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Effect of natural and synthetic noise on evoked vocal responses in a frog of the temperate austral forest

MARIO PENNA, HANS POTTSTOCK & NELSON VELASQUEZ

Programa de Fisiología y Biofísica, Facultad de Medicina, Universidad de Chile

Animals using sound communication have developed different strategies to overcome noise interference, but studies have rarely examined animals behaving in their natural environments. Males of the leptodactylid frog *Eupsophus calcaratus* exposed to natural noises of wind, rain, creek and sea surf and to a band-pass noise encompassing the main spectral components of the conspecific advertisement call increased their call rate in the presence of noises of moderate level, and this effect was particularly strong for the band-pass noise. Frogs exposed to band-pass noise of different intensities increased their call rate in response to exposures of 66–78 dB RMS sound pressure level. Call duration followed similar trends, but the effects of noise exposure on this measure of evoked vocal response were not as strong as those on call rate. The vocal responsiveness of males of this species in the presence of noise denotes adaptations to cope with high interference, in spite of the relatively simple acoustic environment of the austral temperate forest.

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Animals that communicate by means of acoustic signals confront the difficulty of conveying information in environments with different noise levels and qualities. Noise sources of biotic origins are especially important in terrestrial environments of tropical latitudes, where a diversity of organisms build up a complex sound environment at different phases of the circadian cycle (Narins & Zelick 1988; Owings & Morton 1998). In temperate latitudes, the diversity of taxa is more restricted and sources of abiotic noise, like wind, rain and running water are likely to have a higher importance (e.g. Klump 1996).

Vertebrates have developed strategies to overcome noise interference, thus facilitating the transmission of acoustic signals to potential receivers. Various vertebrates, including humans, 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). Some anurans and birds dwelling in environments having high levels of stream noise produce vocalizations containing remarkable frequency modulations and/or high frequencies beyond the noise spectral range (Penna et al. 1983; Dubois & Martens 1984; Penna & Veloso 1990; Feng et al. 2000; Hödl & Amézquita 2001). Other birds increase the emission rate and duration of their

vocalizations to communicate in environments with high wind noise levels (Potash 1972; Lengagne et al. 1999).

Acoustic signals are the principal mediators of anuran social behaviour. Male frogs and toads in chorusing aggregations produce advertisement calls that attract females (e.g. Rand 1988). Also, vocal interactions between males serve to defend a territory or calling site that is used to broadcast advertisement calls (e.g. Wells 1988).

Interference from biotic noise has been shown to affect the vocal behaviour of males. During vocal interactions, males compete with opponents by increasing the duration, amplitude, complexity and rate of emission of their calls and by modifying their dominant frequency (López et al. 1988; Wells 1988; Schwartz et al. 2002). Males also typically alter the timing of their calls to avoid overlap with their neighbours (Narins & Zelick 1988; Klump & Gerhardt 1992; Grafe 1996). High-intensity (above 90 dB sound pressure level (SPL)) exposure to playbacks of continuous choruses of sympatric species inhibits calling of males of the Central American treefrog *Hyla ebraccata* (Schwartz & Wells 1983a, b). Similarly, males of the Caribbean treefrog *Eleutherodactylus coqui* cease responding to synthesized calls if they are accompanied by intense broadband noise (Narins 1982). However, that study found that noise of moderate level could increase evoked vocal responses.

The phonotactic responses of female frogs are also affected in different ways by exposure to synthetic noise imitating the background activity of conspecific choruses.

Correspondence: M. Penna, Programa de Fisiología y Biofísica, Facultad de Medicina, Universidad de Chile, Casilla 70005, Santiago, Chile (email: mpenna@med.uchile.cl).

Compared to males, females of *Hyla cinerea* (Ehret & Gerhardt 1980) and *H. ebraccata* (Wollerman 1999) require higher stimulus intensities to respond to synthetic calls in the presence of noise. However, the study with female *H. cinerea* found a result resembling the effect on males reported by Narins (1982): females preferred a loudspeaker broadcasting synthetic calls accompanied with broadband noise at moderate levels to synthetic calls presented alone (Ehret & Gerhardt 1980). In addition, discrimination by females of *Pseudacris crucifer* between synthetic calls of different frequencies is facilitated in the presence of low levels of broadband noise (Schwartz & Gerhardt 1998).

The effect of natural abiotic noises on sound communication in terrestrial environments has received limited attention. Surprisingly, the structure of these ubiquitous noises has not been thoroughly analysed by students of animal sound communication, and only few quantitative descriptions are available in the literature (e.g. Klump 1996). Most studies on the effect of abiotic noise on vocal behaviour have been conducted in the laboratory (e.g. Klump & Langemann 1995; Langemann et al. 1998), and most field studies have used artificial noise (e.g. Cynx et al. 1998; Brumm & Todt 2002). To our knowledge, just one experimental study on effects of natural abiotic noise on vocalization has been conducted in natural settings (Pytte et al. 2003). That study reported that the hummingbird *Lampornis clemenciae* increases its call amplitude in response to increasing levels of creek-noise playback.

Noises from abiotic sources are thought to affect anuran vocal behaviour in different ways. Some anurans associated with creek environments produce calls with certain spectral characteristics, as outlined above, but some species lack advertisement calls altogether, a tendency that may constitute an extreme adaptation to noisy environments (Penna et al. 1983; Penna & Veloso 1990; Hödl & Amézquita 2001). In contrast with a potential inhibitory effect of creek noise on vocal activity, rain has been associated with the stimulation of frog calling (Bogert 1960). To the best of our knowledge, no associations have been proposed to occur between other noises of abiotic origin, like wind and sea surf, and frog vocal activity.

Our study subject, *Eupsophus calcaratus*, is a leptodactylid frog from the temperate forests of southern Chile. In these latitudes, a small number of species call simultaneously at any breeding site and the level of background noise is generally low (Penna & Veloso 1990; Penna & Solís 1998). *Eupsophus calcaratus* breeds in the austral temperate forest from mid-winter to mid-spring (August–October). During most of this period, no other anurans are active in the region. Males of this and related species call from inside burrows excavated among mosses and ferns in bogs. The advertisement call of this frog consists of a single note, approximately 250 ms long, produced at a rate of up to approximately 0.5 calls/s. The spectrum has a harmonic structure: the second and third harmonics are near 1300 and 1900 Hz, respectively, and have the highest amplitudes. The call has a frequency-modulated structure typically having an ascending–descending pattern (Formas 1985; Penna 2004). Occasionally, males of this and related species interacting at short distances in breeding

aggregations give longer vocalizations having a pulsed structure (Penna & Veloso 1990; M. Penna, unpublished data).

