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ORIGINAL PAPER

Geographic variation in the advertisement call of *Hypsiboas cordobae* (Anura, Hylidae)

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Abstract Geographic variation in the advertisement call of anuran is commonly observed among conspecific populations. We analyzed the geographic variation of advertisement calls in six populations of the Argentinean treefrog species *Hypsiboas cordobae* throughout its geographic distribution. The advertisement calls of this species consisted of three, four or five tonal notes. Spectral call variables showed significant differences among populations, as in the first and second internote intervals. Discriminant function analysis demonstrated significant multivariate differences among populations. All spectral variables exhibited clinal variation, with frequencies increasing significantly from north to south. These same variables were negatively correlated with the altitudes of the six populations. Mantel tests showed no significant correlation between geographic distances and bioacoustic distances or between altitudinal distances and bioacoustic distances, attributable to that call variations are due to different levels of latitudinal and altitudinal populations studied, and not to the distances between pairs of localities. Altitudinal variation in spectral properties may be attributable to an inverse relation with body size, which varies clinally along the same geographical axis.

Keywords *Hypsiboas cordobae* · Geographic variation · Advertisement call · Altitude · Latitude

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Introduction

Acoustic communication is an important feature of anuran social behaviour (Schneider and Sinsch 1992; Pargana et al. 2003; Friedl and Klump 2005). Calls are the primary mating display of anurans and play a very important role in their biology and evolution (Cocroft and Ryan 1995; Brenowitz and Rose 1999), constituting the major pre-mating reproductive isolating mechanism in anurans (Blair 1958; Gerhardt 1974).

Several studies of geographic variation have demonstrated intraspecific differences in the advertisement call among populations of widespread species (Narins and Smith 1986; Ryan and Wilczynski 1991; Ryan et al. 1996; Castellano and Giacoma 2000; Wycherley et al. 2002; Smith et al. 2003a, b; Bernal et al. 2005; Smith and Hunter 2005; Bionda et al. 2006; Baraquet et al. 2007; Pröhl et al. 2007). In species with large distributions relative to their dispersal abilities, isolation by distance takes place, and geographic variation takes the form of gradients or clines (Bernal et al. 2005). The study of this variation has proven to be crucial for the understanding of mating signals evolution in anurans (Loftus-Hills and Littlejohn 1992; Boul and Ryan 2004).

The genus *Hypsiboas* Wagler 1830 contains 84 species, most of which are included in seven species groups. The *Hypsiboas pulchellus* group currently contains 36 species (Frost 2012; Köhler et al. 2010; Lehr et al. 2010, 2011) including *Hypsiboas cordobae* (Barrio 1965). This species was resurrected from the synonymy of *Hyla pulchella* by Faivovich et al. (2004). The distribution of *Hypsiboas cordobae* is restricted to Córdoba and San Luis provinces, Argentina (Barrio 1965; Cei 1980; Gallardo 1974, 1987; di Tada et al. 1996; di Tada 1999; Langone and Lavilla 2002; Faivovich et al. 2004). This restricted distribution, to highlands of central Argentina and with a broad altitudinal range, together with those reported by The IUCN Red List of

Threatened Species, as species with insufficient data, makes this species interesting for study.

The structure of the advertisement call of *H. cordobae* has previously been described (Barrio 1965; Cei 1980; di Tada et al. 1996; Hänsel et al. 2000; Baraquet et al. 2013). However, inter-population variation has not been previously studied in this species. Here, we report our observations of geographic variation in the advertisement calls of *H. cordobae* along a latitudinal and altitudinal gradient in Cordoba and San Luis provinces, Argentina.

Materials and methods

Field work

Advertisement call recordings for *H. cordobae* were collected in six localities of Cordoba and San Luis Provinces (Argentina), between September 2006 and May 2011. The study area cover a latitudinal gradient across an area of approximately 20,000 km^2, with an altitudinal range between 800 m and 2300 m elevation. The studied localities were: Los Linderos (2,310 m asl, 32°00′54.05″ S–64°56′42.97″ W), Pampa de Achala (2,150 m asl, 31°49′41.8″ S–64°51′44.9″ W), Los Tabaquillos (2,107 m asl, 32°23′59.75″ S–64°55′33.69″ W), La Carolina (1,634 m asl, 32°48′43.94″ S–66°05′48.15″ W), Las Guindas (930 m asl, 32°35′35.22″ S–64°42′38.92″ W), Achiras (808 m asl, 33°09′28.64″ S–64°58′55.13″ W) (Fig. 1).

