucao confront this natural interference. The 67-dB root-mean-square (RMS) sound pressure level (fast weighting scale) chosen for the exposures to different types of noise (see below) was within the range of the natural noises recorded.

Stimuli Preparation

The editing procedures of natural noises followed those of Penna et al. (2005a), except that each of the five synthetic stimulus bouts lasted 30 s instead of the 60 s. Thus, the total duration of the noises to which the frogs were exposed was 150 s instead of 180 s. In addition, we created a 150-s band-pass noise encompassing the spectra of the advertisement calls of *E. emiliopugini*, with cutoff frequencies of 400 and 2400 Hz, instead of 700 and 2700 Hz as used in the previous study, using a waveform generator (WG1, Tucker–Davis Technologies, Alachua, Florida, U.S.A.) and a programmable filter (PF1, Tucker–Davis Technologies). An oscillogram and a power spectrum of this noise are shown in Fig. 1.

A synthetic call was generated with the Soundmaker 1.0.4 software (Ovolab, Torino, Italy) to resemble the natural advertisement call of this species (Fig. 2). The signal was composed of 6-ms pulses with rise and fall times of 1 and 5 ms, respectively. The total duration of the call was 250 ms and contained 48 pulses. The interpulse period increased progressively from the beginning to the end of the signal, from 3 to 8 ms. For the initial periods, it was necessary to reduce the duration of the pulse fall time, taking care to avoid discontinuities in the sinusoidal waveform. For subsequent periods (between 6 and 8 ms), intervals of silence were added. The call envelope had rise and fall times of 50 and 100 ms, respectively, and a plateau of 100 ms. We generated bouts of 20 calls, with an intercall interval of 1.5 s, and a total duration of 30 s, which is a realistic periodicity based on data from duetting interactions and playbacks with natural calls (Penna et al. 2005b; M. Penna, unpublished data). We recorded 150-s noises and synthetic calls on separate channels on successive
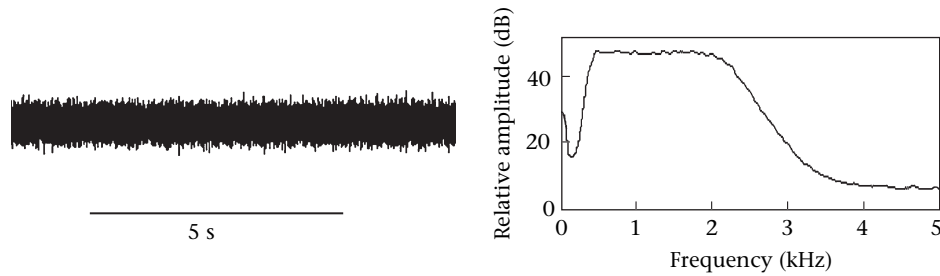
Figure 1. Oscillogram and power spectrum of the band-pass noise to which males of *E. emiliopugini* were exposed.

tracks of an audio compact disc (CD). The first track lasted 60 s and contained a bout of 20 synthetic calls on the left channel (30 s), followed by 30 s of silence on both channels. The following tracks lasted 270 s and started with 150 s of noise on the right channel. On the left channel, a 30-s bout of 20 calls started 60 s after the noise onset. The 150 s of noise was followed by 120 s of silence on both channels. Five such tracks containing the different noises were presented in the following order: wind, rain, creek, sea surf and band-pass noise (see Fig. 4). After the track containing the band-pass noise, we repeated the initial track containing a bout of 20 synthetic calls to control for changes in vocal activity during the experiment. We did not randomize the order of presentation of the different noises because of the lack of effect of the sequence of noise presentations on the EVRs reported for *E. calcaratus* (Penna et al. 2005a). Furthermore, the EVRs to the presentation of the band-pass noise at the same intensity (67 dB) during the first and second experimental sequences should provide an indication of the repeatability of the effect of this noise under different schedules (see Results).

After completing the first experimental sequence, we presented a series of band-pass noises at different intensities. The track used for this experiment was similar to the noise tracks described above, except that the total duration of the track was 210 s and the silent period at the end of the track lasted 60 s instead of 120 s. A shorter interval of silence between noise presentations was chosen to reduce the total duration of the experiment. Seven such tracks containing band-pass noise were presented in the order of increasing intensity at 49, 55, 61, 67, 73, 79 and 85 dB RMS SPL (fast weighting scale, linear frequency weighting), measured at the position of the experimental subject (see Fig. 5).

The total time of stimulation for the series of different noises, from the onset of the bout of synthetic calls presented in the absence of broadcast noise until the end of the presentation of this same stimulus after the exposure to the five different noises, was 24 min. The total time of stimulation for the series of band-pass noise at different intensities, from the onset of the noise at 48 dB RMS SPL that followed the second bout of synthetic calls in the absence of noise until the end of the final bout of synthetic calls presented in the absence of broadcast noise, was 25 min.

Instrumentation and Experimental Settings

We used the same instrumentation to broadcast the synthetic calls and noises as that used by Penna et al. (2005a), except that we used a Sennheiser ME 66 instead
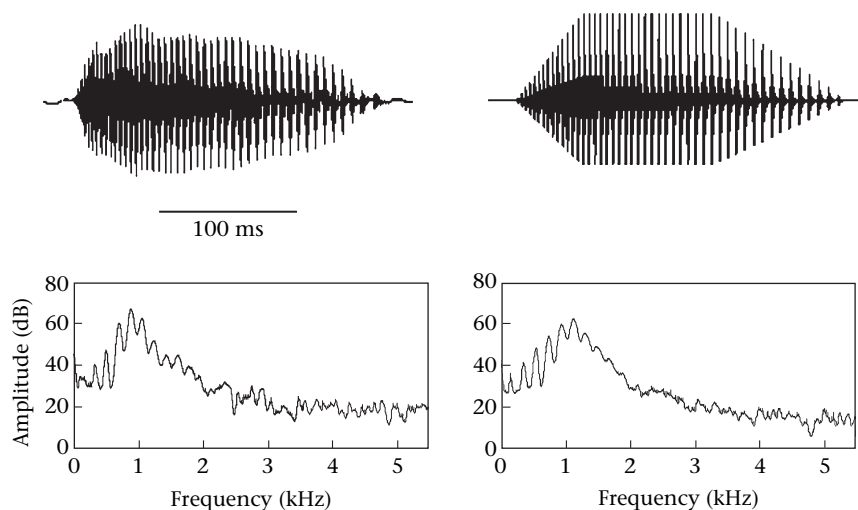
Figure 2. Oscillograms and power spectra of a natural advertisement call of *E. emiliopugini* (left) and a synthetic imitation of this signal used as stimulus (right). Power spectra are taken at the midpoints of both sounds. Recording temperatures of the natural call: air 5.8°C, substrate 8.3°C. Power spectra analysis bandwidth: 20 Hz.