This study explores communication strategies used by frogs confronting potential sources of acoustic interference in natural settings. We report two playback experiments in which males of *E. calcaratus* called in response to a synthetic imitation of the conspecific advertisement call presented with different noises. In the first experiment, we tested the responsiveness of frogs to a variety of natural abiotic noises and a synthetic band-pass noise encompassing the frequency range of the main spectral components of the advertisement call, to explore effects on frogs' evoked vocal responses (EVRs). In the second experiment, the susceptibility of the EVRs to noise intensity was evaluated with band-pass noise, to allow comparisons with the effect of this parameter on the vocal behaviour of other vertebrates.

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. The study site was a bog in which males of *E. calcaratus* called from burrows hidden among mosses (*Rhacomytrium*), grasses (*Scyrpus* and *Myrteola*) or ferns (*Blechnum*) along the borders of small streams. Bioacoustical studies with *E. calcaratus* 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 with the microphone of a sound-level meter (Bruel & Kjaer 2230) fitted with a windscreen (UA 0237) and connected with an extension cable (UA 0028). The AC output of the sound-level meter was connected to a digital tape recorder (Sony TC D10 PROII). Wind noise was recorded with the microphone positioned with a stand at ground level, surrounded by bushes to avoid direct impact of the wind. Rain noise was recorded with the microphone placed at ground level, protected from direct impact of raindrops with a 2-m² foam pad positioned 0.5 m above the ground. Creek noise was recorded from streams of different widths with the microphone positioned 0.5 m from the water border. Noise from the sea surf was recorded at Cucao (43°40′S, 74°00′W) in the National Park of Chiloé, with the microphone placed 1 m above the water surface on the tide border. Although frogs at our study site are not exposed to surf noise, we included this noise in the experimental design because populations of *E. calcaratus* in coastal localities such as Cucao confront this natural interference. Several recordings of these noises were obtained as follows (number of recordings and ranges of intensities measured with the fast RMS weighting scale in parenthesis): wind ($N = 13$, 50–70 dB SPL), rain ($N = 6$, 48–72 dB SPL), creeks ($N = 13$, 61–76 dB

SPL), sea surf ($N = 4$, 74–78 dB SPL). The 66-dB RMS SPL chosen for the exposures to different types of noise (see below) was within the range of the natural noises recorded.

Stimuli Preparation

Recordings of the noises were input to a Power PC G4 computer with the Peak 2.52 software (Bias, Inc., Petaluma, California, U.S.A.) at a 44-kHz sampling rate, using an anti-aliasing filter (FT6-2, Tucker-Davis Technologies, Alachua, Florida, U.S.A.) and an analogue–digital interface (Motu 828). Segments of 10-s duration judged to have spectra representative of each noise type were selected and pasted to create noise durations up to 180 s. Care was taken to avoid discontinuities of the waveform at the points where the segments were added. This procedure was chosen instead of using continuous recordings of 180 s to avoid exposure to extraneous noises or large amplitude fluctuations in the noise level during prolonged recordings. In addition, a band-pass noise encompassing the spectra of the advertisement calls of *E. calcaratus*, with cutoff frequencies of 700 and 2700 Hz was generated with a waveform generator (WG1, Tucker-Davis Technologies) and a programmable filter (PF1, Tucker-Davis Technologies). Oscillograms and power spectra averaged over 10 s for the five noises used in the playback experiments 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. Two harmonically related sinusoids of 1250 and 1875 Hz, having the same amplitude, were added and a 250-ms tone was generated. The tone had 50-ms rise–fall times. The synthetic call and a natural call of *E. calcaratus* are shown in Fig. 2. Although the natural call has an asymmetrical temporal structure, with a longer rise time, a symmetrical temporal structure was chosen as the stimulus to allow a more schematic signal-to-noise ratio during the presentation of this stimulus in the presence of noise. Bouts of 20 calls, having an intercall period of 3 s (and a total duration of 1 min) were generated. This periodicity was chosen because, in duetting interactions, males of this species follow rhythms up to this level for prolonged periods (M. Penna, unpublished data). Synthetic calls and 180-s noises were recorded on separate channels on successive tracks of an audio compact disk (CD). The first track lasted 120 s and contained a bout of 20 synthetic calls on the left channel (60 s) followed by 60 s of silence on both channels. The following tracks lasted 300 s and started with 180 s of noise on the right channel. On the left channel, a 60-s bout of 20 calls started 60 s after the noise onset. The 180-s 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. After the track containing the band-pass noise was played, the initial track containing a bout of 20 synthetic calls was repeated, to control for changes in vocal activity during the experiment. The order of presentation of the different

noises was not randomized because of the difficulty in testing a sufficient number of individuals in calm weather conditions at a time of the year when rainy conditions prevail. However, the similar EVRs to the presentation of the band-pass noise at the same intensity (66 dB) during the first and second experimental sequences provide an indication of the repeatability of the effect of this noise under different schedules (see Results). Also, preliminary evidence on the lack of effect due to the noise-presentation sequence is reported in Results. After completing the first experimental sequence, a series of band-pass noise at different intensities was presented. The track used for this stimulation was similar to the noise tracks described above, except that the total duration of the track was 240 s, with silence at the end of the track lasting 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 order of increasing intensity at 48, 54, 60, 66, 72, 78 and 84 dB RMS SPL (fast weighting scale), as measured at the position of the experimental subject (see below).

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 28 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 absence of noise until the end of the final bout of synthetic calls presented in the absence of broadcast noise, was 29 min.

Instrumentation and Experimental Settings

The instrumentation used to broadcast the synthetic calls and noises was as follows. The compact disk containing these sounds was played back with a portable CD player (Sony walkman D-E356CK). The output signal was passed through a two-channel impedance-matched operational amplifier and two sets of attenuators (Hewlett–Packard 355 C and D for the synthetic calls and Hewlett–Packard 350 D for the noises). The synthetic call and noises were mixed with an electronic adder and fed into a power amplifier (Alpine 3540) and a two-way loudspeaker (Dynaudio BM6, frequency response: 38–20 000 Hz). The loudspeaker was positioned 0.8–1.2 m in front of the experimental subject. Evoked vocal responses were recorded with a directional microphone (AKG CK9), the tip of which was placed 0.2–0.5 m in front of the opening of the burrow occupied by the experimental subject. Evoked vocal responses were recorded on the left channel of a cassette recorder (Sony TC-D5M). The synthetic calls were recorded on the right channel of this recorder via a connecting cable from the CD player.

