

## ORIGINAL ARTICLES

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## Frog call intensities and sound propagation in the South American temperate forest region

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**Abstract** Sound pressure levels and the spectral structure of the advertisement calls of five species of frogs from the South American temperate austral forest were analyzed. Males of *Eupsophus emiliopugini*, *Batrachyla antartandica* and *B. leptopus* call from the ground in bogs, while males of *Hylorina sylvatica* and *Pleurodema thaul* call from the water surface in marshes. Calling males of the species from bogs and marshes spaced at average distances that were shorter and longer than 2 m, respectively. The properties of these habitats for sound propagation were evaluated by broadcasting pure tones, broadband noise and tape-recorded advertisement calls of the three species from bogs and of *H. sylvatica*. Excess attenuation and spectral degradation were higher for calls broadcast in bogs than in the marsh. The calls of *B. antartandica* and *B. leptopus*, with dominant frequencies of about 2 kHz, were more affected than those of *E. emiliopugini* and *H. sylvatica*, with dominant frequencies below 1.5 kHz. These results show the lack of an optimal relationship between properties of habitats for sound transmission and the spectral structure of these anuran calls. Body size imposes an important constraint on call spectra and propagation, which frogs counteract by distribution patterns and auditory capabilities.

**Key words** Anurans · Frog calls · Sound propagation · Temperate forest

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### Introduction

The range over which acoustic communication signals propagate depends on the power generated by the sound source. However, the physical properties of the environment through which sounds are transmitted also affect the propagation distance and the actual structure of signals reaching potential receivers. Different acoustic signals of birds and primates broadcast in a given environment experience dissimilar rates of attenuation, or decrease in sound pressure level (SPL) (e.g., Waser and Waser 1977; Brenowitz 1982b; Waser and Brown 1986) and their spectral and temporal structure are degraded differently (e.g., Brenowitz 1982a; Wiley and Richards 1982; Dabelsteen et al. 1993; Brown et al. 1995). Reciprocally, vocalizations of birds dwelling in different environments have been shown to possess structural features that contribute to improving the transmission of these sounds in their respective habitats (e.g., Chappuis 1971; Morton 1975; Bowman 1979; Wasserman 1979; Gish and Morton 1981; Shy 1983; Sorjonen 1986a,b).

Male frogs and toads produce intense advertisement calls towards which females orient and to which other males respond antiphonally. Comparative studies from Australia, North America and Africa (Loftus-Hills and Littlejohn 1971; Gerhardt 1975; Passmore 1981) have documented the variation in SPL of frog and toad calls. Experimental studies have shown that the SPLs of the calls affect both females' phonotactical responses and males' antiphonal responses (reviewed in Gerhardt 1988; Wells 1988). In addition to these behavioral effects, the SPLs of calls determine spacing patterns of males in chorusing assemblages of various anurans (Brenowitz et al. 1984; Robertson 1984; Wilczynski and Brenowitz 1988; Brenowitz 1989; Gerhardt et al. 1989).

In spite of the extensive field research on anuran vocal behavior conducted during recent years, the influence of the physical environments where toads and frogs communicate on the structure of vocal patterns remains a largely unexplored issue. A single experi-

mental study aimed specifically at evaluating the influence of habitat on the design of advertisement calls has been conducted (Ryan et al. 1990). This study reported that the vocalizations of a subspecies of the North American frog *Acris crepitans* propagate more efficiently in its native habitat relative to calls of an allopatric subspecies.

Frogs from the South American temperate forest in Chile are amenable for studies of habitat influences on vocalizations. Chorusing assemblages are always composed of a small number of species (four as a maximum), which produce a relatively simple acoustic environment. This condition contrasts with anuran aggregations from tropical forests, where about 15 species often call synchronously (e.g., Hödl 1977; Duellman and Pyles 1983; Zimmerman 1983). The extant vocal diversity among species of frogs from southern Chile is likely to have resulted from independent evolutionary processes in isolated refugia during Pleistocene glaciations. In such circumstances, it is probable that interactions among sympatric taxa have not determined the diverse vocal patterns of the different taxa (Penna and Veloso 1990). Such a restricted role of selective pressures arising from interference among sympatric species provides a suitable opportunity to explore the extent to which the physical characteristics of the environment influence frogs' sound communication.

The habitats in which different anurans vocalize in southern Chile can be classified into two types. A number of species vocalize from the ground in bogs and swamps, hidden among low vegetation or from inside burrows, whereas other taxa call from the water surface in marshes and large pools, perched on emergent vegetation (Penna and Veloso 1990).

In the current study, the SPLs and spectral composition of the advertisement calls of five frog species from the temperate forest in southern Chile are characterized. The physical properties for sound transmission of the habitats in which these species breed and vocalize were explored by broadcasting pure tones, white noise, and natural calls. Our aim was to examine relationships between habitat, the structure of advertisement calls, and spacing patterns of these frogs in breeding areas.

## Methods

### Study sites

Advertisement calls of the leptodactylid frogs *Eupsophus emiliopugini*, *Batrachyla antartandica*, *B. leptopus*, *Hylorina sylvatica*, and *Pleurodema thaul* were studied in four localities in southern Chile: Puyehue (latitude 40°35' S, longitude 72°20' W, altitude 440 m), La Picada (latitude 41°06' S, longitude 72°30' W, altitude 700 m), Río Chaicas (latitude 41°37' S, longitude 72°40' W, altitude 240 m), and Cucao (latitude 43°40' S, longitude 74°00' W, altitude 20 m). The calls of *P. thaul* were also recorded in Agua Buena in central Chile (latitude 34°42' S, longitude 70°53' W, altitude 600 m). In these localities, *E. emiliopugini*, *B. antartandica*, and *B. leptopus* called from the ground, and *H. sylvatica* and *P. thaul* called from the water surface of marshes and pools.

Propagation of pure tones, white noise and tape-recorded calls of *E. emiliopugini*, *B. antartandica*, *B. leptopus*, and *H. sylvatica* was studied in Puyehue, La Picada, and Cucao. This field work was conducted during November and December 1990–1992.