of an AKG CK9 microphone to record the EVRs. Playback experiments were conducted nightly between 2100 and 0400 hours. The basal vocal activity of the subjects was recorded for at least 3 min before playbacks began. Subsequently, the CD containing the stimulus and noises was played back and the animal's EVR recorded. During playbacks, special care was taken to suppress vocal activity of neighbouring frogs by gently tapping the substrate near their burrows, so that the EVR of the focal frog could be recorded with minimum interference. After completing the playback experiment, we recorded the basal vocal activity of the subjects for at least 1 min.

We presented bouts of synthetic calls at intensities of 70 dB RMS SPL and bouts of different noises at 67 dB RMS SPL (fast weighting scale) at the position of the subject. We chose the 70 dB RMS SPL intensity for the synthetic call stimulus because this value is within the range of intensities of nearest neighbours at the position of burrow openings in chorusing aggregations of this species (average: 80.3 dB peak SPL, Penna & Solís 1998). This value corresponds to about 70 dB RMS SPL (M. Penna & R. Solís, unpublished data). We chose a noise intensity of 67 dB RMS SPL because background abiotic noise at the study site on nights with calm weather was typically below 50 dB RMS SPL, assuring that the broadcast noise was well above background level. Also, the 3-dB signal-to-noise ratio was appropriate to evoke consistent vocal responses to the synthetic call in a related species (Penna et al. 2005a). Before starting the experiment, we measured the SPL of the synthetic call and the SPLs of the noises by placing the microphone of the sound level meter as close as possible to the burrow opening and pointing towards the loudspeaker, without disturbing the frog. These initial exposures were as brief as possible, lasting only a few seconds, to minimize effects on the subsequent vocal activity of the experimental subjects. The basal vocal activity of the subjects after these initial measurements was apparently unaltered (see Results). We maintained a constant level of intensity during playback of the synthetic call and noises by adjusting the attenuator's settings for each subject. The exposures to band-pass noise at intensities of 49–85 dB RMS SPL included the lowest threshold for eliciting EVRs to natural calls (60 dB peak SPL, corresponding to about 50 dB RMS SPL; Penna et al. 2005b) and the highest SPLs measured for nearest neighbours (90 dB peak SPL, corresponding to about 80 dB RMS SPL; Penna & Solís 1998). The environmental noise and the intensity of the calls of nearest neighbours of the experimental subjects were also measured from this position at the end of the experiment.

Because the opening of the burrows occupied by the subjects was typically hidden among mosses, grasses and ferns, its position was determined by monitoring the intensities of the calls given by the subject, then scanning the area with the microphone of the sound level meter on the substrate surface. The entrance of the burrow was considered to have been located at the position where the call intensity was 95–100 dB peak SPL. The intensity of the calls of the frogs measured at disclosed burrow openings with the sound level meter microphone pointing towards the bottom of the cavities is about 110 dB peak SPL (Penna & Solís 1996, unpublished data).

Analysis of Evoked Vocal Responses

Recordings of frogs' vocalizations and stimuli were digitized as in Penna et al. (2005a) with a Macintosh computer (G4 Power PC) with Peak 2.52 software at 44 kHz-sampling rate, using an antialiasing filter (FT6-2, Tucker-Davis Technologies) and an analogue–digital interface (Motu 828). Two parameters used to assess the EVR of a frog (call rate and duration) were measured with Signalyze 3.12 software (Infosignal, Inc., Charlestown, Massachusetts, U.S.A.) throughout the experimental sequence. The third parameter (call amplitude) was measured with Canary 1.2.4 software (Cornell Bioacoustics Workstation, Ithaca, New York, U.S.A.). We also measured the dominant frequency during the recording of basal activity before exposure to noise from power spectra with Signalyze software (0–5500 Hz, frequency resolution: 20 Hz). Dominant frequency during exposure to noises was not analysed, because of the masking of the signal during the presentation of these interfering sounds.

EVRs recorded during the presentation of noise at high intensity levels were embedded in the broadcast noise, so we corrected the amplitude values of the vocalizations as follows. In a semianechoic room in the laboratory, the instrumentation used to record the EVRs was set up in a disposition similar to the one used in the field. The directional microphone (Sennheiser ME 66), connected to a digital tape recorder (Sony TC D10 Pro II), was positioned pointing to a loudspeaker (JBL T50, 10-cm diameter) through which a natural call of a male of *E. emiliopugini* was broadcast repetitively at a rate of 0.5 calls/s. The loudspeaker (Dynaudio BM6) used to broadcast the noise and the synthetic calls in the field was positioned at 1.2 m from the JBL loudspeaker and behind the directional microphone, with the two loudspeakers facing each other. The distance between the tip of the directional microphone and the loudspeaker broadcasting the natural call was 20 cm and the level of the natural call at this position, measured with the sound level meter (Brüel & Kjaer 2230), was 83 dB RMS SPL. The band-pass noise used in the field experiments (0.4–2.4 kHz) was delivered through the Dynaudio BM6 loudspeaker at six attenuations, in 6-dB steps. This setting was intended to reproduce the experimental situation, recording via the directional microphone and the digital tape recorder a call of constant amplitude with the different noise levels used in the field. At the lowest attenuation used, the intensity of the noise at the tip of the directional microphone was 85 dB RMS SPL, and decreased correspondingly with increasing 6-dB attenuation steps. At the lower attenuation levels (noise levels of 85, 79, 73 and 67 dB RMS SPL), the amplitude of the call embedded in noise, as measured in the recorded sounds, increased by 4.6, 1.6, 0.5 and 0.3 dB, respectively (i.e. 87.6, 84.6, 83.5 and 83.3 dB RMS SPL, respectively), and the amplitude ratio between the signal plus noise and the broadcast noise measured in the recordings was 2.7, 5.3, 10.1 and 15.7 dB, respectively.