Advertisement calls were recorded with a Sony™ Cassette-Corder Walkman TCM-465 V and Sony™ Digital Walkman Audio Tape (DAT) TCD-100 with a Sony™ stereo microphone ECM-MS907 Sony™, at a sampling frequency rate of 44.1 kHz, resolution 16 bit. Air temperature at the each calling site was recorded with a digital thermometer (precision=0.1°C; range=9.7–21°C).

Call analysis

Calls were analyzed using Adobe® Audition™ 1.0 through examination of oscillograms, sonograms and spectrograms. Spectra were calculated using a Fast Fourier transform (FFT) with 1,024 points from the 44.1-KHz, 16-bit resolution digital audio files.

Calls (Fig. 1) were characterized by the following parameters (Duellman and Pyles 1983; Heyer et al. 1990)

1. Number of notes per call (N/C): number of notes each call has
2. Call duration (CD): time each acoustic unit of vocalization lasts
3. Note duration (ND): time each individual note of the call lasts
4. Inter-note interval (IN): period of time between notes
5. Inter-call interval (IC): period of time between calls
6. Call rate (CR): frequency of production of calls (calls/min)
7. Call dominant frequency (DFC): frequency that contains the highest energy for the call
8. Note dominant frequency (DFN): frequency that contains the highest energy for each note

Statistical analyses

Descriptive statistics were calculated for every call character in each population. Linear regressions between call variables and air temperature were performed to assess the effect of temperature on attributes of advertisement calls. Residuals from these regressions were used to standardize call attribute data to the values that would be expected at a temperature of 14 °C (average temperature of all call recordings), for all variables that were significantly correlated with temperature (Heyer and Reid 2003). All data were processed using Statgraphics Plus 5.0.

Call variation between populations

We compared the populations using the variables available for all individuals, seven temporal (CD, ND1, ND2, ND3, IN1, IN2, CR) and four spectral variables (DFC, DFN1, DFN2, DFN3). For inter-population comparisons, we performed univariate analyses of variance (ANOVAs). If the ANOVA revealed significant differences between populations, pairwise Tukey's HSD tests were used to determine which groups differed significantly from one another.

We used a discriminant function analysis to determine whether the overall structure of the advertisement call varied among populations.

Analysis of geographic variation

We correlate each call parameter with latitude and altitude of the study sites to investigate clinal variation.

Mantel tests (Mantel tests for Windows 1.18) (Calvalcanti 2005) were used to estimate the correlations between linear geographic distances among populations and bioacoustic distances among populations; and between altitudinal distances and bioacoustic distances. Ten thousand permutations determined the statistical significance of the correlation coefficients. The Mantel test calculates correlations among similarity/dissimilarity and distance matrices considering that the same data point is used for multiple comparisons, and has proven to be an effective method for analysis in patterns of association between similarity/dissimilarity matrices (Castellano and Balletto 2002; Bernal et al. 2005; Pröhl et al. 2006). We used a dissimilarity matrix

