Frequency-Modulated Vocalizations of *Eupsophus queulensis* (Anura: Cycloramphidae)

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Abstract.—The advertisement calls of the recently described frog *Eupsophus queulensis* (Cycloramphidae) are analyzed, based on recordings of seven males. *Eupsophus queulensis* emits an advertisement call consisting of a harmonic-rich frequency modulated note, with dominant second and third harmonics. The temporal parameters of the calls had large intra- and interindividual variation relative to the spectral parameters. The frequency modulations follow four different patterns, as described previously for *Eupsophus calcaratus* and *Eupsophus roseus*. Individual frogs produce calls having different frequency modulation patterns, and the proportions of each pattern vary individually. A discriminant analysis positions the calls of *E. queulensis* closer to *E. roseus* than to *E. calcaratus*, which is congruent with the geographic and phylogenetic affinities, as well as with the relative body sizes of these taxa.

Anurans have been used as models for acoustic communication studies because of their limited vocal repertoires and the stereotyped responses that these signals evoke as compared to birds and mammals (Gerhardt and Huber, 2002). However, recent work has reported rich vocal repertoires and complex vocalization patterns for some anuran species. For example, males of the endemic Madagascar Treefrog, *Boophis madagascariensis*, have a hyperextended vocal repertoire, with 28 call types differing both in temporal and spectral features (Narins et al., 2000). The Chinese frog, *Amolops tormotus*, produces vocalizations having high individual variability with conspicuous frequency modulations, including ultrasonic components, which expand the frequency range formerly attributed to anuran sound communication (Feng et al., 2002, 2006).

Various studies have shown that anuran advertisement calls are modified during interactions with conspecific or heterospecific neighbors (e.g. López et al., 1988; Wells, 1988; Schwartz et al., 2002) and when confronted with abiotic sources of acoustic interference (Narins, 1982; Dubois and Martens, 1984; Penna et al., 2005). In particular, species inhabiting stream environments having high noise levels produce calls containing high frequencies beyond the noise spectral range or remarkable frequency modulations (Penna et al., 1983; Dubois and Martens, 1984; Feng et al., 2002).

Frog species of the cycloramphid genus *Eupsophus*, endemic inhabitants of stream envi-

ronments in the South American temperate forest, are divided in the *Vertebralis* and *Roseus* groups (Formas, 1991; Formas et al., 1992; Cuevas and Formas, 1996), with species of the *Roseus* group producing frequency-modulated advertisement calls (Formas, 1985; Penna and Veloso, 1990; Formas and Brieva, 1994). Márquez et al. (2005), in a comparative study on the vocalizations of *Eupsophus roseus* and *Eupsophus calcaratus*, reported a high variability in the frequency modulation patterns of their advertisement calls, with four different call types within each population.

The phylogenetic status of *Eupsophus queulensis* within the genus has not been clarified, although relevant comparative cytogenetic, morphologic and bioacoustic evidences have been reported for some species of this genus (Formas, 1992, 1993; Formas et al., 1992). Veloso et al. (2005) suggested the affinity of *E. queulensis* with *E. calcaratus* within the *Roseus* group on the basis of 12S mtDNA sequences. However, in a recent study of the phylogenetic relationships of Chilean leptodactylids, Correa et al. (2006) positioned *E. queulensis* closer to *E. roseus* than to *E. calcaratus* within the *Roseus* group, in agreement with the proximity of the geographical distributions of both species.

In this study, we describe the advertisement call of *E. queulensis* in natural settings, analyzing individual variation in its frequency modulation patterns, an issue that has not been addressed in the literature on anuran sound communication. In addition, we compare these vocalizations with those described for the related species *E. roseus* and *E. calcaratus*, to contribute to the understanding of the phylogenetic relationships within this group. Because the frogs call along

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creeks, we also characterized the background noise produced by the fast flowing water.