### Call SPLs and spectra

Peak SPLs of advertisement calls of the five species under study were measured, in order to compare levels of sounds having different temporal structure. A sound level meter (Brüel & Kjør 2230) fitted with a flexible microphone extension rod (UA 0196), a foam wind shield (UA 0237), and a 10-m extension cable (UA 0028) was used. The instrument was calibrated with a portable calibrator (Brüel & Kjør 4230) before and after each recording session. SPLs of the advertisement calls were obtained with the microphone positioned 0.5 m in front of a calling male (0°). Five to 30 calls were measured for each position of the sound level meter relative to a calling frog. A few vocalizations produced at the beginning of a bout of calling generally had lower intensities and were not considered for statistical analysis. The signal detected with the sound level meter was recorded on one channel of a Uher 4400 IC stereo tape recorder, and the SPL values read on the display of the sound level meter were dictated onto the second channel of the tape recorder.

In addition to the measurements used for interspecific comparisons, peak SPLs of the calls produced by the nearest conspecific neighbors were recorded at the position of a given frog. These measurements were taken with the sound level meter microphone placed at the position of the focal subject, pointing towards the calling neighbor. Five to 30 peak SPL values were computed and an average was calculated for each individual. To compute averages and standard deviations of SPLs, dB readings were converted to sound pressure (N/m<sup>2</sup>) and the resulting means and standard deviations reconverted to dB SPL. Reverting linear values to the dB scale resulted in standard deviations asymmetrical around the mean. Coefficients of variation of SPL measurements were calculated by dividing the larger of the standard deviations by the average in dB, following the procedure used by Wilczynski and Brenowitz (1988).

Power spectra of three calls were analyzed for each frog, and an average for the dominant frequency and a secondary spectral peak, when applicable, was calculated for each individual. The software and hardware used for spectral analysis are detailed below.

Distances between a calling frog and the sound level meter microphone, and between neighboring frogs were measured with a steel tape to the nearest centimeter. Snout-vent lengths and body masses of frogs whose calls were recorded were measured within the first 48 h of captivity with a Vernier caliper to the nearest 0.1 mm and a scale (Acculab 333) to the nearest 0.1 g, respectively. Air and substrate temperatures were measured after each recording with a telethermometer (Digi-Sense 8528-20) to the nearest 0.1 °C.

### Sound propagation experiments

Experiments on sound propagation were conducted during daytime in Puyehue (marsh), La Picada site 1 (bog A), La Picada site 2 (bog B), and Cucao (bog C) between 1030–1230, 1800–2100, 1700–1900, and 0730–0930 hours, respectively. Air temperatures measured at 5 and 100 cm above the ground varied between 12.7–14.6 °C and 12.5–14.3 °C in marsh, between 9.2–13.5 °C and 9.6–12.8 °C in bog A, and between 9.8–13.5 °C and 9.5–13.5 °C in bog C. In bog B, a single reading for each height was taken at the end of the experiment, and temperatures at 5 and 100 cm above the ground were 16.1 °C and 14.7 °C, respectively. Temperature differences between both heights were within ±1.5 °C in the four sites. During the experiments, the atmosphere was calm. Only slight gusts of wind occurred occasionally, during which measurements were suspended. These recordings were conducted during daytime to avoid interference from vocal activity of frogs in the tested areas at night. These measurements are assumed to apply to night hours during which frogs vocalize, assuming that air temperature and humidity have negligible effects on sound propagation at the frequencies and

distances from the source tested (Harris 1966; Piercy and Daigle 1991).

Continuous tones were generated with a portable sine wave generator based on a 2206 integrated circuit. White noise was generated with a 5837 integrated circuit. Six repetitions of a single complete call or call subunits of each of four species (*E. emiliopugini*, *B. antartandica*, *B. leptopus*, and *H. sylvatica*) contained on a metallic cassette tape were played back with a cassette recorder (Sony TCD-5M). The continuous tones, white noise, and playback calls were passed through attenuators (Hewlett-Packard 355 D and E), an audio amplifier (Alpine 3540) and a 10-cm-diameter loudspeaker (JBL T-50). Distortion products of this instrumentation measured at 0.5 m from the speaker in a semianechoic room were 32 dB below the amplitude of the tones generated.

In the marsh, the speaker was placed on the edge of a pool at the approximate position where a male *H. sylvatica* called during the night before. In bogs A, B, and C, the speaker was placed at ground level at the position from which males of *E. emiliopugini*, *B. antartandica*, and *B. leptopus* had been calling, on nights previous to the days when the experiments were carried out. SPLs of the sounds were measured with the sound level meter positioned at 0.5, 1, 2, 4, and 8 m in front of the speaker. Fast root-mean-square (RMS) and peak SPLs were measured for continuous tones and playback calls, respectively. The height of the microphone was constant at 5 cm for all distances. Signals detected were fed into one channel of an Uher 4400 IC tape recorder. The recording level of the tape recorder was kept constant for all measurements, and the sensitivity of the sound level meter was increased at distant locations from the loudspeaker, in order to provide detectable signals into the tape recorder. In the marsh, the measuring microphone was placed along the border of a 3 × 16 m pool with sparse emergent rushes (*Juncus*). In bogs A and B, the microphone was placed on a surface where mosses (*Sphagnum* and *Hygroamblystegium*) predominated. In bog C, the surface was covered with grasses (*Scyrpus*) and ferns (*Blechnum*).

Excess attenuations relative to spherical spreading of pure tones and playback calls were calculated for distances of 1, 2, 4, and 8 m from the loudspeaker, relative to measurements at 0.5 m. Values predicted by spherical attenuation were calculated with the equation: dB attenuation = 20 log[far distance (m)/0.5 (m)]. This value was subtracted from the difference between the values measured in dB SPL at 0.5 m from the loudspeaker and those measured at the corresponding far distances. Positive and negative values indicated that the sound attenuated at rates higher and lower, respectively, relative to SPLs predicted by spherical attenuation for each distance. A single measurement was taken for each pure tone frequency at a given distance from the source, assuming that the readings for these determinations were essentially constant. SPLs of six repetitions of a single call of each of the four species tested were measured at each distance from the source, and the values measured also showed little variation for repetitions of a call at a given distance from the loudspeaker (see Results).

Maximum RMS and peak SPLs of ambient noise were measured in the four study sites prior to the sound propagation experiments, with the sound level meter microphone placed on the transect along which natural and synthetic sounds were broadcast. These readings were taken during 1-min periods when no frogs were calling.