These measured values were used to generate a best-fit curve: $Y = 5.9129 \times e^{-0.2097x}$, in which Y (dB) is the increment in the call amplitude produced by the noise (i.e. the value to be subtracted from the amplitude values of the evoked calls measured) and X (dB) is the ratio between

the amplitude of the evoked call embedded in noise and the amplitude of the broadcast noise. This correction was applied to the field recordings for which this ratio was below 10 dB. This occurred for presentations of band-pass noise at 79 and 85 dB RMS SPL in most of the experimental subjects.

To analyse the effect of the exposure to different kinds of noise presented at the same level, we performed Friedman nonparametric ANOVAs and multiple comparisons between treatments (Siegel & Castellan 1988) for the three EVR measures, considering five time intervals as treatments: the no-playback interval preceding the noise presentation (120 s), the noise exposure before synthetic call onset (60 s), the noise exposure during the presentation of the bout of synthetic call (30 s), the noise exposure after the presentation of the synthetic call (60 s) and the no-playback interval after noise exposure (120 s). To analyse the effects of the exposure to band-pass noise of different intensities, we made the same comparisons, except that the silent intervals were 60 s instead of 120 s. We refer to these five time intervals as S1 ('silence 1'), N1 ('noise 1'), C ('call'), N2 ('noise 2') and S2 ('silence 2'). A no-playback interval between two noise exposures was considered as S2 for the preceding exposure and as S1 for the subsequent exposure (Fig. 3).

To evaluate the effect of prolonged noise exposure on EVRs during the entire experimental sequence, we used Wilcoxon matched-pairs signed-ranks tests (Siegel & Castellan 1988) to compare subjects' EVRs to synthetic calls before and after the series of five exposures to noises of different structure. We also compared subjects' EVRs to synthetic calls after exposure to the five noise series and after exposure to band-pass noise at different levels.

To compare graphically the EVRs of different individuals to a series of stimuli, we normalized the call rate, duration and amplitude to the maximum response for each individual. Namely, we divided a given subject's EVR at a particular time interval by the maximum EVR value produced by that frog across all intervals, and multiplied by 100.

RESULTS

Environmental Conditions and Basal Vocal Activity

The background noise at the position of the 15 experimental subjects, measured after the noise exposures and when these individuals and their neighbours were silent, averaged 41.0 dB RMS SPL (range 33−57 dB RMS SPL). The intensity of the nearest neighbours' calls at the position of the experimental subjects was on average 63.6 dB RMS SPL (range 47−85 dB RMS SPL). The air and substrate temperatures during the recordings were on average 7.0°C (range 4.0−10.6°C) and 8.2°C (range 6.7−10.5°C), respectively.

Before presentation of the initial bout of stimuli, the 15 subjects produced an average of 6.0 calls/min (range 1.5−34.7 calls/min), with an average call duration of 279 ms (range 218−446 ms) and dominant frequency of 1050 Hz (range 778−1395 Hz), during the recording period (average = 250 s, range 48−420 s). When presented with the initial bout of stimuli in the absence of broadcast noise, subjects significantly increased calling rate (25.9 calls/min, range 9.9−40.0 calls/min; Wilcoxon matched-pairs signed-ranks test: $T = 0$, $P = 0.0007$) and call duration (304 ms, range 254−565 ms; $T = 19$, $P = 0.0199$) relative to prestimulus values.

To evaluate the dependence of the EVR measures (call rate, call duration and amplitude) on environmental factors (air temperature, substrate temperature, relative humidity, background noise level and level of the nearest neighbours' calls at the position of the experimental subjects), we performed multiple regressions between these determinants and the EVR measures, and none of them was statistically significant (call rate: $F_{2,4} = 0.8645$, $P = 0.5615$; call duration: $F_{2,4} = 0.1340$, $P = 0.9771$; call amplitude: $F_{2,4} = 0.7505$, $P = 0.6198$).

EVRs during Exposure to Noises of Different Structure

Most of the frogs called persistently during the series of exposures to different noises at a constant level. One frog ceased responding during exposure to creek noise but resumed calling during the rest of the experiment. Another frog ceased responding during exposure to the band-pass noise and remained silent thereafter. Subjects' EVRs to bouts of synthetic calls did not differ before and after exposure to noises of different structure (Wilcoxon matched-pairs signed-ranks test: call rate: $T = 59$, $P = 0.9547$; call duration: $T = 43$, $P = 0.3343$; call amplitude: $T = 41$, $P = 0.2805$).

Calling rates in response to bouts of synthetic calls were higher in the presence of noise delivered at a constant level than in the absence of generated noise. Calling rate
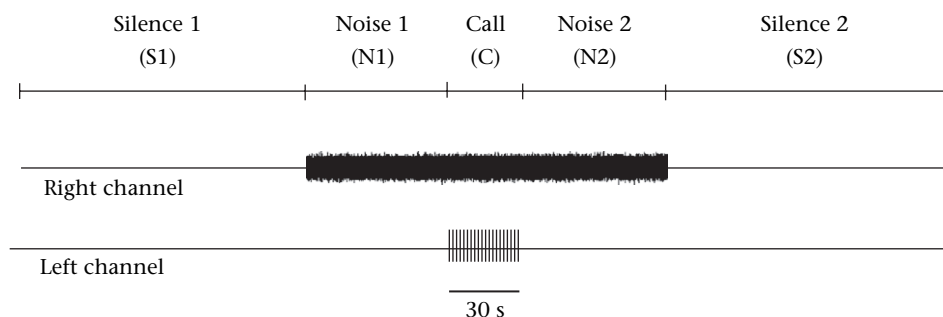
Figure 3. Schematic diagram of the time intervals for which measures of evoked vocal responses (EVRs) were compared during exposure to different kinds of noise. For exposures to band-pass noise of different intensities, the intervals of silence lasted 60 s instead of 120 s (see text).