MATERIALS AND METHODS

Advertisement calls of *E. queulensis* were recorded in the National Reserve Los Queules, VII Region, Chile (35°37′S, 72°21′W) on 18 October 2003. Advertisement calls emitted by seven males calling from inside burrows along the borders of a creek were recorded with a directional microphone (Sennheiser ME 66) at an estimated distance of 0.5–1.0 m from the burrow openings and stored on a digital recorder (Sony TC D10 PROII). Background noise produced by the creek was also recorded at the position of one burrow opening with an omnidirectional microphone (Realistic 33-3303, 8 mm diameter, 16 mm length). This microphone was calibrated before recording the background noise with a sound calibrator (Brüel and Kjær 4230), by fitting the microphone into the calibrator with a plastic bearing that adapted the 8-mm microphone diameter to the 12.5-mm opening of the sound calibrator. The 1-kHz tone produced by this device, having a root-mean-square sound pressure level (RMS SPL) of 93.8 dB, was recorded, and subsequently, the creek noise was recorded using the same recording level as for the calibration tone to calculate the noise RMS SPL. Air and substrate temperatures during the field recordings were 8.8–9.7°C and 11.4–12.0°C, respectively.

Vocalization and noise recordings were digitized with a Macintosh G4 computer using Peak 2.5.2 software at a 44.1 kHz sampling rate, using an anti-aliasing filter (FT6-2, Tucker-Davis Technologies) and an analog-digital interface (Motu 828). Oscillograms and power spectra (512 points, filter bandwidth 124 Hz) were obtained using the Raven 1.2 software (Cornell Laboratory of Ornithology) for at least 20 calls per subject. The parameters measured were as follows: (1) call duration (time from call onset to call end); (2) rise time proportion (time from call onset to time at which the peak amplitude occurred, expressed as percentage of the total call time); (3) lowest frequencies of the second and third harmonics (LF2 and LF3); (4) highest frequencies of the second and third harmonics (HF2 and HF3); and (5) intercall period (time between the onset of two successive calls). In addition, we established a frequency modulation pattern (FM) for each call analyzed. This was analyzed by measuring the frequency of the second harmonic in power spectra taken at three different times as follows: T_1 was within the first 10th of the total duration of the signal; T_2 was within the midportion of the signal, either at about the maximum amplitude or at the maximum of the second harmonic if this occurred within this time period; and T_3 was within the last 10th of the total duration of the signal. Frequency modulated calls were considered to occur when the value of the second harmonic differed by at least 7% between any of the frequency measurements at T_1, T_2, and T_3. This percentage was chosen because it provided a reliable estimate of the shape of the sonograms. We used the second harmonic for this analysis because in most cases this was the spectral component having the largest amplitude. The calls were classified following the four FM patterns defined by Márquez et al. (2005) for *E. calcaratus* and *E. roseus*: upward-downward (UD); upward (U); downward (D); and flat (F). To compare intraindividual versus interindividual variation, we calculated coefficients of variation (CV = $100 \times$ SD/mean) for the different call parameters within (CV_w) and among (CV_a) individuals (Márquez et al., 2005; Pröhl et al., 2007).

The spectral parameters of the advertisement calls of *E. queulensis* were compared to those of *E. calcaratus* and *E. roseus* reported by Marquez et al. (2005) with a discriminant analysis (Statistica version 6.0). The canonical scores obtained for each species were compared with a one-way ANOVA. In addition, the sizes of the three species were compared with a one-way ANOVA. For this purpose, the snout–vent lengths (SVL) were measured in a sample of 18 males of *E. roseus* and 18 *E. calcaratus* from the localities where the calls of these species were recorded by Márquez et al. (2005). The sample of *E. queulensis* corresponds to the SVL reported for seven males by Veloso et al. (2005). Means are given ± 1 SD.