SPL readings of pure tones and playback calls that fell within 3–10 dB RMS and peak SPLs of ambient noise, respectively, were corrected after Hassal and Zaveri (1988). SPLs less than 3 dB above background noise were excluded from analysis. This procedure was necessary for measurements of pure tones between 3.0 and 5.0 kHz and playback calls of *B. antartandica* and *B. leptopus* obtained in Cucao, at 4 and 8 m from the loudspeaker (see Results).

#### Spectral analysis

Power spectra of the advertisement calls recorded at 0.5 m, and power spectra of white noise and of playback calls rerecorded at different distances from the sound source were analyzed with a

286 PC computer fitted with a Data Translation 2821 board. Fast Fourier transform of the signals was done with a J. Dempster software package modified for the requirements of our study. The frequency range of the spectrograms was 20–5000 Hz, and the frequency resolution 20 Hz.

#### Statistical analysis

Kruskal-Wallis one-way ANOVA ( $P < 0.05$ ) was used to test for statistical differences among species in the following acoustical parameters of the advertisement calls recorded in the field: peak SPL (dB), dominant frequency (Hz), frequency of secondary spectral peak (Hz), relative amplitude of spectral peaks (dB). This statistic was also used to assess the significance of differences in SPLs of nearest neighbors' calls and in distances between nearest neighbors among the five species. The statistical significance of correlations between the acoustical parameters analyzed and snout-vent length and body mass of the frogs whose calls were recorded was assessed with Pearson's correlation coefficient ( $P < 0.05$ ).

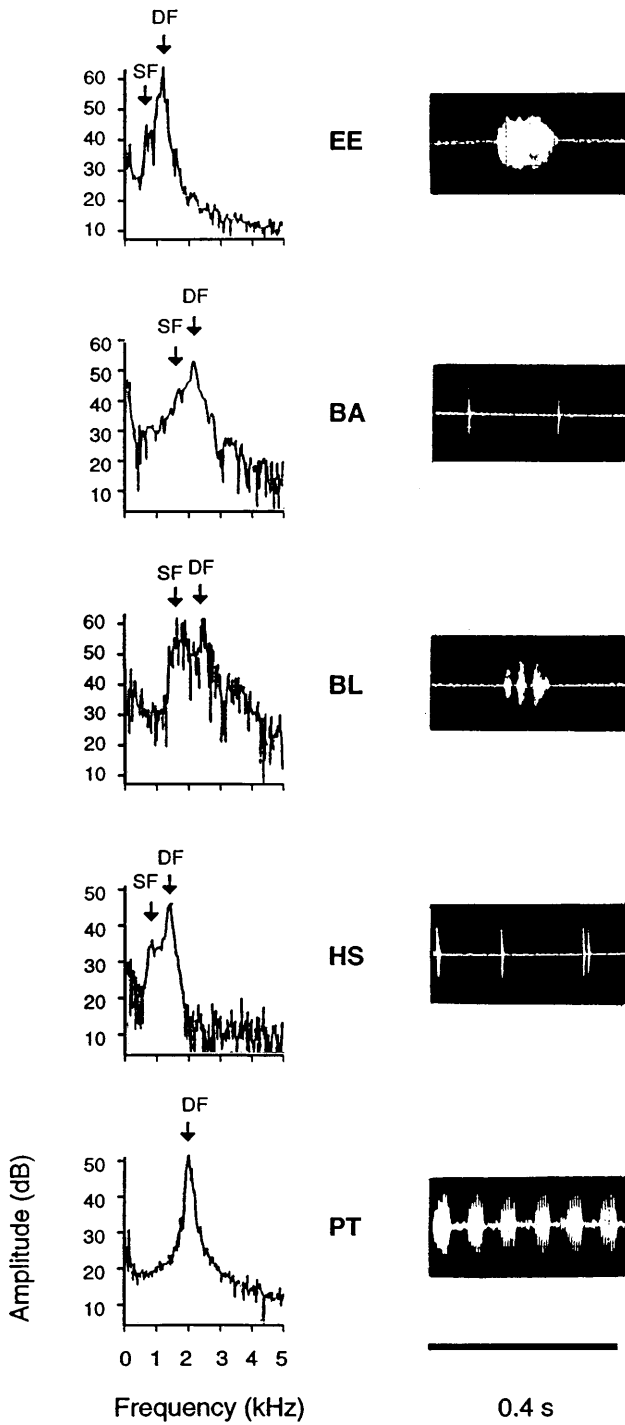
## Results

### Call SPLs, spectra, and spacing patterns

Males of the species studied occupied different calling sites within the temperate forest region in southern Chile. *E. emiliopugini*, *B. antartandica*, and *B. leptopus* called from burrows along the borders of small streams in bogs, while *H. sylvatica* and *P. thaul* called from the water surface in marshes. Descriptions of the temporal structure of the advertisement calls of these frogs are given in Penna and Veloso (1990), Penna and Solís (1996), and Penna (1997). A dominant frequency is evident in the spectra of the calls of all five species, and a secondary spectral peak occurs at lower frequencies in all species but *P. thaul*. Oscillograms and spectrograms of the calls of the five species studied are shown in Fig. 1. SPLs of the calls produced by an individual during a bout of calling, measured at 0.5 m in front of the frog, were generally stable, varying within  $\pm 2$  dB. SPLs differed considerably among individuals within a species, encompassing ranges of 16, 15, 13, 8, and 10 dB in *E. emiliopugini*, *B. antartandica*, *B. leptopus*, *H. sylvatica*, and *P. thaul*, respectively (Table 1).

Significant differences occurred among the SPLs of the calls of the five species (Kruskal-Wallis test,  $P < 0.05$ ). *E. emiliopugini* and *H. sylvatica* had the lowest and highest peak SPLs, respectively (Table 1). Call spectra also differed among the five species: *E. emiliopugini* and *B. leptopus* had the lowest and highest dominant frequencies, respectively (Table 1). The Kruskal-Wallis test yielded significant differences ( $P < 0.05$ ) for the dominant frequency and for the secondary frequency peak among species.