Playback experiments were conducted nightly between 2100 and 0400 hours. Air and substrate temperatures were monitored with a telethermometer (Digi-Sense 8528-20)

Wind

Rain

Creek

Sea surf

Band-pass

5 s
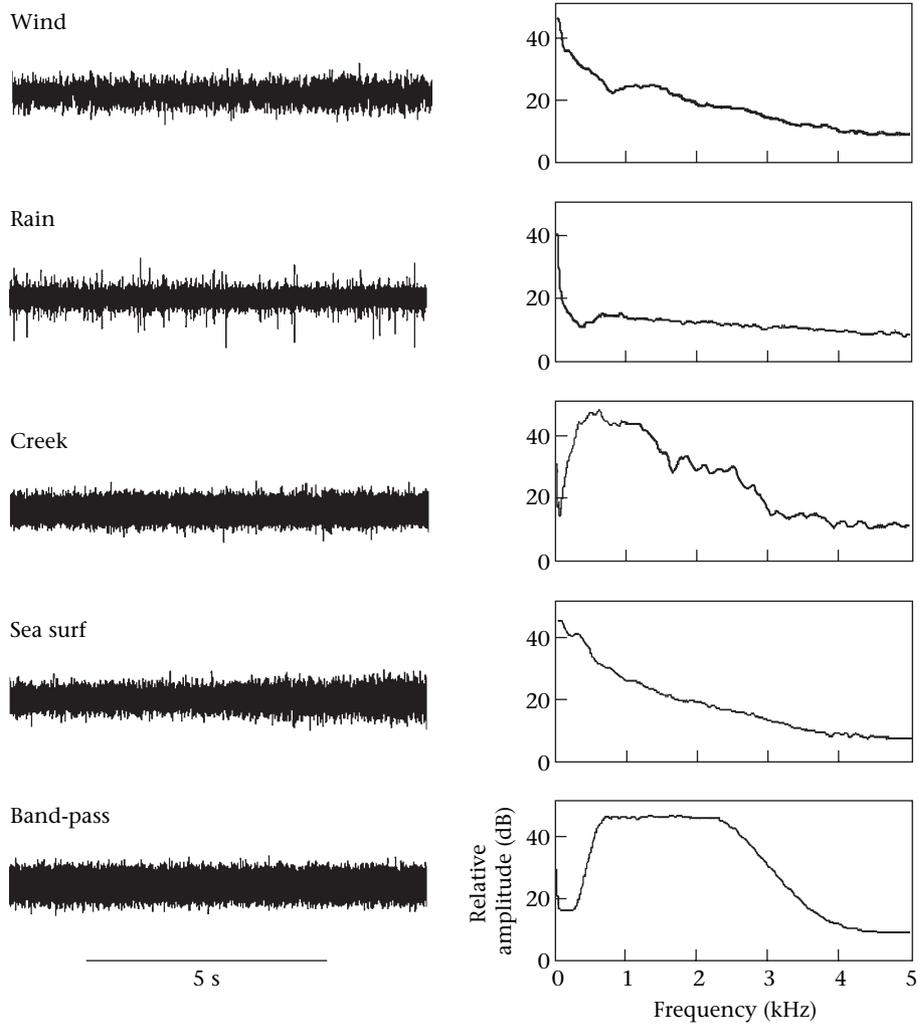
Figure 1. Oscillograms and power spectra of four natural noises recorded in the field and band-pass noise used to create the noise tracks to which males of *E. calcaratus* were exposed. Power spectra analysis bandwidth: 20 Hz.

during recordings. The basal vocal activity of the subjects was recorded for at least 3 min prior to playbacks. Subsequently, the recording of the stimulus and noises was played back and the EVRs were 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

100 ms
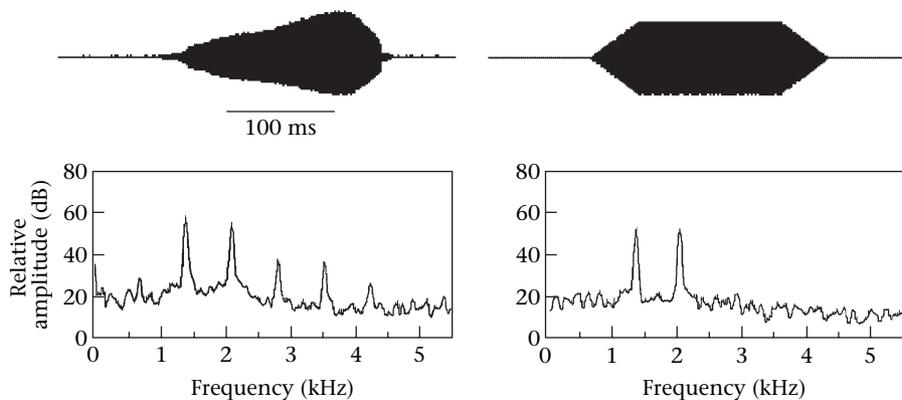
Figure 2. Oscillograms and power spectra of a natural advertisement call of *E. calcaratus* (left) and a synthetic imitation of this signal used as stimulus (right). Power spectra were taken at the midpoints of both sounds. Temperatures during recording of the natural call: air 6.2°C, substrate 8.9°C. Power spectra analysis bandwidth: 20 Hz.

the playback experiment, the basal vocal activity of the subjects was recorded for at least 1 min.

The bouts of synthetic calls and the different noises were presented at intensities of 69 and 66 dB RMS SPL (fast weighting scale), respectively, at the position of the subject. The intensity of the synthetic call was chosen because this value is within the range of intensities of nearest neighbours at the position of burrow openings in chorusing aggregations of this species (M. Penna, unpublished data). Noise intensity was chosen because background abiotic noise at the study site on nights with calm weather was typically below 50 dB RMS SPL, and using 66 dB RMS SPL assured 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. Before starting the experiment, the SPLs of the synthetic call and noises were measured by placing the microphone of the sound-level meter as close as possible to the burrow opening and pointing it towards the loudspeaker, without disturbing the frog. These initial exposures were as short 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 constant levels of these playback sounds at 69 and 66 dB RMS fast SPL, respectively, for the different experimental subjects by adjusting attenuator settings. The environmental noise was also measured from this position at the end of the experiment.