RESULTS

At the study site, males of *E. queulensis* called from inside burrows along the borders of a stream that produced considerable background noise. Advertisement calls were the only vocalizations heard at the study site and consisted of single notes rich in harmonics (Fig. 1), with different FM patterns (see below). In most vocalizations, the harmonics having the highest amplitudes corresponded to the second and third. The fourth and fifth harmonics were also clearly identified in most of the calls analyzed. However, the fundamental frequency had a very small amplitude (except in individual number 1) and, therefore, was not subjected to analysis. In the calls of individual number 1, the fundamental frequency was modulated between an average lowest and highest frequency of 532.0 ± 13.4 Hz and 611.9 ± 10.9 Hz, respectively. The acoustic parameters analyzed
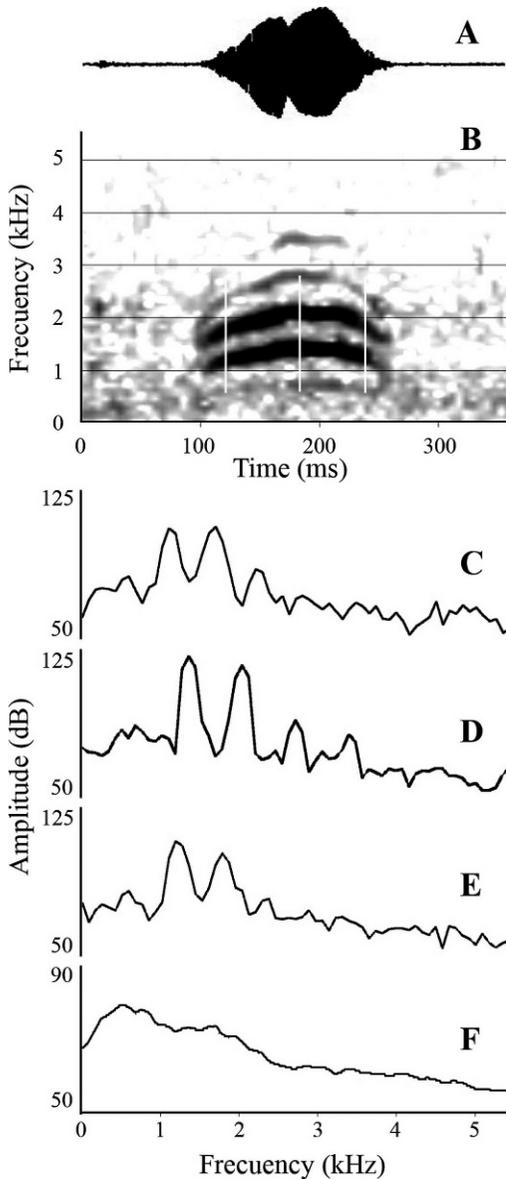
FIG. 1. Oscillogram (A), sonogram (B), and power spectra (C, D, and E) of an advertisement call of *Eupsophus queulensis*. Power spectra were taken at the times indicated by the white bars in (B). An averaged power spectrum of the background noise averaged over 4 sec, at an interval during which no frogs were calling in the vicinity produced by the creek is also shown (F). Filter bandwidth for the sonogram and power spectra was 124 Hz and FFT size 512 points.

for the advertisement calls of seven individuals are listed in Table 1.

The dominant harmonic of individual calls was calculated from the average amplitude of the most prominent spectral components (second and third) at T_1, T_2, and T_3. The second was

the dominant harmonic for three animals (1, 2, and 3) in all the calls analyzed. This spectral peak was also dominant in 90.0% and 88.0% of the calls analyzed for two other individuals (4 and 6, respectively), and the third harmonic was dominant in 80.0% and 73.3% of the calls of two individuals (5 and 7, respectively). Overall, for 151 of the 197 calls analyzed (76.7%), the second harmonic had the largest amplitude, whereas for 46 calls (23.3%), the third harmonic had the largest amplitude.

Intraindividual variations of the measured temporal parameters (CV_w: 7.6, 17.7, and 83.2%, for call duration, rise time, and intercall period, respectively) were greater than those of the spectral parameters, all having CV_w below 7%. Interindividual variations of the temporal parameters (>20%) were also greater than those of the spectral parameters (<11%). Intercall period had the largest CV_a and CV_w ($CV > 80\%$). The $CV_a : CV_w$ ratios for most of the acoustic parameters were slightly above 1, with the exception of call duration, having a ratio of about 3 (Table 1).