For *P. thaul*, the dominant frequency of the call was significantly correlated with snout-vent length ( $r = -0.871$ ,  $P < 0.02$ ,  $n = 7$ ) and body mass ( $r = -0.876$ ,  $P < 0.01$ ,  $n = 7$ ). The SPL of the call was not significantly correlated ( $P > 0.05$ ) with the body attributes for this species. No significant correlations were found be-



**Fig. 1** Power spectra and oscillograms of the advertisement calls of five leptodactylid frogs from the South American temperate forest. (*EE* *Eupsophus emiliopugini*, *BA* *Batrachyla antartandica*, *BL* *B. leptopus*, *HS* *Hylorina sylvatica*, *PT* *Pleurodema thaul*, *DF* dominant frequency peak, *SF* secondary frequency peak). Oscillograms show entire calls of *E. emiliopugini*, *H. sylvatica*, and *B. leptopus*, two pulses of the call of *B. antartandica*, and six notes of the call of *P. thaul*

tween the dominant frequency of the calls or SPL and snout-vent length or body mass for conspecific individuals of *E. emiliopugini*, *B. antartandica*, *B. leptopus*, and *H. sylvatica*. This lack of covariance is likely due to the

**Table 1** Body sizes and weights, recording temperatures, sound pressure levels (SPLs) at 0.5 m and spectral parameters of the advertisement calls of five species of frogs from the South American temperate forest. Numbers of individuals correspond to animals for which body size and weight, SPLs, and spectral parameters were measured respectively. Data listed are averages, with ranges in parentheses. Relative amplitude of frequency peaks corresponds to the difference: dominant frequency peak–secondary frequency peak (*A* air, *S* substrate)

Species	Locality	Temperature (°C)	Number of individuals	Snout-vent length (mm)	Body mass (g)	Peak sound pressure level (dB SPL)	Dominant frequency peak (Hz)	Secondary frequency peak (Hz)	Relative amplitude of frequency peaks (dB)
<i>Eupsophus emiliopugini</i>	La Picada	5.3–10.4	5/11/13	47.8 (45.5–50.1)	11.5 (9.8–14.5)	82.6 (71.9–87.9)	971 (645–1222)	651 (449–912)	4.9 (–10.0–16.7)
	Puyehue, Río Chaicas	2.9–11.1	5/15/15	35.1 (31.9–36.7)	3.4 (2.1–3.9)	95.1 (86.2–100.7)	2092 (1701–2333)	1585 (1056–1929)	10.3 (4.6–19.3)
<i>B. leptopus</i>	Cucao	5.5–12.8	3/8/8	28.2 (26.9–29.5)	1.8 (1.6–1.9)	89.5 (80.3–93.4)	2445 (2183–2612)	1904 (1668–2053)	5.4 (–0.75–13.0)
	Puyehue, La Picada	4.7–10.2	4/6/8	57.1 (52.6–62.7)	14.2 (10.1–19.3)	109.2 (105.1–113.0)	1358 (1048–1596)	752 (502–886)	9.4 (–2.56–14.7)
<i>Pleurodema thaul</i>	Agua Buena, La Picada	7.0–13.1	7/15/13	31.7 (27.5–39.9)	3.7 (2.4–7.1)	97.2 (91.6–101.1)	2002 (1636–2161)		

small sample sizes of individuals for which the physical attributes were measured ( $n = 3\text{--}5$  per species; see Table 1).

Across species, significant correlations were found between average snout-vent length and average dominant frequency, and between body mass and average dominant frequency calculated for each species from individuals whose body attributes were measured ( $r = -0.879$ ,  $P < 0.05$ ,  $n = 5$  and  $r = -0.927$ ,  $P < 0.05$ ,  $n = 5$ , respectively). No significant correlations ( $P > 0.05$ ) occurred between the averages of body attributes versus average call SPLs for each species.

Males of the different species showed distinct spacing patterns in breeding aggregations. Minimum distances between nearest calling neighbors varied considerably within and among species (Table 2). Males of *B. antartandica* and *B. leptopus* were spaced at average interindividual distances of about 1 m, males of *E. emiliopugini* were spaced at average distances of 1.7 m, whereas males of *P. thaul* were found at distances above 2 m apart. *H. sylvatica* males were also typically spaced at distances of above 2 m, as exemplified by the two cases measured for this species. Distances between conspecific neighboring males varied widely, as shown by the coefficients of variation for this measure (Table 2). The maximum SPLs of the neighbors' calls at the position of a calling male varied considerably within a species. Ranges for this measure spanned from 11 dB in *H. sylvatica* to 32 dB in *E. emiliopugini*. These differences, however, were smaller than ranges for distances among nearest neighbors, as can be seen by comparing the coefficients of variation between both measures. Nearest neighbor's distances and nearest neighbor's SPLs varied significantly among the five species (Kruskal-Wallis test,  $P < 0.05$  for both measures).

## Sound propagation experiments

### Pure tones

Tests of sound propagation showed that pure tones of frequencies above about 1 kHz experienced higher rates

of attenuation across bogs than across the marsh surface. Negative excess attenuation values were measured at 1, 2, 4, and 8 m for most frequencies tested at the marsh (Fig. 2). Propagation of pure tones across bog surfaces followed a different pattern; excess attenuations for frequencies above about 1 kHz increased steadily with distance, from 1 to 8 m from the loudspeaker. Maximum excess attenuations of 20–30 dB were measured at 8 m in bogs A and B. In bog C, SPLs of tones between 2.2 kHz and 2.8 kHz and above 1.6 kHz could not be measured at 4 and 8 m from the loudspeaker, respectively, due to high levels of low-frequency background noise at this site, situated about 1 km from the seashore (Fig. 2C, D).

### Playback calls and white noise

The vocalizations used for the experiments on sound propagation were an entire single-note call of *E. emiliopugini*, an entire four-note call of *H. sylvatica*, two pulses of a call of *B. antartandica*, and an entire three-note call of *B. leptopus*. Peak SPLs measured for six repetitions of a given playback call showed little variation at 0.5, 1, 2, and 4 m from the loudspeaker in the four test sites. For 64 presentations of six single-call repetitions (four single calls at four distances in the four test sites), 61 presentations yielded differences in SPL readings that were within  $\pm 1$  dB. Differences higher than 2 dB were measured only for *B. antartandica* at 0.5 m in bog A, *H. sylvatica* at 2 m in bog C, and *B. leptopus* at 4 m in bog C. At 8 m from the source, for 15 presentations of six single-call repetitions (four single calls in four test sites, excluding the call of *B. leptopus* in bog C), 11 presentations yielded differences in SPL readings that were within  $\pm 1$  dB. Differences higher than 2 dB were measured for *H. sylvatica* and *B. leptopus* in the marsh, and *B. antartandica* in bogs A and C. The highest difference for repetitions of a single call was 3.3 dB for *B. antartandica* at 8 m in bog C.