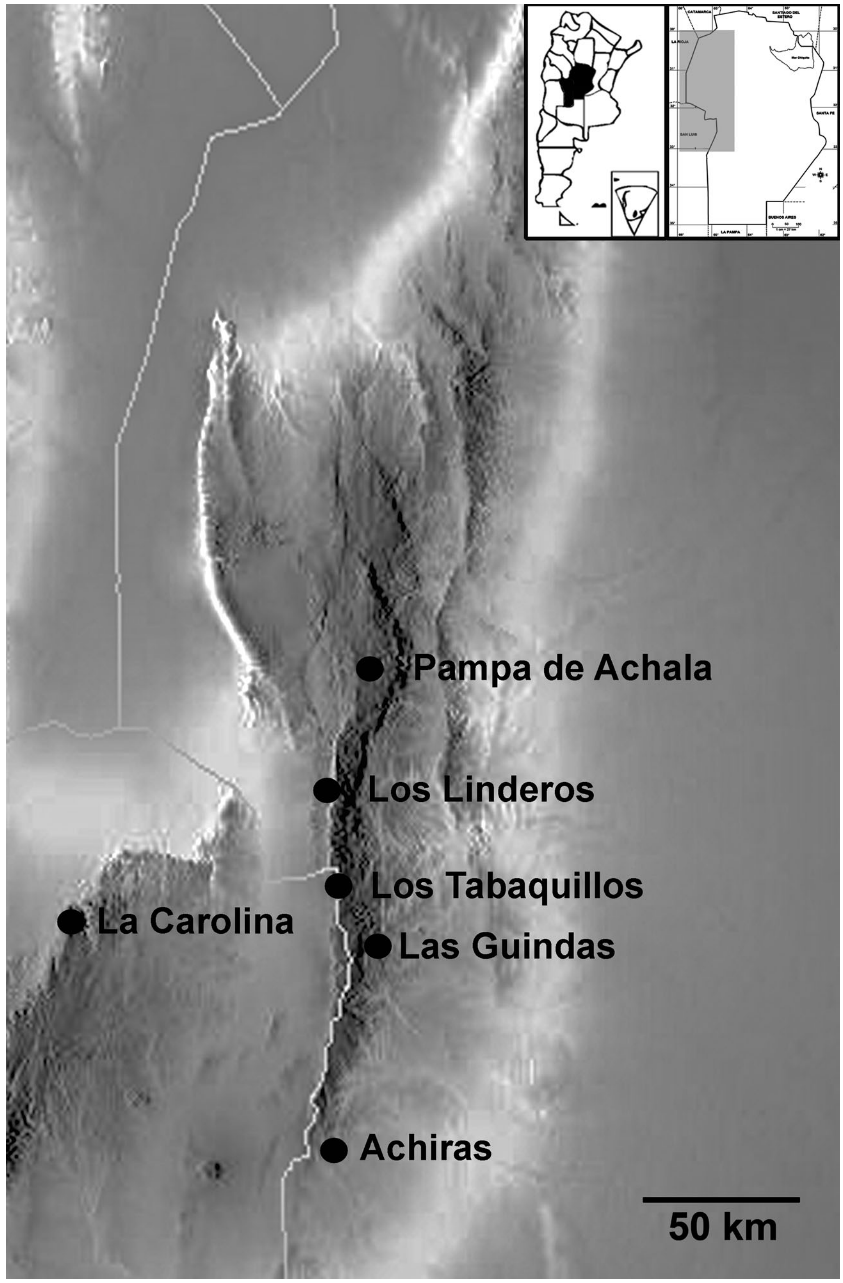

Fig. 1 Map of the study area (localities of Cordoba and San Luis Provinces, Argentina) showing the distribution of *H. cordobae*

of Mahalanobis distances between acoustics variables, and correlated it with matrices of altitudinal (meters) and geographical (kilometers) distances between all pairs of study sites. Analyses were performed using Statgraphics Plus 5.

Results

General description of the advertisement call

The advertisement call of *H. cordobae* had the same basic structure in all populations. The results obtained revealed that calls consisted of either three, four or five notes calls, alternating regularly; meaning that a single frog can produce calls with different numbers of notes (Fig. 2). Means, standard deviation and ranges of acoustic properties of advertisement calls for each population are presented in Table 1.

Simple regression analyses showed that CD, ND1, ND2, ND3, ND4, DFC, DFN1, DFN2 and DFN3 were negatively correlated with temperature (Table 2). The fitted regression equations were used to standardize these variables to the values that would be expected at 14°C. Temperature was uncorrelated with CR, IN1, IN2, IN3, IN4, ND5, DF4, DF5 and IC (Table 2).