The four FM patterns of the calls occurred in different proportions in the males of *E. queulensis* analyzed (Fig. 2). For five of seven individuals, the UD pattern was the most common, ranging between 56.5% and 95.0% of its calls, whereas for the other two individuals, the U and the D patterns predominated (63.3% and 76.7% of its calls, respectively). Overall, the highest proportion (62.4% of the calls) corresponded to the UD modulation pattern, whereas the U, D, and F modulation patterns occurred in 17.3%, 16.2%, and 4.1% of the calls analyzed, respectively. As presented in Table 2, one frog produced calls having the four FM patterns, three frogs emitted three FM patterns, and three frogs emitted two FM patterns.

The discriminant analysis performed on the spectral parameters of the advertisement calls of *E. queulensis* (LF2, HF2, LF3, and HF3), and the corresponding parameters of the calls of *E. calcaratus* and *E. roseus* reported by Márquez et al. (2005) yielded significant differences among species (Wilks' $\lambda = 0.30$; $F_{8,80} = 8.34$; $P < 0.0001$). *Eupsophus queulensis* is closer to *E. roseus* than to *E. calcaratus*, CV1 being the root accounting for most of the variation (Eigenvalue $= 2.17$; explained variance $= 97\%$). Only the Canonical Scores of CV1 were significantly different among species ($F_{2,43} = 34.25$; $P < 0.0001$). The Canonical Score of *E. calcaratus* differed significantly from *E. roseus* (Tukey's test: $P < 0.001$) and *E. queulensis* (Tukey's test: $P < 0.001$) and was similar between *E. roseus* and *E. queulensis* (Tukey's test: $P = 0.66$). Among the parameters analyzed, only HF2 was relevant to discriminate among species (Wilks' $\lambda = 0.44$;

TABLE 1. Temporal and spectral parameters of the advertisement calls of *Eupsophus queulensis*. Abbreviations: CD: call duration, RT: rise time, IC: intercall period, LF2: lowest frequency of the 2° harmonic, HF2: highest frequency of the 2° harmonic, LF3: lowest frequency of the 3° harmonic, HF3: highest frequency of the 3° harmonic.

Acoustic parameter	Mean $\pm$ SD (Range)	CV_w	CV_a	CV_a/ CV_w
CD (msec)	135 $\pm$ 31 (46–182)	7.60	22.91	3.02
RT (%)	59.4 $\pm$ 12.0 (23.1–97.8)	17.66	20.19	1.14
IC (sec)	1.96 $\pm$ 1.69 (0.65–26.36)	83.21	85.77	1.03
LF2 (Hz)	1040.6 $\pm$ 65.3 (861.3–1205.9)	4.85	6.28	1.30
HF2 (Hz)	1210.2 $\pm$ 124.8 (947.5–1550.4)	6.64	10.31	1.55
LF3 (Hz)	1557.4 $\pm$ 88.9 (1292.0–1808.8)	4.63	5.71	1.23
HF3 (Hz)	1818.4 $\pm$ 183.5 (1464.3–2325.6)	6.68	10.09	1.51

$F_{8,80} = 9.35$; $P < 0.001$). Figure 3 shows a graph of CV1 and CV2 for the discriminant analysis performed.

The comparison performed on the SVL yielded significant differences among these three congeneric species ($F_{2,40} = 5.12$, $P = 0.01$). *Eupsophus calcaratus* was smaller than *E. roseus* (Tukey's test: $P = 0.02$) and *E. queulensis* (Tukey's test: $P = 0.04$), and the sizes of *E. roseus* and *E. queulensis* did not differ significantly (Tukey's test: $P = 0.88$). Body sizes together with acoustical parameters for the calls of the three congeneric species are listed in Table 3.

The sound pressure level of the noise produced by the creek along which the burrows of *E. queulensis* are found, measured at the approximate calling position of one individual, was 67.7 $\pm$ 0.4 dB RMS SPL, which correspond-

ed to an average value obtained over four intervals lasting 4 sec each. The band-pass spectrum of this sound, with main energy components between about 200 and 2,000 Hz, had a maximum at about 550 Hz. Such spectral shape is also a characteristic of previous recordings of this type of noise (Penna et al., 2005).