Attenuation of playback calls followed patterns concordant with measurements of pure tones. In the marsh, slightly negative excess attenuations occurred for

**Table 2** Nearest distances and sound pressure levels of nearest neighbor's calls at the position of calling males in five leptodactylid frogs from the South American temperate forest. Numbers of in-

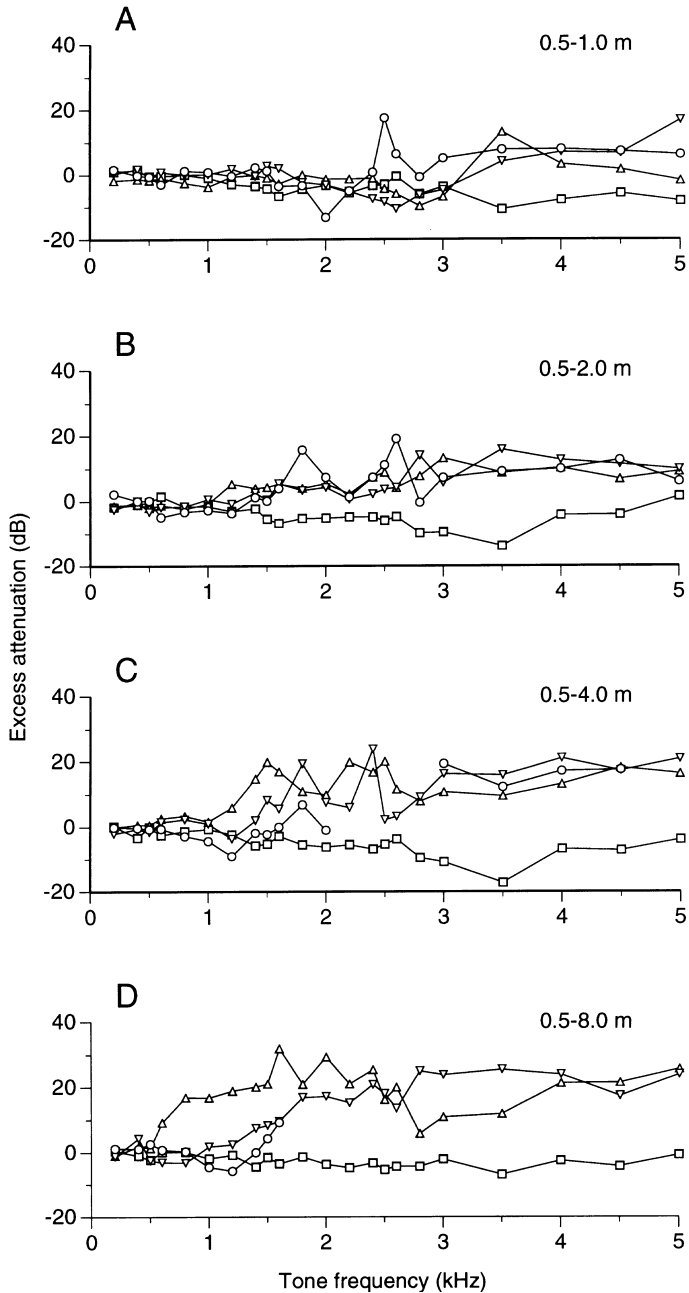
dividuals correspond to focal males for which distance and call sound pressure level of the nearest neighbor were measured, respectively. Data correspond to averages, with ranges in parentheses

Species	Number of individuals	Nearest distances (m)	Coefficients of variation (%)	Peak sound pressure levels (dB SPL)	Coefficients of variation (%)
<i>Eupsophus emiliopugini</i>	8/8	1.75 (0.2–3.9)	89.1	80.3 (58.2–90.0)	15.4
<i>Batrachyla antartandica</i>	8/8	1.00 (0.6–1.7)	46.0	85.3 (75.7–89.4)	5.3
<i>Batrachyla leptopus</i>	9/9	1.04 (0.4–1.6)	49.2	80.5 (74.8–89.4)	5.5
<i>Hylorina sylvatica</i>	2/7	2.35 (2.0–2.7)	–	89.7 (84.6–95.6)	3.9
<i>Pleurodema thaul</i>	6/6	3.27 (1.9–4.7)	30.4	81.1 (67.0–86.3)	8.8

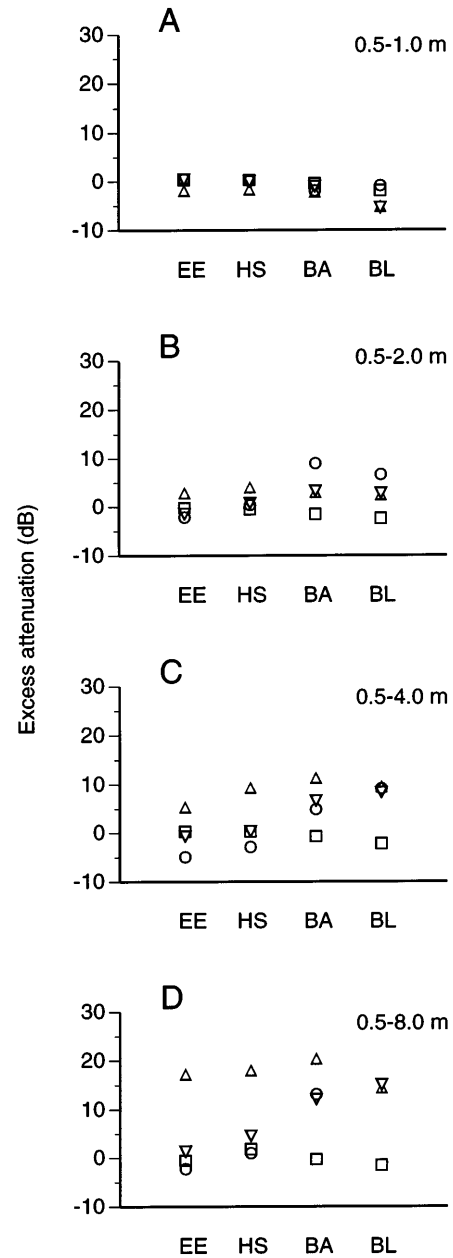
the calls of the four species tested at all distances from the sound source. For the experiments conducted in the bog environments, excess attenuations increased steadily with distance, from 1 to 8 m from the sound source. In bog A, excess attenuations of about 10 dB and 20 dB occurred for all four calls at 4 and 8 m, respectively. In bogs B and C, the calls of the two *Batrachyla* species, with high dominant frequencies, also experienced rela-

tively high attenuation rates. However, in these two sites, the calls of *E. emiliopugini* and *H. sylvatica*, with lower dominant frequencies, were propagated at rates similar to those observed in the marsh, with excess attenuation values close to 0 dB (Fig. 3).