differed significantly between time intervals (S1, N1, C, N2 and S2) during exposure to wind (Friedman ANOVA: $\chi^2_4 = 27.9$, $P < 0.0001$), rain ($\chi^2_4 = 40.7$, $P < 0.0001$), creek ($\chi^2_4 = 15.8$, $P = 0.0033$), sea surf ($\chi^2_4 = 34.3$, $P < 0.0001$) and band-pass noise ($\chi^2_4 = 21.8$, $P = 0.0002$). The multiple comparison tests showed that the call rate during interval C was higher than that during intervals S1, N1 and N2 for the five types of noise. The call rate during C was also higher than that during S2 for rain, sea surf and band-pass noises. Call rate was higher during N1 than during N2 for rain noise. Call rate did not differ between interval S1 and intervals N1, N2 and S2 or between intervals N2 and S2 for the five types of noise (Fig. 4a, Table 1).

Although differences in call duration paralleled those of call rate, they were generally smaller than those obtained for call rate. Call duration differed between time intervals (S1, N1, C, N2 and S2) for exposures to wind ($\chi^2_4 = 15.3$, $P = 0.0042$), rain ($\chi^2_4 = 26.6$, $P < 0.0001$), creek ($\chi^2_4 = 30.5$, $P < 0.0001$), sea surf ($\chi^2_4 = 26.8$, $P < 0.0001$) and band-pass noise ($\chi^2_4 = 16.9$, $P = 0.0021$). Call duration was longer during C than during S1 and S2 for the five types of noise, and longer during C than during N2 for rain, sea surf and band-pass noises. Call duration did not differ between interval S1 and intervals N1, N2 and S2, between interval N1 and intervals C, N2 and S2, or between intervals N2 and S2 for any type of noise (Fig. 4b, Table 1).

In contrast to the results for call rate and duration, call amplitude showed no systematic changes as a result of noise exposure. However, there was an overall tendency for call amplitude to decrease during the series of exposures to noises of different structure. Call amplitude was significantly higher during N2 than during S1 and S2 for creek noise ($\chi^2_4 = 15.0$, $P = 0.0046$), but did not differ significantly between other time intervals (Fig. 4c, Table 1).

To compare subjects' EVRs to noise of different structure during corresponding intervals of exposure, we made comparisons between intervals N1 and C using Friedman ANOVAs. These intervals were chosen for comparisons because interval N1 corresponded to the first exposure to a given noise in the absence of synthetic calls and interval C was the one that elicited the highest level of vocal activity, thus facilitating comparisons between exposures. Across N1 intervals, there was no difference in call rate ($\chi^2_4 = 7.0$, $P = 0.1349$), call duration ($\chi^2_4 = 5.0$, $P = 0.2919$) or call amplitude ($\chi^2_4 = 4.7$, $P = 0.3211$). However, comparisons between C intervals yielded significant differences for call rate ($\chi^2_4 = 19.6$, $P = 0.0006$) and call amplitude ($\chi^2_4 = 11.6$, $P = 0.0203$), but no difference for call duration ($\chi^2_4 = 7.0$, $P = 0.1331$). Multiple comparison tests showed that call rate was higher during exposure to wind noise than during exposure to creek noise, and higher during exposure to sea-surf noise than during exposures to rain and creek noise. Call amplitude was higher during exposure to creek noise than during exposure to wind noise (Table 2).

EVRs during Exposure to Band-pass Noise at Different Intensities

Fourteen frogs were exposed to this experimental series. For one individual, the experiment was interrupted at the
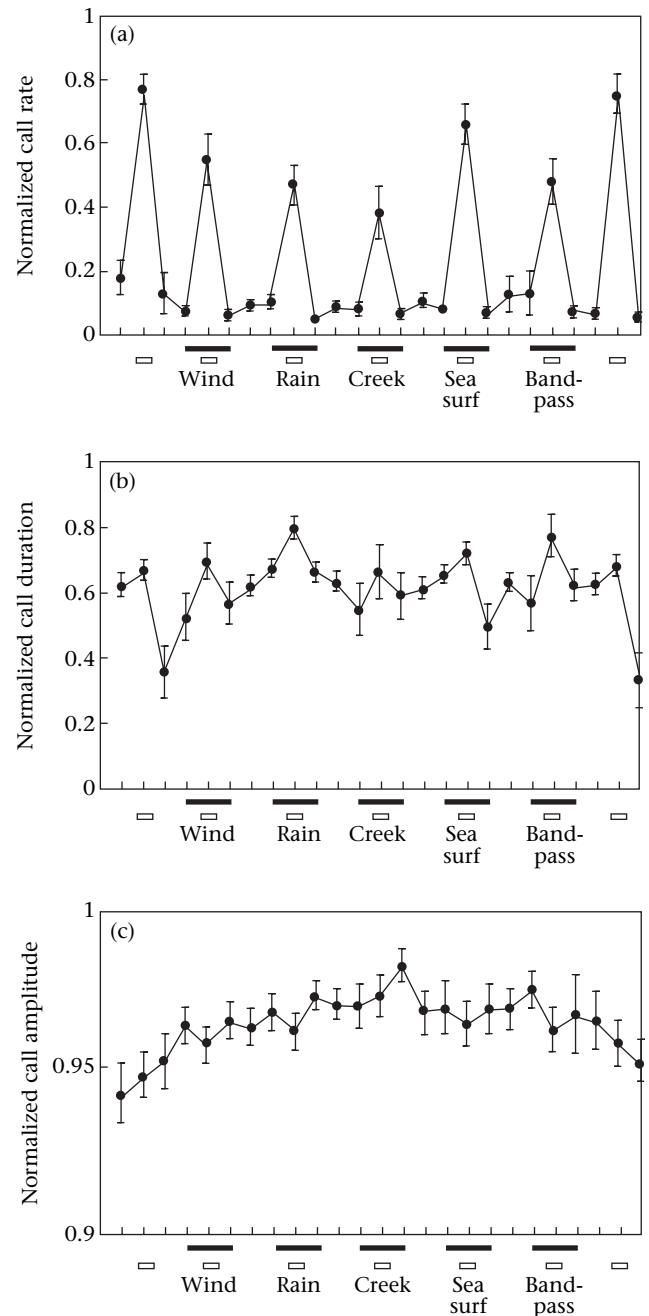
Figure 4. Normalized measures of evoked call response (call rate (a), call duration (b) and call amplitude (c)) of 15 male *E. emiliopugini* during the experimental sequence of exposure to noises of different structure. Horizontal open bars at the beginning and at the end of the sequence indicate 30-s intervals during which a bout of 20 synthetic calls was presented with an intercall period of 1.5 s. Filled bars indicate 270-s intervals during which noises of different structure were presented and open bars below indicate bouts of 20 synthetic calls during the middle 30 s (see Methods). Intervals between bars indicate 2-min intervals during which no prerecorded noise or stimulus was delivered to the experimental subjects. Intervals after the presentation of the initial and final stimulus bout lasted 30 s, and the interval before the initial stimulus bout had an average duration of 250 s, depending on the subject (see Methods). Filled circles and vertical bars represent averages and standard errors, respectively. The sound levels of the synthetic call and noises measured at the position of the subjects were 70 and 67 dB RMS SPL, respectively.