Analysis of Evoked Vocal Responses

Recordings of frog vocalizations and stimuli were digitized with a Macintosh computer (G4 Power PC) with the Peak 2.52 software at a 44-kHz sampling rate, using an anti-aliasing filter (FT6-2, Tucker-Davis Technologies) and an analogue–digital interface (Motu 828). The three parameters used to assess the EVR of a frog (call rate, duration and amplitude) were measured with the Signalyze 3.12 software (Infosignal, Inc., Charlestown, Massachusetts, U.S.A.) throughout the experimental sequence. Spectral components during the recording of basal activity prior to noise exposure were also measured from power spectra (0–5500 Hz, frequency resolution: 20 Hz). Call spectra during the exposure to noises were not analysed, due to their masking during the presentation of these interfering sounds.

Because the EVRs recorded during the presentation of noise at high-intensity levels were embedded in the broadcast noise, the amplitude values of the vocalizations were corrected 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 (AKG CK9) was positioned pointing towards a loudspeaker (JBL T50, 10 cm diameter) through which a natural call of a male of *E. calcaratus* was broadcast repetitively at a rate of 0.5 calls/s. The loudspeaker (Dynaudio BM6) used to deliver the noise and synthetic calls in the field was positioned 1.2 m from the JBL loudspeaker and behind the directional

microphone, such that the two loudspeakers faced 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 75 dB RMS SPL. The band-pass noise used in the field experiments (0.7–2.7 kHz) was delivered through the Dynaudio BM6 loudspeaker at six attenuations, in 6-dB steps. This setting was intended to reproduce the experimental situation, by recording a call of constant amplitude with the different noise levels used in the field. At the lowest attenuation, the intensity of the noise at the tip of the directional microphone was 84 dB RMS fast SPL, and intensity decreased correspondingly with increasing 6-dB attenuation steps. At the lower attenuation levels (noise levels of 84, 78, 72 and 66 dB RMS SPL), the amplitude of the call embedded in noise as measured increased by 5.3, 2.7, 1.1 and 0.3 dB RMS SPL, respectively, and the ratio between the signal plus noise and the broadcast noise was 0.6, 3.4, 7.4 and 12.9 dB, respectively.

These measured values were used to generate a best-fit curve: $Y = 5.9124e^{-0.2244X}$, where Y (dB) is 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 broadcast noise. This correction was applied to the field recordings having ratios between these measurements below 10 dB. This occurred in most of the subjects for presentations of band-pass noise at 72 dB RMS SPL and higher.

To analyse the effect of the exposure to different kinds of noise presented at the same level, ANOVAs for repeated measures (Statistica 5.0 software, Statsoft, Inc., Tulsa, Oklahoma, U.S.A.) were performed for the three EVR measures, using as treatments five time intervals: (1) the no-playback interval preceding the noise presentation (120 s); (2) the noise exposure before synthetic call onset (60 s); (3) the noise exposure during the presentation of the synthetic call bout (60 s); (4) the noise exposure after the presentation of the synthetic call (60 s); and (5) the no-playback interval after noise exposure (120 s). To analyse the effects of the exposure to band-pass noise of different intensities, the same comparisons were made, except that the duration of the intervals of silence were 60 s instead of 120 s. The five time intervals are hereafter called 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. These time intervals are shown in Fig. 3.

To evaluate the effect of prolonged noise exposure on EVRs during the entire experimental sequence, comparisons were performed between EVRs to the bout of synthetic calls presented in the absence of broadcast noise at the beginning of the experiment and EVRs to the same bout of stimuli presented after completing the series of five exposures to noises of different structure. Also, the EVRs to this second presentation of the bout of synthetic calls were compared to those evoked by the same bout of synthetic calls presented after the exposures to band-pass noise at different levels. The two comparisons were chosen instead
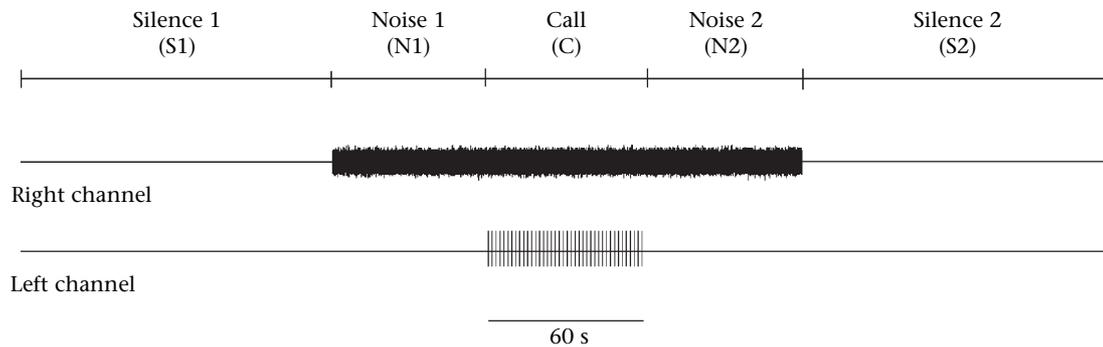
Figure 3. Schematic diagram of the time intervals for which measures of evoked vocal responses (EVRs) were compared during exposure to different kinds of noise. For exposures to band-pass noise of different intensities, the intervals of silence lasted 60 s instead of 120 s (see text).

of an ANOVA comprising the three measurements because two frogs ceased calling after the exposure to band-pass noise at the highest intensity and the sample size was smaller than the one available for the three presentations of the bout of synthetic calls (see Results).

To compare graphically the EVRs of different individuals to a series of stimuli, the call rate, duration and amplitude were normalized to the maximum response for each individual. Specifically, the value of an EVR measure for a given subject in response to a particular time interval was divided by the maximum value of that EVR measure produced by the frog to any one of the analysed intervals and multiplied by 100.

RESULTS

Basal Vocal Activity

Calls produced by the 13 subjects recorded over a period ($\overline{X}\pm SD=317\pm72.7$ s) prior to the presentation of the initial bout of stimuli had a mean $\pm$ SD rate of 9.4 ± 4.14 calls/min. The mean $\pm$ SD duration of advertisement calls for the 13 individuals was 286 ± 56 ms. The call spectra had a harmonic structure, with the second ($\overline{X}\pm SD=1396\pm96.7$ Hz) and third ($\overline{X}\pm SD=2094\pm 145.4$ Hz) harmonic having the highest amplitudes. Males of *E. calcaratus*, when stimulated during the initial bout of stimuli in the absence of broadcast noise, produced advertisement calls at a mean $\pm$ SD rate of 17.8 ± 6.36 calls/min. Mean $\pm$ SD call duration was 322 ± 56 ms. The background noise at the position of the experimental subjects, measured when no nearby individuals called, was on an average 49.5 dB RMS SPL (range 38–62 dB RMS SPL). Three of the experimental subjects were tested during nights having increased noise levels (55, 59 and 62 dB RMS SPL) produced by light rain and/or wind or increased creek currents after storms on previous days. At the study site, frogs were observed to call during stormy nights with background noise levels up to 70 dB RMS SPL. Air and substrate temperatures during recordings were -0.2–$5.8\,°C$ and 3.7–$6.9\,°C$, respectively.