White noise broadcast across bog environments showed spectral changes that followed the patterns measured with pure tones, with attenuation of high



**Fig. 2** Propagation of pure tones in different habitats: marsh (squares), bog A (standing triangles), bog B (inverted triangles), and bog C (circles). Excess attenuations measured at 1(A), 2(B), 4(C) and 8(D) m relative to SPLs at 0.5 m from the loudspeaker. Excess attenuations in bog C at 4 and 8 m from the loudspeaker were not measured for frequencies between 2.2 and 2.8 kHz and above 1.6 kHz, respectively, due to high levels of background noise (see Results)



**Fig. 3** Excess attenuation of playback calls of four species in different habitats measured at 1, 2, 4, and 8 m relative to SPLs at 0.5 m from the loudspeaker. Symbols indicate different test sites as in Fig. 2. Each symbol represents an average for six repetitions of a call. Abbreviations of species names as in Fig. 1. Species on the horizontal axis follow an order of increasing dominant frequency. Excess attenuation of the call of *B. leptopus* was not measurable at 8 m in Cucao due to high levels of low-frequency background noise (see Results)

frequencies in the three bog sites. Power spectra of the broadcast white noise measured 8 m from the sound source showed a relatively flat frequency response in the marsh, and low-pass functions for the three bog sites, with a cutoff frequency that was manifestly lower for bog A than bogs B and C (Fig. 4).

The different spectral components of the calls, i.e., the dominant frequencies and the secondary frequency peaks, experienced attenuation rates that differed between bogs and marsh. Spectra were obtained from the entire single-note call of *E. emiliopugini*, the first note of the four-note call of *H. sylvatica*, the second of two call notes of *B. antartandica*, and the second note of a three-

note call of *B. leptopus*. Power spectra of the four natural calls rerecorded at 0.5 and 8.0 m from the loudspeaker in the four test sites are shown in Fig. 4. The call of *B. antartandica* used for sound propagation experiments did not have a clear secondary spectral peak as typically observed in this signal (see Fig. 1). The amplitude of this component was measured in a small deflection observed in the spectra at about 1250 Hz. This value is within the range of the secondary frequency peak of the call of this frog (Penna et al., 1997b). The positions of the spectral peaks were relatively constant for playback calls rerecorded at different distances from the sound source. For 16 comparisons (four calls in the four test sites), the shift of the secondary frequency peak along the frequency axis was on average 19.6 Hz (range = 0–79 Hz), and the shift of the dominant frequency peak was on average 63.0 Hz (range = 0–195 Hz).

The differences between the ratios, amplitude of the dominant frequency peak/amplitude of the secondary frequency peak, measured at 8.0 and 0.5 m are listed in

**Fig. 4** Power spectra of broadcast white noise and playback calls recorded at 0.5 and 8.0 m from the loudspeaker in different habitats. Abbreviations of species names as in Fig. 1 (WN white noise). Arrows indicate dominant frequency peak and secondary frequency peak for each spectrum. Species follow an order of increasing dominant frequency from top to bottom. Maxima amplitudes of the power spectra do not represent the absolute levels of the signals