Table 1. Results of Friedman ANOVA and multiple comparisons for evoked vocal response, EVR, measures (call rate, duration and amplitude) between time intervals during exposures to noises of different structure

EVR measure	Noise	χ^2	P	S1/N1	S1/C	S1/N2	S1/S2	N1/C	N1/N2	N1/S2	C/N2	C/S2	N2/S2
Call rate	Wind	27.9	<0.0001		*			*			*		
	Rain	40.7	<0.0001		*			*	*		*	*	
	Creek	15.8	0.0033		*			*			*		
	Sea surf	34.3	<0.0001		*			*			*	*	
	Band-pass	21.8	0.0002		*			*			*	*	
Call duration	Wind	15.3	0.0042		*							*	
	Rain	26.6	<0.0001		*						*	*	
	Creek	30.5	<0.0001		*							*	
	Sea surf	26.8	<0.0001		*						*	*	
	Band-pass	16.9	0.0021		*						*	*	
Call amplitude	Wind	7.7											
	Rain	6.9											
	Creek	15.0	0.0046			*							*
	Sea surf	8.2											
	Band-pass	7.7											

S1: no-playback interval preceding the noise exposure; S2: no-playback interval after the noise exposure; N1: noise exposure preceding synthetic call onset; N2: noise exposure after the presentation of the bout of synthetic calls; C: noise exposure during the presentation of the bout of synthetic calls. Nonsignificant P values (>0.05) for the Friedman ANOVA are omitted. Asterisks indicate significant differences (P < 0.05) for multiple comparisons.

end of the exposure to noise at 67 dB SPL because of technical problems. Call rate was significantly higher in response to synthetic calls before exposure to band-pass noise than it was after exposure to band-pass noise of different intensity (Wilcoxon matched-pairs signed-ranks test: $T = 15$, $P = 0.0331$). However, there was no difference in call duration ($T = 43$, $P = 0.8613$) or call amplitude ($T = 25$, $P = 0.1520$) in response to synthetic calls before and after exposure to band-pass noise of different intensity.

Call rate also differed significantly between the five time intervals during exposures to band-pass noise at 49 dB SPL ($\chi^2_4 = 35.2$, $P < 0.0001$), 55 dB SPL ($\chi^2_4 = 25.3$, $P < 0.0001$), 61 dB SPL ($\chi^2_4 = 20.3$, $P = 0.0045$), 67 dB SPL ($\chi^2_4 = 25.6$, $P < 0.0001$), 73 dB SPL ($\chi^2_4 = 22.0$, $P = 0.0002$), 79 dB SPL ($\chi^2_4 = 32.4$, $P < 0.0001$) and 85 dB SPL ($\chi^2_4 = 20.3$, $P = 0.0004$).

Call rate was significantly higher during C than during N2 for all levels of exposure and higher during C than during S1 and S2 for levels of exposure between 49 and 79 dB RMS SPL. Call rate was also higher during C than during N1 for exposures between 49 and 73 dB RMS SPL, and

higher during N1 and N2 than during S2 for the 85 dB RMS SPL exposure. There were no significant differences in call rate between interval S1 and intervals N1 and N2, between intervals N1 and N2, or between intervals S1 and S2 for any of the noise exposure levels (Fig. 5a, Table 3).

Call duration of EVRs to band-pass stimuli at different levels showed trends resembling those of call rate, but the significance of the differences was lower. Significant differences in this parameter occurred only for band-pass noise at 67 dB SPL ($\chi^2_4 = 25.2$, $P < 0.0001$) and 73 dB SPL ($\chi^2_4 = 19.9$, $P = 0.0005$). Call duration was significantly longer during C than during S1 and S2 for noise exposures at 67 and 73 dB SPL. Call duration was also significantly longer during C than during N2 for noise exposure at 67 dB SPL. There were no significant differences in call duration between interval S1 and intervals N1, N2 and S2, between interval N1 and intervals C, N2 and S2, or between intervals N2 and S2 for any of the noise levels (Fig. 5b, Table 3).

Although there was no systematic change in call amplitude of EVRs during exposure to different levels of band-pass noise, there was an overall increase in call amplitude during this experimental series. Significant differences in

Table 2. Results of Friedman ANOVA and multiple comparisons for evoked vocal response, EVR, measures (call rate, duration and amplitude) among intervals N1 and C during exposures to noises of different structure

EVR measure	Interval	χ^2	P	W/R	W/C	W/S	W/B	R/C	R/S	R/B	C/S	C/B	S/B
Call rate	N1	7.0											
	C	19.6	0.0006		*				*		*		
Call duration	N1	5.0											
	C	7.0											
Call amplitude	N1	4.7											
	C	11.6	0.0203		*								