DISCUSSION

Eupsophus queulensis emits an advertisement call consisting of a harmonic-rich single note, with dominant second and third harmonics, displaying four basic FM patterns. The temporal parameters measured in the advertisement calls of *E. queulensis* showed great variability relative to the spectral parameters. Intercall period has
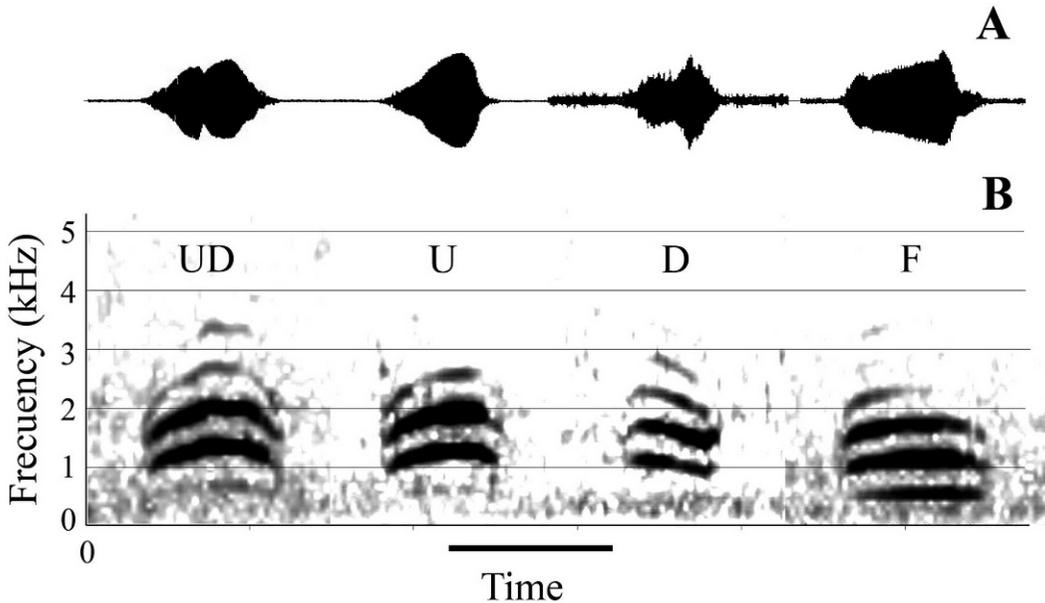

FIG. 2. Oscillograms (A) and sonograms (B) of the four frequency modulation patterns in calls of *Eupsophus queulensis*. Abbreviations: UD: upward-downward; U: upward; D: downward; F: flat. The horizontal bar corresponds to 200 msec.

TABLE 2. Proportions of frequency modulation types in the calls of seven males of *Eupsophus queulensis*. Abbreviations as Figure 2.

Individual (number of calls)	UD (%)	U (%)	D (%)	F (%)
1 (24)	83.3	0	16.7	0
2 (23)	56.5	4.3	21.7	17.4
3 (30)	36.7	63.3	0	0
4 (20)	85.0	10.0	0	5.0
5 (20)	95.0	5.0	0	0
6 (50)	74.0	22.0	0	4.0
7 (30)	20.0	0	76.7	3.3
TOTAL (197)	62.4	17.3	16.2	4.1

the largest variation, having average CV_w and CV_a above 80%, which contrasts with the low variability observed in the spectral parameters, with values below about 10% for both coefficients. Such larger variation in temporal relative to spectral parameters also occurs in other anurans (Gerhardt, 1991; Pröhl, 2003; Pröhl et al., 2007), including species of *Eupsophus* (Márquez et al., 2005).