Exposure to Noises of Different Structure

A preliminary test of the relevance of the presentation order of noises of different structure indicated that this factor does not exert a critical influence on EVRs. Two frogs other than the experimental subjects were exposed to 1-min noise presentations at 66 dB RMS SPL, separated by 1-min no-broadcast intervals in the following schedule: wind, band-pass, wind, band-pass. Both frogs responded with lower call rates during the first and second wind noise exposures (mean = 11.3 and 9.1 calls/min, respectively) relative to the corresponding band-pass noise exposures (mean = 20.1 and 21.6 calls/min, respectively).

Most of the frogs called persistently during the series of exposures to different noises at a constant level. Two frogs ceased responding during and after the exposure to sea surf noise and one frog ceased responding during and after the exposure to the band-pass noise. These three frogs and a fourth individual were not presented with the final bout of synthetic calls in the absence of broadcast noise. This stimulus was presented to the remaining nine frogs, and the three EVR measures (call rate, duration and amplitude) to bouts of synthetic calls previous to noise exposure and after the exposure to noises of different structure were similar (*t* test for dependent samples: $t_8 = 1.449$, $P = 0.185$, $t_8 = -0.675$, $P = 0.518$, $t_8 = 0.945$, $P = 0.372$, respectively).

Frogs increased their calling rates during the presentation of the synthetic stimulus in the presence of the five noise types delivered at a constant level. Call rates differed significantly between the five time intervals (S1, N1, C, N2 and S2) during exposure to wind, rain, creek, sea surf and band-pass noise ($F_{4,44} = 17.466$, $P < 0.00001$; $F_{4,48} = 27.045$, $P < 0.00001$; $F_{4,48} = 22.792$, $P < 0.00001$; $F_{4,40} = 12.562$, $P < 0.00001$; $F_{4,36} = 27.642$, $P < 0.00001$, respectively). The natural noises of wind and sea surf did not produce significant differences in call rate during N1 relative to S1. However, rain, creek and band-pass noise produced significant increases in call rate during N1 relative to S1. The band-pass noise produced the largest increase in call rate during N1, and this rate did not differ significantly from the call rate evoked during C by this noise. However, this difference was significant for the other four noises. Exposure to noise during N1 yielded average call rates that were higher than those produced during N2 and S2, and these differences were significant for the rain and band-pass noise. The call rate evoked during C was higher than the call rate during S1, N2 and S2 for the five types of noise. The call rate during N2 did not differ from either S1 or S2 and the call rate did not

differ between S1 and S2 for the five types of noise (Fig. 4a, Table 1).

Call duration showed trends of change that parallelled those of call rate. Call duration differed between the
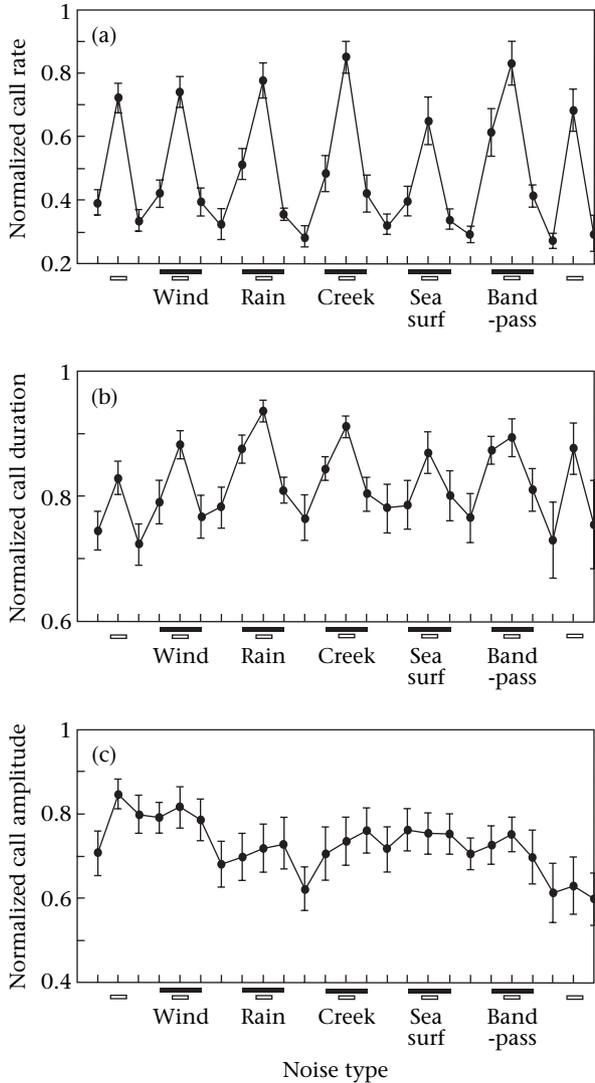
Figure 4. Normalized measures of evoked call response (call rate (a), call duration (b) and call amplitude (c)) of 13 male *E. calcaratus* during the experimental sequence of exposure to noises of different structure. Horizontal open bars at the beginning and at the end of the sequence indicate 1-min intervals during which a bout of 20 synthetic calls was presented at a rate of three calls/s. Filled bars indicate 3-min intervals during which noises of different structure were presented and open bars below indicate bouts of 20 synthetic calls during the second min (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 1 min, and the interval before the initial stimulus bout had an average duration of 317 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 69 and 66 dB RMS SPL, respectively.