W: wind; R: rain; C: creek; S: sea surf; B: band-pass. Nonsignificant P values (>0.05) are omitted. Asterisks indicate significant differences (P < 0.05) for multiple comparisons.
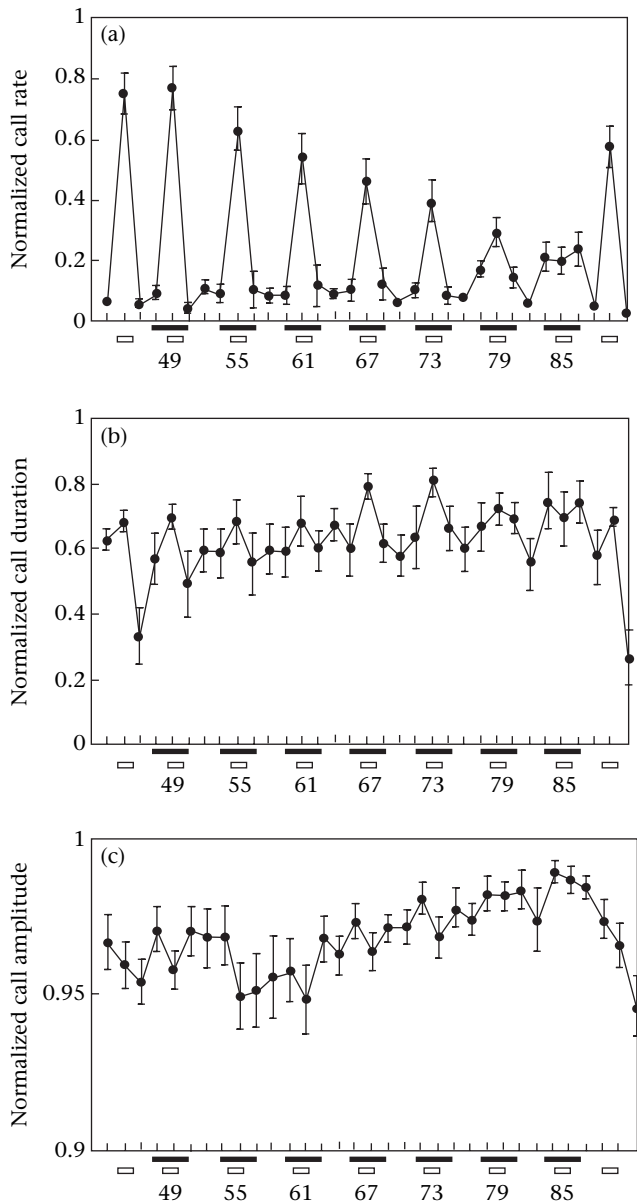
Figure 5. Normalized measures of evoked call response (call rate (a), call duration (b) and call amplitude (c)) of 14 male *E. emiliopugini* during the experimental sequence of exposure to band-pass noise delivered at different RMS SPLs measured at the position of the subjects, as indicated on the horizontal axis. Horizontal open bars at the beginning and at the end of the sequence indicate 30-s intervals during which a bout of 20 synthetic calls was presented with an inter-stimulus period of 1.5 s. Filled bars indicate 270-s intervals during which noises of different structure were presented and open bars below indicate bouts of 20 synthetic calls during the middle 30 s (see Methods). The levels of the synthetic call measured at the position of the subjects was 70 dB RMS SPL. Intervals between bars indicate 1-min intervals during which no noise or stimulus was delivered to the experimental subjects. Intervals after the final bout of stimuli had an average duration of 210 s, depending on the subject (see Methods). The initial bout of stimuli of this sequence is the same as the last stimuli of the sequence of presentations of noises of different structure (Fig. 4). Filled circles and vertical bars represent averages and standard errors, respectively.

call amplitude occurred only for band-pass noise at 55 dB SPL ($\chi_4^2 = 11.7$, $P = 0.0206$), 73 dB SPL ($\chi_4^2 = 13.7$, $P = 0.0084$) and 79 dB SPL ($\chi_4^2 = 12.3$, $P = 0.0151$). Call amplitude was significantly larger during N1 than it was either during S1 for exposure at 79 dB SPL, during C for the 55 dB SPL exposure, or during S2 for the 79 dB SPL exposure (Fig. 5c, Table 3).

Subjects' EVRs to band-pass noise at different intensities differed significantly between N1 intervals for call rate (Friedman ANOVA: $\chi_6^2 = 18.9$, $P = 0.0043$) but not for call duration ($\chi_6^2 = 5.0$, $P = 0.1177$) or call amplitude ($\chi_6^2 = 10.2$, $P = 0.1153$). Multiple comparisons showed that call rate during N1 was higher during exposure to 79 dB SPL noise than it was during exposures to 61 and 67 dB SPL noise. In addition, call rate during N1 was higher during exposure to 85 dB SPL noise than it was during exposure to noise at 49, 61 and 67 dB SPL (Table 4).

Call rate during the C intervals showed a tendency to decrease with the intensity of noise exposures. Comparisons between the C intervals during noise exposures at different intensities yielded significant differences for call rate ($\chi_6^2 = 37.5$, $P < 0.0001$), call duration ($\chi_6^2 = 16.5$, $P = 0.0112$) and call amplitude ($\chi_6^2 = 25.2$, $P = 0.0003$). Multiple comparison tests showed that call rate was higher during the 49 dB SPL exposure than during the 73, 79 and 85 dB SPL exposures, higher during the 55, 61 and 67 dB SPL exposures than during the 79 and 85 dB SPL exposures, and higher during the 73 dB SPL exposure than during the 85 dB SPL exposure (Table 4).

In contrast, call duration showed no tendency to decrease with increasing intensity of noise exposure; the longest durations corresponded to intermediate noise levels. Multiple comparisons showed that call duration was longer during the 67, 73 and 85 dB SPL exposures than during the 49 dB SPL exposure and longer during the 67 and 73 dB SPL exposures than during the 55 dB SPL exposure.

Call amplitude was not clearly related to noise level; however, the highest amplitudes occurred during the 79 and 85 dB SPL exposures. Multiple comparisons showed that call amplitude was higher during the 79 and 85 dB SPL exposures than during the 49 dB SPL exposure and higher during the 73, 79 and 85 dB SPL exposures than during the 55 and 61 dB SPL exposures. Variation in call amplitude during exposures to band-pass noise at different intensities was also analysed with a Spearman correlation between the amplitude of the calls produced during the N2 interval of each exposure and during the following silent period. The correlation was highly significant ($r_S = 0.97$, $P = 0.001$), indicating that the changes in amplitude during noise exposure persisted after the cessation of this interference. The higher amplitudes measured during the intervals between noise broadcasts at the higher levels also indicated that the corrections used to measure call amplitudes during the noise exposures were appropriate (see Fig. 5).