The spectral parameters of the advertisement call of *E. queulensis*, having low CV_w, could be considered static properties, as defined for these signals by Gerhardt (1991, 1994) as those having intraindividual coefficients of variation below 5%. Among the temporal parameters, rise time and intercall period have large high CV_w, corresponding to Gerhardt's dynamic proper-ties, with intraindividual coefficients of variation above 10%. However, call duration, having the lowest intraindividual variability among the temporal properties, with an average CV_w of 7.6%, could be regarded as a static property. A low variability for this parameter has been reported for *Hyla cinerea* and *Pseudacris crucifer* (Gerhardt, 1991), which also produce single-note advertisement calls. In addition, call duration had a $CV_a : CV_w$ ratio of 3, well above the ratios measured for the other parameters, indicating that this is an individual trait for calling males. Such variation may be related to the different densities or background noise levels at which the different subjects called. Penna et al. (2005) reported that the duration of the advertisement call of males of *E. calcaratus* increased in response to synthetic calls or in the presence of continuous noises. The constancy of the spectral parameters measured suggests that these are features relevant for signal recognition, an attribute of static call properties (Gerhardt 1991, 1994). However, the variation in the FM patterns indicates that the spectral structure of these signals is highly plastic in *E. queulensis*.

In agreement with previous studies on other species of *Eupsophus* (Márquez et al., 2005), we found four FM patterns in the advertisement calls of *E. queulensis*: upward-downward (UD), upward (U); downward (D); and flat (F). The UD pattern predominates in most individuals.
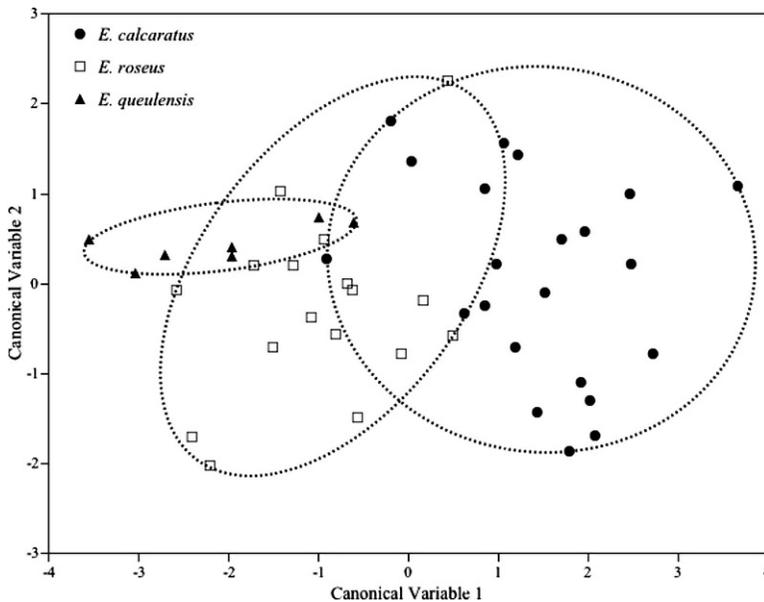

FIG. 3. Discriminant analysis for spectral parameters of the advertisement calls of *Eupsophus queulensis*, *Eupsophus calcaratus*, and *Eupsophus roseus*, showing canonical variables 1 and 2. The discriminant analysis was performed on four spectral parameters: lowest frequency of the second and third harmonics (LF2 and LF3) and highest frequency of the second and third harmonics (HF2 and HF3; see text).

TABLE 3. Comparison of body sizes and acoustical parameters of the calls of three species of *Eupsophus*. Averages, with ranges in parenthesis. *N*s listed for CD apply to the five acoustical parameters. Abbreviations: SVL: snout–vent length. Other abbreviations as in Table 1. Acoustical parameters for *Eupsophus roseus* and *Eupsophus calcaratus* are from Márquez et al. (2005). SVLs of *Eupsophus queulensis* are from Veloso et al. (2005). SVLs of *E. roseus* and *E. calcaratus* were measured for individuals of the same populations studied by Márquez et al. (2005).