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

EVR measure	Noise	F	P*	S1/N1	S1/C	S1/N2	S1/S2	N1/C	N1/N2	N1/S2	C/N2	C/S2	N2/S2
Call rate	Wind	17.466	<0.00001		0.00013			0.00039			0.00013	0.00013	
	Rain	27.047	<0.00001	0.00862	0.00013			0.00039	0.03626	0.00067	0.00013	0.00013	
	Creek	22.792	<0.00001	0.01722	0.00013			0.00039			0.00013	0.00013	
	Sea surf	12.562	<0.00001		0.00013			0.00188	0.00553	0.00013	0.00013	0.00013	
	Band-pass	27.642	<0.00001	0.00013	0.00013						0.00013	0.00013	
Call duration	Wind	5.535	0.00107		0.00061						0.01303	0.02450	
	Rain	6.510	0.00029		0.00344					0.02953	0.03384	0.00093	
	Creek	6.772	0.00021	0.04901	0.00060						0.02862	0.00165	
	Sea surf	4.627	0.00364		0.00548							0.00571	
	Band-pass	4.596	0.00422	0.04072	0.02654							0.03035	
Call amplitude	Wind	3.841	0.00920							0.03901			
	Rain	1.879											
	Creek	4.321	0.00458	0.01922			0.02920					0.00815	0.03960
	Sea surf	0.314											
	Band-pass	0.927											

S1: no-playback interval preceding the bout of synthetic calls; 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) are omitted.

different time intervals (S1, N1, C, N2 and S2) for the exposures to wind, rain, creek, sea surf and band-pass noise ($F_{4,44} = 5.535$, $P = 0.00107$; $F_{4,48} = 6.510$, $P = 0.00029$; $F_{4,48} = 6.772$, $P = 0.00021$; $F_{4,40} = 4.627$, $P = 0.00364$; $F_{4,36} = 4.596$, $P = 0.00422$, respectively).

The natural noises of wind and rain did not produce significant differences in call duration during N1 relative to S1, but creek and band-pass noises produced significant differences for the same comparison. The band-pass and creek noises produced increases in call duration during N1 relative to S1, and these call durations did not differ significantly from the call duration evoked by these noises during C. Exposure to noise during N1 yielded call durations that were on an average longer than those produced during N2, however, none of these differences reached levels of significance. Duration of evoked calls was longer during N1 than during S2 for the rain and band-pass noises. Duration of evoked calls was also longer during C than during N2 for all noises, and this difference was significant for the wind, rain and creek noises. The call duration during N2 did not differ from either S1 or S2, and call duration during S1 and S2 was similar for the five types of noise (Fig. 4b, Table 1).

In contrast with call rate and duration, call amplitude did not show systematic trends of change within the exposure to a particular noise. However, there was an overall decrease in call amplitude during the series of exposures to noise of different structure. Significant differences in this parameter between time intervals (S1, N1, C, N2 and S2) occurred only for the exposures to wind and creek noise ($F_{4,44} = 3.84$, $P = 0.00920$; $F_{4,48} = 4.321$, $P = 0.00458$, respectively). For the exposure to wind noise, the call amplitude during S2 was lower relative to amplitudes produced during N1, C and N2. For the exposure to creek noise, the call amplitude during S1 was lower relative to the call amplitude during C and N2 (Fig. 4c, Table 1).

Exposure to Band-pass Noise at Different Intensities

Most of the frogs exposed to this series ($N = 11$) called persistently during the exposures to band-pass noise presented at different levels. One frog was not exposed to the band-pass noise at 48 dB RMS SPL, one frog was not exposed to the noise at 72 dB RMS SPL and two frogs were not exposed to the noise at 84 dB RMS SPL. Two other frogs ceased responding during and after the exposure to this noise level. The three measures of EVR (call rate, duration and amplitude) were similar between the presentation of synthetic calls prior to noise exposure and after the exposure to noises of different intensity (t test for dependent samples: $t_8 = -0.817$, $P = 0.451$, $t_8 = 0.313$, $P = 0.767$, $t_8 = -1.188$, $P = 0.288$, respectively).

During the series of exposures to band-pass noise at different levels, frogs increased their calling rates during the presentation of the synthetic stimulus in the presence of noise. Call rates differed significantly between the five time intervals during exposures to

band-pass noise at 48, 54, 60, 66, 72, 78 and 84 dB RMS SPL ($F_{4,32} = 15.509$, $P < 0.00001$; $F_{4,28} = 27.045$, $P = 0.00005$; $F_{4,36} = 7.624$, $P = 0.00015$; $F_{4,36} = 19.845$, $P < 0.00001$; $F_{4,36} = 10.105$, $P < 0.00001$; $F_{4,36} = 9.911$, $P = 0.00002$; $F_{4,24} = 2.827$, $P = 0.04710$, respectively).

The exposure to band-pass noise during N1 produced significant increases in call rate relative to S1 for exposures to noise at 66, 72 and 78 dB RMS SPL. The call rate during C was significantly different relative to S1 for all intensities, except for the 84-dB RMS SPL exposure. No significant differences in call rate occurred between N2 and S1, N2 and S2, and S1 and S2 for any of the noise exposure levels. Call rate was higher during C relative to N1 only for the noise exposures at 48 and 60 dB SPL. The call rate during N1 was higher than during N2 only for the 66-dB SPL exposure. The call rate during N1 was higher than during S2 for the exposures at 66, 72 and 78 dB SPL. The call rate during C was higher than during N2 for the exposures at 48, 54, 60, 66 and 72 dB SPL. Call rate during C was higher than during S2 for exposures at all levels (Fig. 5a, Table 2).

Call durations of EVRs to band-pass stimuli at different levels tended to resemble those of call rate. Significant differences in this parameter occurred only for band-pass noise at 48, 54, 60 and 66 dB SPL ($F_{4,32} = 3.137$, $P = 0.02766$; $F_{4,28} = 12.108$, $P < 0.00001$; $F_{4,36} = 4.730$, $P = 0.00359$; $F_{4,36} = 2.980$, $P = 0.03182$, respectively).

No significant differences in call duration occurred between S1 and N1 for any of the noise levels. Call duration was significantly longer during C than during S1 for noise exposures at 54 and 60 dB SPL only. No significant differences in call duration occurred between S1 and N2 or between S1 and S2. Call duration was significantly longer during C than during N1 and N2 for exposures at 48 and 54 dB SPL. Call duration was also significantly longer during C relative to S2 during exposures at 48, 54 and 60 dB SPL. No differences occurred in call duration between N2 and S2, N2 and N1, or N2 and S1 for any of the exposure intensities (Fig. 4b, Table 2).

Call amplitude of EVRs to band-pass noise at different levels did not show systematic trends of change within the exposure to any particular level. However, there was an overall increase in call amplitude during this experimental series. Significant differences in call amplitude occurred only for band-pass noise at 60 and 78 dB SPL ($F_{4,36} = 2.856$, $P = 0.03736$; $F_{4,36} = 4.305$, $P = 0.00600$, respectively). Call amplitude was significantly larger during C relative to S1 for exposure at 60 dB SPL and it was also larger during C relative to S2 and during N2 relative to S2 for the 78-dB SPL exposure (Fig. 5c, Table 2).