DISCUSSION

Results of this study show that different types of noise presented at a moderate level (67 dB RMS SPL) do not have

Table 3. Results of Friedman ANOVA and multiple comparisons for evoked vocal response, EVR, measures (call rate, duration and amplitude) between time intervals during exposures to band-pass noise at different levels

EVR measure	Noise level (dB SPL)	χ^2	P	S1/N1	S1/C	S1/N2	S1/S2	N1/C	N1/N2	N1/S2	C/N2	C/S2	N2/S2
Call rate	49	35.2	<0.0001		*			*			*	*	
	55	25.3	<0.0001		*			*			*	*	
	61	20.3	0.0045		*			*			*	*	
	67	25.6	<0.0001		*			*			*	*	
	73	22.0	0.0002		*			*			*	*	
	79	32.4	<0.0001		*						*	*	
	85	20.3	0.0004							*	*		*
Call duration	49	2.9											
	55	8.4											
	61	7.7											
	67	25.2	<0.0001		*						*	*	
	73	19.9	0.0005		*							*	
	79	9.3											
	85	8.4											
Call amplitude	49	6.9											
	55	11.7	0.0206					*					
	61	5.9											
	67	6.3											
	73	13.7	0.0084										
	79	12.3	0.0151	*						*			
	85	6.0											

Abbreviations as in Table 1. Nonsignificant P values (>0.05) for the Friedman ANOVA are omitted. Asterisks indicate significant differences (P < 0.05) for multiple comparisons.

excitatory effects on the vocal activity of *E. emiliopugini*. No changes in the EVR measures were observed during the intervals when noise alone was presented in the absence of synthetic calls (intervals N1 and N2). Changes in subjects' EVRs occurred only during the presentation of bouts of synthetic calls, regardless of whether these calls were accompanied by generated noise. However, although there was no effect of the noise per se on the subjects' EVRs, the frogs' responses to synthetic calls (interval C) differed depending on the type of background noise: call rate was higher during exposure to wind and sea surf noise than during exposure to rain and creek noise.

During exposure to noises of different structure, call rate was the EVR measure that showed the largest variation, call duration having more restricted ranges. In contrast, the amplitude of the evoked calls did not show changes related to the presentation of the synthetic stimulus or to particular noises.

The level of the natural noises used in the experiments (67 dB RMS SPL) was within the range of wind, rain and creek noise levels recorded during stormy nights at the study site (Penna et al. 2005a). The sea surf noise does not occur in the mountainous area where the study was conducted, but as mentioned in Methods, coastal populations of this species are exposed to this interference. The average background noise from abiotic sources is usually lower, and during the experiments, it was on average about 41 dB RMS SPL. The noise produced by the conspecific choruses is the predominant noise to which males of *E. emiliopugini* are exposed in the breeding areas. The level of the neighbours' calls at the position of calling males is highly variable in this species (Penna & Solís 1998), and for the experimental subjects in this study, averaged

65 dB RMS SPL. However, the EVRs of the subjects during the experiments were not related either to the levels of abiotic noise or to the neighbours' call levels. Subjects' responses to the band-pass noise, which was intended to emulate the noise of conspecific choruses, were similar to their responses to abiotic noises, in that their vocal activity was not affected by the noise itself.

These results contrast with those of Penna et al. (2005a), who used the same noises and a similar experimental protocol to examine EVRs in a related species, *E. calcaratus*, at the same study site. In that study, rain, creek and especially band-pass noises, presented at about the same level used in the present study, had a marked excitatory effect on EVRs of *E. calcaratus*, as indicated by increases in call rate and duration.

Vocal activity of *E. calcaratus* is not affected by the presentation order of different noises (Penna et al. 2005a), so differences between our results and those of Penna et al. (2005a) are unlikely to be due to differences in order of presentation of the noises of different structure.

In the present study, subjects' levels of response during exposure to band-pass noise of different intensities were similar to their levels of response during exposure to noise of different structure: call rate increased during presentation of synthetic calls (interval C) and band-pass noises of 49−79 dB RMS SPL. However, the increase in call duration during interval C was moderate and significant only for the exposures at 67 and 73 dB SPL. Call rate decreased during interval C with subsequent exposure to noise of higher intensity. In contrast to the decrease in the call rate during interval C, call amplitude showed a tendency to increase with the intensity of the band-pass noise. This association between the decrease in call rate and the increase in call

Table 4. Results of Friedman ANOVA and multiple comparisons for evoked vocal response, EVR, measures (call rate, duration and amplitude) among intervals N1 and C during exposures to band-pass noise at different levels

EVR measure		χ^2	P	Band-pass noise exposure (RMS SPLs)																			
				49/55	49/61	49/67	49/73	49/79	49/85	55/61	55/67	55/73	55/79	55/85	61/67	61/73	61/79	61/85	67/73	67/79	67/85	73/79	73/85	79/85
Call rate	N1	18.9	0.0043					*	*				*			*	*	*		*	*			
	C	37.5	<0.0001			*	*	*	*			*		*		*	*	*		*	*		*	
Call duration	N1	5.0				*	*	*	*		*													
	C	16.5	0.0112																					
Call amplitude	N1	10.2																						
	C	25.2	0.0003				*	*				*	*			*	*	*						

Nonsignificant *P* values (>0.05) for the Friedman ANOVA are omitted. Asterisks indicate significant differences (*P* < 0.05) for multiple comparisons. RMS SPL: root-mean-square sound pressure level.

amplitude with increasing noise levels could indicate that the noise partially masked the broadcast calls. Alternatively, given the high energetic cost of vocal effort in anurans (e.g. Wells 2001), subjects may have compensated for the higher effort needed to produce louder calls by decreasing their calling rate.