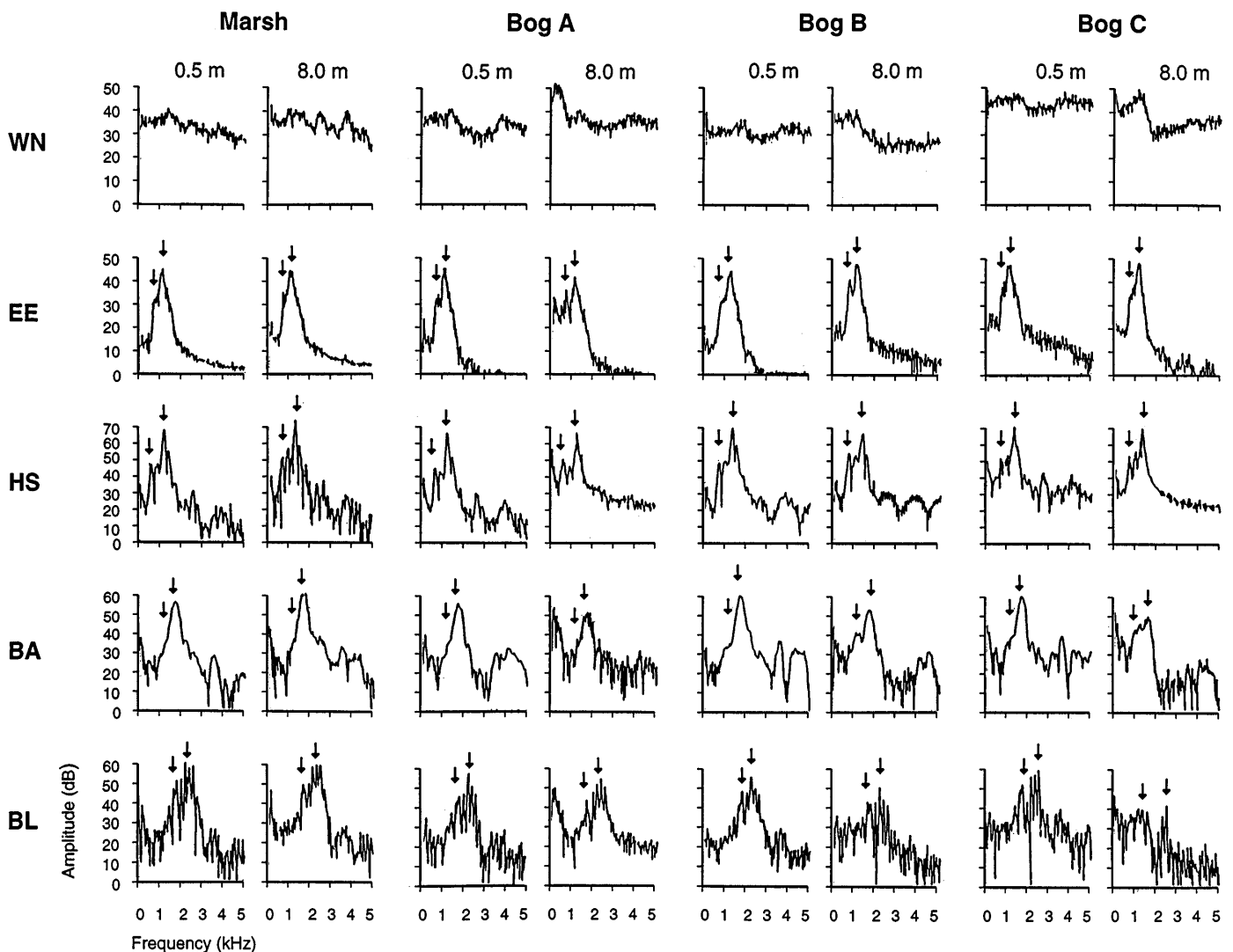


Table 3. In the marsh, the amplitude of the dominant frequency peak relative to the secondary spectral peak of all the four calls at 8.0 m was similar to the ratio observed in the power spectra recorded at 0.5 m from the loudspeaker. In contrast, in the three bog sites, the calls of *E. emiliopugini*, *H. sylvatica*, and *B. antartandica* experienced predominantly a decrease in the amplitude of the dominant frequency peak relative to the amplitude of the secondary frequency peak, as indicated by the negative sign of these differences. However, the relative amplitudes of the frequency peaks of the call of *B. leptopus* at 8.0 m were similar to those measured at 0.5 m in the bog sites.

Background noise measured during 1-min periods before the experiments of sound propagation yielded maxima RMS SPL (fast-weighting scale) and peak SPL values of 56.2 dB and 62.6 dB in the marsh, 48.3 dB and 59.3 dB in bog A, 42.6 and 50.8 dB in bog B, and 66.7 dB and 74.9 dB in bog C.

## Discussion

### Call SPLs and spectra, and spacing patterns

SPLs of the calls of the frogs from the South American temperate forest analyzed in this study show ranges of variation comparable to those reported for vocalizations of anurans from other continents. The calls of *H. sylvatica* have the highest SPLs among the species studied, reaching about 110 dB peak SPL at 0.5 m. This level is within the range of SPLs measured for a number of North American and African frogs (Gerhardt 1975; Passmore 1981). The call of *E. emiliopugini* has the lowest SPLs among the five species studied, reaching about 80 dB peak SPL. This level is similar to the lowest values reported for Australian and North American frogs (Loftus-Hills and Littlejohn 1971; Gerhardt 1975).

**Table 3** Differences between the ratio (amplitude of the dominant frequency peak/amplitude of the secondary frequency peak) of power spectra of playback calls measured at 8.0 m and at 0.5 m from the sound source. Positive and negative values indicate increases and decreases of the amplitude of the dominant frequency peak relative to the amplitude of the secondary frequency peak, respectively. Species are listed in order of increasing dominant frequency

Species	Habitat			
	Marsh	Bog A	Bog B	Bog C
<i>Eupsophus emiliopugini</i>	-3.3	-7.8	-6.4	4.6
<i>Hylorina sylvatica</i>	1.2	-4.2	-9.2	-2.6
<i>Batrachyla antartandica</i>	3.3	-5.4	-12.2	-17.4
<i>Batrachyla leptopus</i>	1.0	-0.4	0.7	5.2

Variation in call SPLs among species of the South American temperate forest is not related to differences in body size between these species. A lack of relationship between these two variables has also been reported to occur in other anuran groups (Gerhardt 1975; Passmore 1981). Anatomical and functional differences in the vocal apparatus between taxa may have a predominant influence on the intensity of vocalizations.

Call SPLs measured 0.5 m in front of the emitter varied widely among individuals within a species. Ranges for this measure among conspecific individuals of *E. emiliopugini*, *B. antartandica*, and *B. leptopus* were 16, 15, and 13 dB, respectively (see Table 1). Such dispersion is probably related to the heterogeneity of the substrate of bogs from which these species call, in which grasses, mosses, and ferns are distributed in patches along the borders of small streams. The SPLs of the calls of *H. sylvatica* and *P. thaul* showed a narrower range of variation among conspecific individuals (8 and 10 dB, respectively; see Table 1). This relative uniformity is associated with the homogeneous quality of marshes, where sound propagates over a continuous water surface with sparse emergent vegetation.

Distances among calling conspecific males differ between frogs inhabiting marshes and bogs. Nearest neighbors of the marsh species *H. sylvatica* and *P. thaul* usually space further than 2 m. Such sparse distributions are related to the better properties for sound propagation of water surface. In contrast, males of *B. antartandica* and *B. leptopus* typically space at distances shorter than 1 m between conspecific neighbors. This clumping would facilitate the detection of neighbors' signals, in spite of the high attenuation rates affecting the calls of these frogs in bog environments. Neighbors of *E. emiliopugini* distribute at longer average distances than males of the two *Batrachyla* species. Such a broader spacing is associated with the production of low-frequency calls that experience less excess attenuation in these environments. Furthermore, calls of neighboring frogs are amplified inside the burrows occupied by males of *E. emiliopugini* (Penna and Solís 1996), thus providing an additional means to increase the efficiency of acoustic communication in sound-attenuating bogs.

In the frogs studied, differences in distances between conspecific neighbors are large relative to differences in SPLs of the calls of neighbors at the position of other males, as indicated by the coefficients of variation for both measures. This suggests that males in breeding aggregations space themselves in order to maintain the intensities of neighbors' calls at a certain level, as has been reported to occur in North and Central American frogs (Brenowitz et al. 1984; Wilczynski and Brenowitz 1988; Brenowitz 1989; Gerhardt et al. 1989).

The maximum SPLs of neighbors' calls at the position of calling males are on average above 80 dB for the five species analyzed. These values are likely to be well above frogs' auditory thresholds. The only species considered in this study for which electrophysiological measurements have been conducted is *P. thaul*. Auditory



midbrain neurons of this frog tuned to the range of the dominant frequency of its advertisement call have minimum thresholds of about 30 dB SPL peak (Penna et al. 1997a). It is probable that auditory thresholds of the other frogs considered in this study are also well below 80 dB SPL. Electrophysiological recordings of multiunit auditory responses in the midbrain of a number of anurans have reported thresholds below 60 dB SPL at frequencies of the mating calls (Loftus-Hills 1973; Lombard and Straughan 1974; Hubl and Schneider 1979; Walkowiak 1980; Walkowiak et al. 1981; Penna et al. 1990; Diekamp and Gerhardt 1993).