Body size and acoustic parameters	*E. queulensis*	*E. roseus*	*E. calcaratus*
SVL (mm)	38.7 (34.0–41.7) *N* = 7	38.2 (34.0–43.0) *N* = 18	36.2 (33.0–39.0) *N* = 18
CD (msec)	135 (46–182) *N* = 7	158 (124–235) *N* = 18	192 (112–262) *N* = 24
LF2 (Hz)	1040.6 (861.3–1205.9)	1037.4 (875.3–1298.2)	1170.0 (928.7–1351.5)
HF2 (Hz)	1210.2 (947.5–1550.4)	1285.2 (1147.8–1428.6)	1486.1 (1286.1–1682.8)
LF3 (Hz)	1557.4 (1292.0–1808.8)	1618.5 (1194.4–1826.8)	1817.2 (1377.3–2038.3)
HF3 (Hz)	1818.4 (1464.3–2325.6)	1871.0 (1503.1–2166.7)	2157.1 (1804.6–406.8)

In addition, in the current study, we show that males change FM patterns through time, in the absence of detectable changes in their social circumstances or acoustic environment. Playback experiments are needed to explore possible relationships between FM patterns and changes in the acoustic environment to which calling frogs are exposed.

High variability in the spectral features of signals has also been reported for the acoustical signals of species of Ranoidea, in particular for African racophorid and Asian ranid frogs (Narins et al., 2000; Feng et al. 2002, 2006). Our study extends the variability of acoustic signals to Telmatobiinae (Cycloramphidae, Frost et al 2006), a group of Hyloidea (Frost et al., 2006; Correa et al., 2006) from southern South America.

Environmental noise influences anuran vocalizations; in particular, a number of species inhabiting stream environments produce frequency-modulated calls (Penna et al., 1983, 2005; Feng et al., 2002). The presence of frequency-modulated patterns in the advertisement calls of *E. queulensis* contributes to generalize the extent of this association, which, however, is not absolute; FM-calls are also produced by species from environments other than streams and some stream inhabitants produce calls with no FM patterns (e.g., Márquez et al. 1996). The noise level of about 68 dB SPL measured at the calling site of one of the subjects analyzed in our study is a considerable interference to the human ear and is within the range of noise levels to which frogs are exposed in the temperate austral forest (Penna et al., 2005).

The comparative analysis of the vocalizations of *E. queulensis* with two other congeneric species shows that the advertisement calls of this frog are closer to *E. roseus* than to *E. calcaratus*. This result is congruent with the geographic distributional patterns of these frogs. *E. queulensis*, is found in latitude 35°59′S (Veloso et al., 2005), closer to *E. roseus* (with a northern distributional limit at about latitude 37°S in the Cordillera of Nahuelbuta; Nuñez et al., 1999; Veloso and Navarro, 1988) than to *E. calcaratus*, which occurs south of latitude 40°S (Nuñez et al., 1999). Furthermore, our results agree with a molecular phylogeny showing close affinity between *E. queulensis* and *E. roseus* (Correa et al., 2006). The relationships reported here between the spectral parameters of the vocalizations of the three species in addition are in correspondence with their body sizes. Because of the inverse relationship between size and frequency of spectral components in anurans (reviewed in Gerhardt and Huber 2002), the similar spectral structure of the calls of *E. roseus* and *E. queulensis* is congruent with the similar size between these species. Correspondingly, *E. calcaratus* has a smaller size and spectral components centered at higher frequencies.

The similarity of the vocalizations of *E. queulensis* with those of other species of the *Roseus* group is indicative of a relatively recent phylogenetic divergence. Other species of the genus in addition to *E. queulensis* have restricted geographical ranges. The remarkable correspondence of these distributions with proposed forest refuges on the western slopes of the coastal cordillera during the last Pleistocenic glaciation (*Eupsophus contulmoensis*, *Eupsophus insularis*, *Eupsophus migueli*, *Eupsophus septentrionalis*, and *E. queulensis*), or with *Araucaria* forest within this geographic area, arisen during the postglacial warming Holocenic period (*Eupsophus nahuelbutensis*) (Villagrán, 1991, 2001; Vuilleumier, 1968), suggests that the divergence between species of this genus took place during these geological periods. Such divergence is likely to have followed a model of allopatric

speciation in isolation, as proposed by Penna and Veloso (1990) based on the vocal diversity shown by this group of vertebrates.

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