DISCUSSION

Results of this study show that noises of different nature presented at a moderate level (66 dB RMS SPL) have excitatory effects on the vocal activity of E. calcaratus. In this study, these effects were significant for the natural noises of rain and creek, and especially for the band-pass noise encompassing the spectra of the natural advertisement call of this species. The effects of rain noise on EVRs
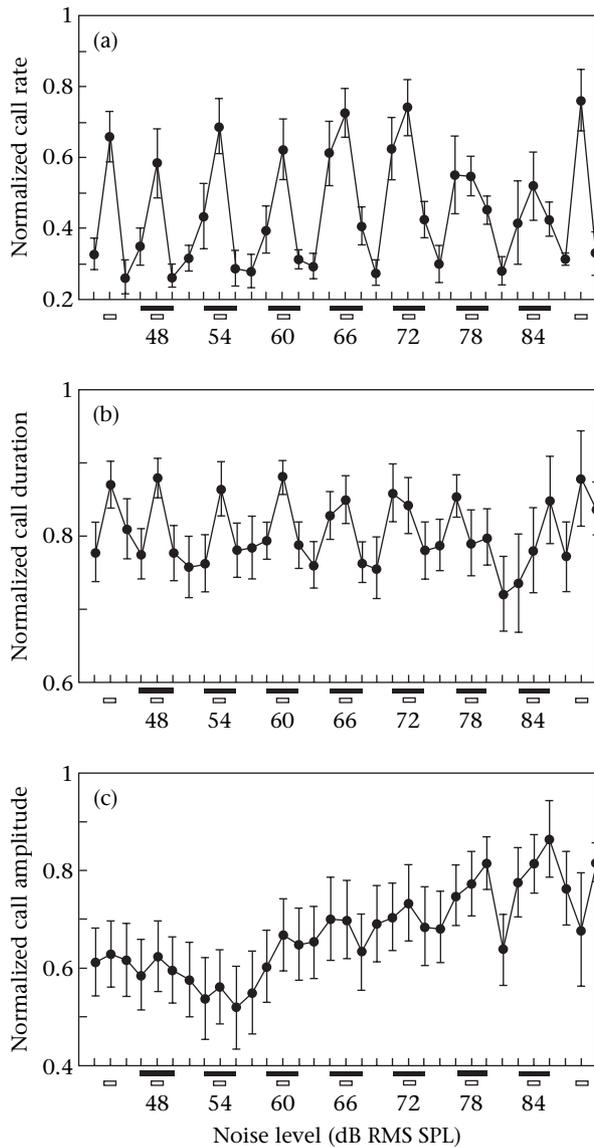
Figure 5. Normalized measures of evoked call response (call rate (a), call duration (b) and call amplitude (c)) of 11 male *E. calcaratus* during the experimental sequence of exposure to band-pass noise delivered at different RMS SPLs measured at the position of the subjects, as indicated on the horizontal axis. Horizontal open bars at the beginning and at the end of the sequence indicate 1-min intervals during which a bout of 20 synthetic calls was presented at a rate of three calls/s. Filled bars indicate 3-min intervals during which noises of different structure were presented and open bars below indicate bouts of 20 synthetic calls during the second min (see Methods). The sound levels of the synthetic call measured at the position of the subjects was 69 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 199 s, depending on the subject (see Methods). The initial bout of stimuli of this sequence was the same as the last stimuli of the sequence of presentations of noises of different structure (see Fig. 3). Filled circles and vertical bars represent averages and standard errors, respectively.

could be related to the temporal structure of this sound, having sharp amplitude modulations that are not present in the other noises to which subjects were exposed. The effect of the creek noise could be explained by its spectral structure, which resembled that of the band-pass noise (see below). Among the EVR measures analysed, call rate was the one that experienced the largest changes during noise exposure. Call duration paralleled the effects on call rate. By contrast, call amplitude did not show changes related to noise exposure. An indication of the repeatability of these effects is provided by the similar profile of the changes in EVR obtained during the exposures to band-pass noise at 66 dB SPL during the sequences of different noise types and during the sequence of band-pass noise of different intensities.

The level of the natural noises employed in the experiments (66 dB RMS SPL) was within the range of wind, rain and creek noise levels recorded during stormy nights at the study site (see Methods). Males of *E. calcaratus* call during agitated weather conditions that produce similar noise levels. The sea surf noise does not pertain to the mountainous area where the study was conducted, but as mentioned in Methods, coastal populations of this species are exposed to this interference. The band-pass noise to which experimental subjects were exposed was intended to mimic the noise of choruses of *E. calcaratus*. The levels of the calls of neighbours at the position of males in chorusing aggregations can reach 70 dB RMS SPL (M. Penna, unpublished data); these calls are the most persistent noise to which frogs are exposed in their breeding areas. The average background noise from abiotic sources is usually lower, and during the experiments was approximately 50 dB RMS SPL on average. The larger increase in vocal activity produced by band-pass noise was not related to a better auditory sensitivity for this frequency range. The auditory system of this species has a similar sensitivity, with thresholds of about 50 dB RMS SPL, throughout the frequency range of conspecific vocalizations (1–2 kHz), and at frequencies below 0.4 kHz. (M. Penna & A. Plaza, unpublished data).

A similar dependence of vocal activity on noise spectrum has been reported for other vertebrates. Birds (Manabe et al. 1998; Brumm & Todt 2002), monkeys (Sinnot et al. 1975) and humans (Egan 1972) produce vocalizations of larger amplitude if exposed to band-pass noise centred at the frequency range of their vocalizations, as compared to noises having a different spectral composition. In anurans, a single study has explored the effects of noise spectra on EVRs (Schwartz & Wells 1983b). This study showed that males of the Central American treefrog *Hyla ebraccata* show a larger decrease in call rate when they are exposed to high-intensity noise (90 and 100 dB SPL) centred in the spectra of their vocalizations than when they are exposed to noises centred at higher or lower frequencies.