Behavioral studies with the North American frogs *Pseudacris crucifer* (Gerhardt et al. 1989) and *Hyla regilla* (Brenowitz 1989) are in agreement with our results and with electrophysiological studies. These authors have shown that SPLs of neighbors' calls at the position of focal males are well above the auditory thresholds of these species. The efficient auditory sensitivity of different anurans in the frequency range of their advertisement calls is likely to facilitate communication in unfavorable environments.

The SPLs of neighbors at the position of a calling frog are higher for *H. sylvatica* than for the other four species. SPLs of neighbors' calls reported in the literature also show differences between species. Average RMS SPLs of nearest-neighbors' calls range from 64.4 dB in the Central American treefrog *Eleutherodactylus diastema* (Wilczynski and Brenowitz 1988) to about 100 dB in the North American frog *P. crucifer* (Gerhardt et al. 1989). Peak SPLs of nearest neighbors have been measured for two Australian myobatrachids *Geocrinia laevis* and *G. victoriana*, and average 93.5 and 102.5 dB, respectively (Harrison and Littlejohn 1985; Littlejohn and Harrison 1985). The diverse intensities to which males of different species are exposed may reflect differences in the sensitivities of their auditory systems. However, neighbors' call SPLs of two allopatric populations of *P. crucifer* in North America have been reported to differ by about 20 dB (Brenowitz et al. 1984; Gerhardt et al. 1989). Such differences in call intensities between populations of the same species suggest that acoustic interactions adjust to densities of breeding aggregations.

### Sound propagation and habitat

The experiments on sound propagation show a trend for the calls of the four species tested to propagate more efficiently in marsh than in bog habitats. The calls of *H. sylvatica* and *P. thaul* experience low attenuation and degradation across the marshes and large pools where these frogs breed. *H. sylvatica* is particularly well adapted for communicating across long distances; males produce the most intense advertisement call among the species analyzed.

In contrast with *H. sylvatica* and *P. thaul*, the three species that breed in bogs call from an environment

across which propagation of frequencies above about 1 kHz is substantially impaired. The calls of the two species of *Batrachyla* are particularly affected, because of their high dominant frequencies. The lack of an optimal relationship between dominant frequencies and physical properties of the environment for sound transmission suggests that no strong environmental selective pressures have contributed to shaping the spectral design of the advertisement calls of these frogs. An optimal relationship between call structure and habitat is also lacking for subspecies of the North American cricket frog *A. crepitans* from open and forested habitats (Ryan et al. 1990).

Correlations between spectral composition of sounds of long-distance communication and habitat characteristics have been shown to occur in birds. Species from forested habitats produce songs that are lower pitched than those sung by birds in open sites (Chappuis 1971; Morton 1975; Bowman 1979; Hunter and Krebs 1979; Wasserman 1979; Shy 1983; Ryan and Brenowitz 1985; Sorjonen 1986a,b; Waas 1988; Smith and Yu 1992). Such differences in the signals accord with the distinct frequency-filtering properties of these habitats (e.g., Marten and Marler 1977; Marten et al. 1977). Broadcast experiments with playback songs of birds from different environments have revealed further correspondences between call characteristics and habitat (Gish and Morton 1981; Cosens and Falls 1984; Sorjonen 1986a,b).

The occurrence of optimal relationships between signal structure and habitat indicate that environmental selective pressures have influenced the evolution of bird songs. By preserving their structure across long distances, birds' vocalizations are perceived by receivers as coming from nearby and thus constitute effective threatening signals for rival males (Morton 1982; Shy and Morton 1986).

Various vertebrates are sensitive to degradation experienced by propagating sounds. Degraded characteristics of vocalizations are used to assess neighbors' distance by certain avian species (Richards 1981; McGregor and Falls 1984; McGregor and Krebs 1984). Frogs can also use degradation of spectral cues to orient towards the sound source. The green treefrog *Hyla cinerea* has an advertisement call with two frequency peaks, and females are attracted at very low SPLs (which mimic long distances from the emitter) by just the low-frequency component of the call. At higher SPLs of the signal (i.e., close to the emitter), females prefer calls that have both low- and high-frequency peaks (Gerhardt 1976, 1981). In addition to spectral changes affecting broadcast signals, degradation of temporal structure has been shown to occur for vocalizations of two North American species of *Bufo* (Ryan and Sullivan 1989). This distortion of signal structure could provide listeners with additional cues to locate the sound source.

The structure of acoustic signals is under influences other than environmental. Zimmerman (1983) has shown that phylogenetic relationships account for dif-

ferences in call structure between Amazonian frogs from open and forested habitats. However, an exhaustive assessment of the effect of phylogeny on call diversity in the South American temperate forest is precluded by the small number of anuran species found in this region compared to tropical environments. Furthermore, a number of species from southern Chile do not produce advertisement calls (Penna and Veloso 1990).

Size is a major factor affecting the spectra of calls; small animals are constrained to produce high-frequency signals despite the disadvantages of such spectral design for propagation in most terrestrial environments. Anurans from the South American temperate forest are no exception to this rule: a strong correlation exists between body size and dominant frequency of the advertisement calls of the different species of this region (see Results and Penna and Veloso 1990). Most of these frogs produce calls having dominant frequencies above 1 kHz, and transmission of their calls across the extensive bog areas in southern Chile is thus limited. However, the differences in frequency filtering between the three bogs analyzed indicate that calling sites with diverse properties for sound broadcast are available for callers within a given habitat.

Overall, our study of calls of five frog species from southern Chile shows that these signals are more efficiently transmitted in the marsh habitat, irrespective of the frogs' native environment. This mismatch between call structure and habitat supports the notion that broadcasting signals at the longest possible distances is not necessarily a condition to be met in the design of advertisement calls of anurans. Such lack of optimization is conceivably related to restrictions on dispersion of these vertebrates, which are dependent on water availability. Frogs communicating in environments unfavorable for sound transmission may rely on high densities of breeding aggregations and on effective auditory sensitivities for detection and recognition of signals of biological importance.

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