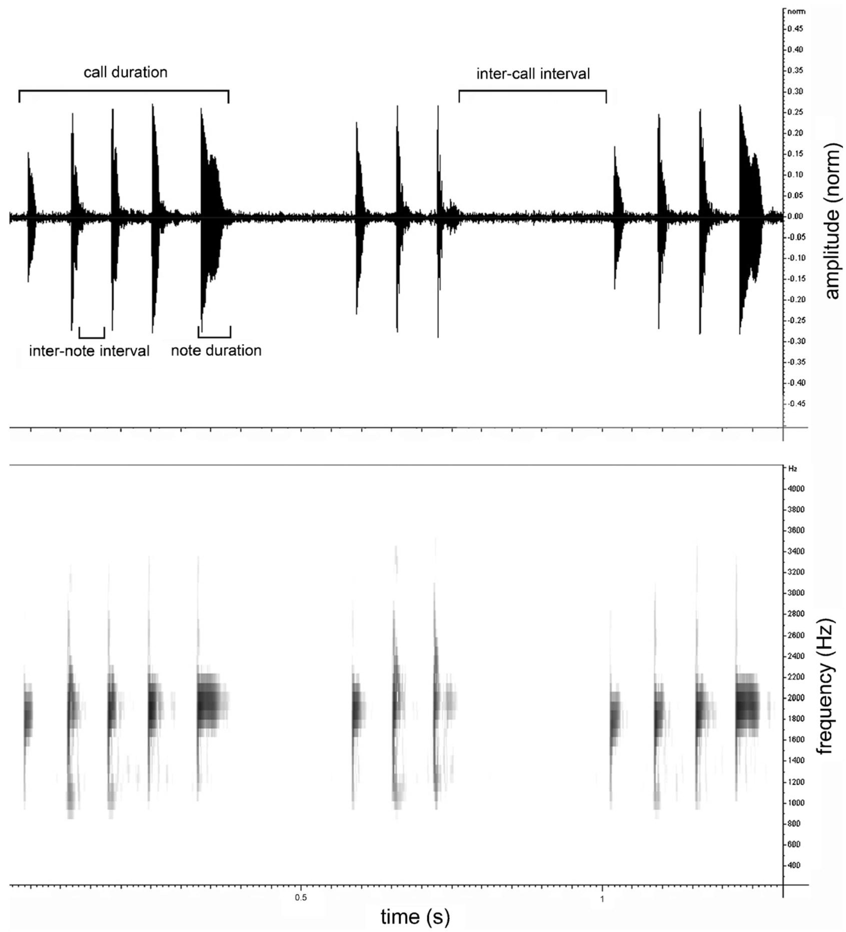

Fig. 2 Oscillogram (*top*) and sonogram (*bottom*) of the advertisement call of *H. cordobae*

Table 1 Mean values and SD of all call characters measured at the six study localities of *Hypsiboas cordobae*

Call variables	Los Linderos Hill	Pampa de Achala	Los Tabaquillos Establishment	La Carolina	Las Guindas	Achiras
CD	328.06±105.56	269.03±28.41	293.23±42.77	303.15±36.50	327.39±53.61	255.92±51.65
ND1	23.64±5.07	23.43±3.02	28.30±12.25	28.10±10.43	26.21±7.13	17.02±5.52
IN1	75.66±38.92	58.89±6.08	56.76±8.84	64.94±17.23	81.19±14.04	61.58±6.91
ND2	23.74±0.15	19.44±2.64	27.79±7.85	26.41±11.53	23.88±4.99	18.86±6.33
IN2	67.18±36.73	53.42±4.93	51.57±10.15	58.43±17.53	67.52±10.49	52.95±5.22
ND3	27.35±2.07	23.84±5.78	36.58±4.81	32.64±15.37	33±7.69	23.83±9.38
IN3	63.78±32.18	50.93±6.26	46.42±12.39	53.67±18.91	58.74±10.53	50.24±5.13
ND4	46.74±18.75	43.28±9.40	52.45±10.68	51.38±10.05	51.67±7.12	35.09±5.57
IN4	41.38	52.75±5.89	48.84±15.18	53.63±12.23	38.59±8.73	50.57±4.87
ND5	41.73	47.82±5.78	49.36±6.08	49.28±7.08	53.44±9.07	37.29±4.01
IC		1,713.15±403.29	1,637.25±740.25	1,741.81±1,699.57	2,652.01±252.82	1,701.94±1,101.43
DFC	1,669.04±469.24	1,709.84±176.80	1,647.17±155.64	1,811.50±152.49	2,223.99±131.60	2,009.08±141.17
DF1	1,595.92±446.06	1,649.82±135.89	1,562.53±130.53	1,752.20±123.90	2,040.92±177.15	1,780.01±123.85
DF2	1,621.60±455.89	1,672.57±149.87	1,598.32±143.93	1,774.21±134.12	2,047.24±233.29	1,885.12±131.42
DF3	1,648.88±469.81	1,706.45±180.80	1,640.47±146.43	1,802.01±146.51	2,173.46±134.39	1,977.74±121.34
DF4	1,677.93±478.27	1,731.45±167.52	1,685.81±159	1,835.51±164.12	2,227.39±206.93	2,033.44±141.96
DF5	1,375.60	1,666.96±91.94	1,741.09±175.79	2,090.33±174.94	1,865.61±451.77	2,004.71±133.65
CR	30±21.21	27.73±5.97	32±8.50	35.13±19.12	23.81±10.60	37.56±21.97