Male *E. emiliopugini* respond consistently to prerecorded natural calls presented at increasing intensity levels by gradually increasing call rate and duration and by producing multiple-note calls (Penna et al. 2005b). However, the amplitude of the evoked calls does not change with the intensity of the stimuli (M. Penna & R. Solís, unpublished data), as reported for other frogs (López et al. 1988). In *E. emiliopugini*, the gradual increases in call rate and call duration are transient effects that recede with the cessation of the stimulus and thus could reflect the caller's motivation to confront a challenger.

In contrast, in the present study, the increase in call amplitude to band-pass noise of different intensity persisted between intervals of exposures to noise. This persistent increase may facilitate communication during prolonged noises, such as background chorusing or stormy weather, potentially generating larger interference for competitors and improving the signals' attractiveness for receptive females.

The decrease in the call rate evoked by synthetic calls in the presence of increasing noise levels could be attributed to an effect of the order of the noise exposures, since the same schedule was used for all subjects. Moreover, the calling rate in response to unmasked calls was lower after exposure to band-pass noise of different intensity than it was before exposure to such noise, indicating an effect of fatigue or habituation during the prolonged stimulation, and thus, a potential flaw of the experimental design. However, this decrease in the responsiveness of male *E. emiliopugini* contrasts with the results of Penna et al. (2005a) for male *E. calcaratus*, in which the call rate was unaltered within a broad range of band-pass noise intensities (48−72 dB RMS SPL). These dissimilar results suggest that the two species use different strategies to confront noise.

Reanalysis of Penna et al.'s (2005a) data showed that *E. calcaratus* also increases call amplitude in response to synthetic calls that are presented simultaneously with band-pass noise of increasing intensity (Friedman ANOVA: $\chi^2_4 = 13.0$, $P = 0.0112$). In that study, call amplitude did not differ significantly between intervals of a given noise exposure, but it did show a sustained increase across the entire experimental series at higher levels of band-pass noise, similar to the present study. This phenomenon corresponds to the Lombard effect, which is a common strategy used by frogs of southern Chile and other vertebrates to confront noise (Sinnot et al. 1975; Cynx et al. 1998; Brumm & Todt 2002; Pytte et al. 2003; Brumm 2004; Brumm et al. 2004).

In the present study, it is unlikely that the increase in call amplitude observed during the experimental series of band-pass noise at different intensities was produced by an approach of the frog towards the sound source. The burrows from which males of *E. emiliopugini* call have a standing wave environment (Penna & Solís 1996, 1999) in which changes of position inside the enclosure

would not alter the SPL of the sound broadcast outside the burrow opening. In addition, three experimental subjects that could be observed inside their burrows during the experiments did not change their position during the entire playback sequence.

Differences in the EVRs produced by *E. emiliopugini* and *E. calcaratus* in the presence of noise could be related to differences in the sound environments where these animals breed. *Eupsophus emiliopugini* males call and mate during late spring through early summer (November–January) at the same sites and often inside the same burrows where *E. calcaratus* breeds from mid-winter to mid-spring (July–October). The atmospheric conditions and levels of abiotic noise during the reproductive period are probably milder for *E. emiliopugini* than they are for *E. calcaratus*. Abiotic noise (at the position of the experimental subjects) was significantly lower in our study (*E. emiliopugini* average: 41.0 dB RMS SPL, range 33–57 dB RMS SPL) than in Penna et al.'s (2005a) study (*E. calcaratus* average: 49.5 dB RMS SPL, range 38–62 dB RMS SPL; Mann–Whitney *U* test: $U = 160.5$, $N_1 = 15$, $N_2 = 13$, $P < 0.05$), suggesting that the remarkable increase in vocal activity of *E. calcaratus* in the presence of generated noise is an adaptation for communicating amid relatively high levels of natural abiotic noises.

Differences in the intensities of the calls of both species may also help to explain the differences in the EVRs in the presence of noise. The average intensity of *E. emiliopugini* calls, measured at 50 cm from the caller, is 87 dB peak SPL, whereas that of *E. calcaratus* is 72 dB peak SPL (Penna & Solís 1998, unpublished data). Thus, the excitatory effect of noise on the vocal activity of *E. calcaratus* may be an adaptation to higher interference from abiotic noises during communication mediated by relatively low-amplitude calls.

Interestingly, the background noises that evoke the largest increases in vocal activity of *E. calcaratus* (creek, rain and band-pass) are those showing the greatest spectral overlap with the call of this species (Penna et al. 2005a). In contrast, noises that are associated with a higher vocal activity in *E. emiliopugini* are those showing a lower degree of overlap with the call spectrum (wind and sea surf). The Central American frog *Hyla ebraccata* decreases its vocal activity when exposed to high levels (90 dB SPL) of noise having a spectrum similar to the conspecific calls (Schwartz & Wells 1983a). In comparison with this frog, the decrease in the vocal responses of *E. emiliopugini*, first manifest at moderate levels of band-pass noise, suggests a high susceptibility to interference.

Birds show different susceptibilities to anthropogenic noise, as reflected in population densities. In areas of traffic noise exposure, species that produce songs with relatively low frequencies suffer larger density declines than species that sing at higher frequencies (Rheindt 2003). In anurans, different strategies of acoustic communication have also been reported in the presence of anthropogenic noise. Three frog species in Thailand decrease their vocal output when exposed to aircraft or motorcycle noise, but the sympatric *Rana taipehensis* increases its vocal activity in the presence of these same intrusions (Sun & Narins 2005). Interestingly, the call of *R. taipehensis* has a much lower

intensity than that of the sympatric taxa, as does the call of *E. calcaratus* relative to that of *E. emiliopugini*.

A radical example of different strategies in confronting natural noise has been recently reported for closely related Chinese frogs living in the same noisy stream environments; *Odorrana livida* produces calls containing ultrasonic components and it has an auditory sensitivity shifted to this frequency range, whereas the signals and auditory responses of *O. schmackeri* are restricted to frequencies below about 8 kHz (Yu et al. 2006). The current study contributes unique experimental evidence on differences in vocal responses to interference from noises in natural settings between related anuran species and prompts interest in the origin and adaptive significance of these diverse communication strategies among vertebrates.

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