The larger effect of the band-pass noise on the EVRs of *E. calcaratus* may depend on a preferential amplification of those frequencies inside burrows from which males of this species call (Penna 2004). However, this effect was not measured in the experiments reported here, because of the difficulty in locating the burrow openings among the

Table 2. Results of ANOVA and post hoc tests 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)	F	P*	S1/N1	S1/C	S1/N2	S1/S2	N1/C	N1/N2	N1/S2	C/N2	C/S2	N2/S2
Call rate	48	15.509	<0.00001		0.00013			0.00013			0.00013	0.00013	
	54	9.749	0.00005		0.00087						0.00013	0.00013	
	60	7.624	0.00015		0.00013			0.04542			0.00145	0.00104	
	66	19.845	<0.00001	0.00013	0.00013				0.00170	0.00013	0.00013	0.00013	
	72	10.105	<0.00001	0.00208	0.00024					0.00544	0.01853	0.00013	
	78	9.911	0.00002	0.00087	0.00533					0.00025		0.00107	
	84	2.827	0.04710									0.05800	
Call duration	48	3.137	0.02766					0.05300			0.00017	0.03357	
	54	12.108	0.00001		0.00017			0.00017			0.03414	0.00017	
	60	4.730	0.00318		0.01638							0.00268	
	66	2.980	0.03182										
	72	2.245											
	78	2.434											
	84	1.131											
Call amplitude	48	1.702											
	54	0.366											
	60	2.856	0.03736		0.03887								
	66	1.799											
	72	0.292											
	78	4.305	0.00600									0.00876	0.01728
	84	1.165											

Abbreviations as in Table 1.
*Nonsignificant P values (>0.05) are omitted.

mossy substrate of the bog where the study was conducted.

Although noise exposure affects the amplitude of bird vocalizations (Cynx et al. 1998; Brumm & Todt 2002; Pytte et al. 2003; Brumm 2004), it does not affect the amplitude of the advertisement call of *E. calcaratus*. Other frogs, however, augment the amplitude of their calls in response to stimuli of increasing intensity (López et al. 1988). The lack of an increase in amplitude in response to noise exposure in *E. calcaratus* could be related to limitations of the vocal apparatus or to the high energetic cost of vocal effort in anurans (e.g. Wells 2001).

Increases in call rate and duration are modalities of confronting interference that increase the duty cycle of the vocal output. In particular, an increase in call duration may signify aggressiveness and a disposition to defend a calling post in the presence of intrusion. In a related species, *E. emiliopugini*, which breeds in our study site during late spring and early summer (November–December), the production of longer, multiple-note calls by males increases gradually with the intensity of a natural call used as a stimulus (Penna et al. 2005). The gradual increase in the production of these signals may denote the readiness of the caller to sustain a vocal challenge. By producing longer calls, frogs potentially generate more interference to competitors.

In the only study on the effect of noise on frog EVRs using moderate intensities, Narins (1982) stimulated males of the Caribbean treefrog *Eleutherodactylus coqui* with a synthetic call in the presence of noise, but not to noise alone, and he therefore could not determine whether the increase observed during stimulation in the presence of noise was due to the effect of noise or to a combined effect of noise and the stimulus. In his study, Narins (1982) defined an effective critical ratio as the quotient between the synthetic call used as a stimulus and the noise level necessary to suppress the EVRs to that stimulus. This term is related to the critical ratio (i.e. the ratio between level of a test tone and the spectrum level of a broadband noise necessary to produce a total masking of the test tone; Scharf 1970). In his study, Narins found that the effective critical ratio that produced a total suppression of the response to the stimulus was between 31 and 40 dB, measured in spectral density (dB/Hz) of the band-pass noise.

In our study, the spectral density (dB/Hz) of the 2-kHz bandwidth noise employed is 33 dB below a pure tone having the same SPL as the noise. The synthetic call used was presented at 69 dB RMS SPL and consisted of two harmonically related tones; the individual level of each tone was approximately 66 dB RMS SPL. The increase in EVR produced by exposure to band-pass noise was manifest up to 78 dB RMS SPL, and this effect disappeared for the exposure of 84 dB RMS SPL. The spectral densities of these exposures (45 and 51 dB/Hz) correspond to signal-to-noise ratios of 21 and 15 dB, respectively, relative to the 66-dB level of each of the harmonics composing the synthetic call. An effective critical ratio between 15 and 21 is considerably lower than the 31–40 dB reported by Narins (1982). The higher responsiveness to noise of *E. calcaratus* relative to *E. coqui* contrasts with the naïve

expectation that animals from tropical environments should have higher tolerance to noise intrusion because they experience higher noise levels. It is possible, however, that *E. calcaratus* confronts a relatively high noise level in its microacoustic environment. Males of this and related species can call in dense aggregations with individuals positioned at distances less than 0.5 m to their nearest neighbours (Penna & Solís 1998; M. Penna, unpublished observations), whereas males of *E. coqui* space themselves at distances of approximately 2 m to their nearest neighbours (Narins & Hurley 1982). Furthermore, the amplification effect of burrows contributes to the increase in noise level of conspecfic choruses of *E. calcaratus* at the position of receivers (Penna 2004).

The enhancement of vocal activity caused by moderate levels of noise found by Narins (1982) and by the present study is similar to effects observed in other studies, where female anurans show a preference for a stimulus embedded in noise relative to a stimulus alone (Ehret & Gerhardt 1980) and an improvement in discrimination of stimuli of different frequencies (Schwartz & Gerhardt 1998). Neurophysiological evidence complements behavioural data showing increased responsiveness in the presence of moderate noise levels. Neurons in the torus semicircularis of ranid frogs respond with higher discharge rates (Ratnam & Feng 1998) or higher synchrony (Bibikov 2002) to stimuli accompanied by broadband noise. Also, plots of multiunit activity versus stimulus frequency for neurons in the torus semicircularis of the frog *Pseudacris crucifer* show a more peaked shape when isointensity tones are presented with moderate levels of background noise than without noise, providing a neural basis for a finer behavioural discrimination by females under the former circumstances (Schwartz & Gerhardt 1998).

The overall tendency for subjects in the present study to decrease call rate and call duration between the exposures to a given noise before and after (N1 and N2) the presentation of the bout of stimuli (C) suggests that the vocal response may habituate to a persistent noise exposure. Experiments with prolonged exposures to noise that are not accompanied by synthetic call presentation would clarify the mechanisms involved in the apparent decrease of response during noise presentation.

The important effects of noise on the vocal activity of *E. calcaratus* indicate that this frog, native to a relatively simple sound environment, is capable of responding actively to considerable levels of interference. Birds apparently use different strategies to cope with urban noise. Some species increase the amplitude (Brumm 2004) or pitch (Slabbekoorn & Peet 2003) of their vocalizations in areas of high noise levels, whereas other bird species seem to habituate quickly to environmental noise exposure (Harms et al. 1997). Declines of some bird populations in areas of high environmental anthropogenic noise have been reported (Forman et al. 2002), but other species have not shown signs of vulnerability to this kind of intrusion (Rheindt 2003). Additional studies on the effect of noise on the vocal behaviour of frogs from the temperate forest would determine whether the responsiveness displayed by *E. calcaratus* to interference from biotic and abiotic noise corresponds to a broadly spread adaptation, or whether

alternative strategies are used by other inhabitants of these biotopes.

Acknowledgments

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