We analyzed 1,090 calls from 58 individuals. All temporal measurements in milliseconds and all spectral measurements in Hz

Table 2 Linear regressions between call properties and air temperature

Call parameter	*r*	R^2	*P*
CD	−0.30	9.01	0.0198
ND1	−0.45	20.57	0.0003
IN1	−0.20	4.13	0.1192
ND2	−0.48	23.59	0.0001
IN2	−0.13	1.81	0.3045
ND3	−0.49	24.31	0.0001
IN3	−0.007	0.005	0.9540
ND4	−0.58	34.74	0.0000*
IN4	0.12	1.63	0.6368
ND5	0.27	7.63	0.2830
IC	0.12	0.69	0.6787
DFC	−0.30	9.50	0.0165
DFN1	−0.35	12.57	0.0054
DFN2	−0.29	8.62	0.0228
DFN3	−0.32	10.61	0.0111
DFN4	−0.25	6.35	0.0539
DFN5	0.22	4.98	0.3181
CR	0.11	1.36	0.3740

Call variation between populations

All variables showed significant differences between populations when compared using ANOVA; except ND2 and CR (Table 3).

Pairwise test showed that calls of Las Guindas individuals were the most different from the remaining populations in all acoustic variables (Tukey test, $P<0.05$). Individuals of this population showed the highest mean values for all call parameters (Fig. 3).

Discriminant analysis generated five functions, the first highly significant accounted for 71.19 % of the total variation (Table 4). The calls from different populations of *H. cordobae* were differentiated primary by the first discriminant function, which was strongly correlated with IN1 and IN2 (Fig. 4).

Table 3 ANOVA of acoustics variables among six population of *H. cordobae*

Variable	*P*	*F*
CD	0.0053	3.77
ND1	0.0333	2.64
ND2	0.1037	1.93
ND3	0.0243	2.83
IN1	0.0000	12.28
IN2	0.0003	5.63
DFC	0.0000	21.65
DFN1	0.0000	13.39
DFN2	0.0000	8.18
DFN3	0.0000	16.60
CR	0.2253	1.44

Fig. 3 Comparison of DFC (ms) in each of the populations studied of *H. cordobae*

Although there was some overlap between populations, when grouping all individuals 65 % were correctly assigned to their original population. The highest number of individuals correctly assigned was from population of Las Guindas. Rates of correct assignment of individuals from Pampa de Achala, Achiras, Los Tabaquillos and Los Linderos ranged from 50 % and 78 %, while individuals from La Carolina were correctly assigned in only 33.33 % of cases (Table 4).

Analysis of geographic variation

Simple regressions between call variables and latitude showed that all measured spectral variables increased significantly from north to south (DFC: $r=0.3604$, $P=0.0047$; DFN1: $r=0.3035$, $P=0.0184$; DFN2: $r=0.2691$, $P=0.0375$; DFN3, $r=0.3097$, $P=0.0160$; DFN4: $r=0.2533$, $P=0.0529$ and DFN5, $r=0.4829$, $P=0.0228$). In contrast, temporal variables did not show significant correlation with the latitude.

The Mantel test comparing the geographic distance and call distance matrices was not statistically significant. The Mantel test correlation was $r=-0.498$ and the one-tail probability was $P=0.0635$.

As was the case of latitude, all spectral call characters were significantly correlated with altitude. However, in this case, the correlation was negative: all spectral variables decreased significantly as altitude increases (DFC: $r=-0.7666$, $P=0.0000$; DFN1: $r=-0.6514$, $P=0.0000$; DFN2: $r=-0.5930$, $P=0.0000$; DFN3: $r=-0.7169$, $P=0.0000$; DFN4: $r=-0.5895$, $P=0.0000$; DFN5: $r=-0.5192$, $P=0.0133$) (Fig. 5).

The Mantel test comparing the altitudinal distance and call distance matrices was not statistically significant ($r=-0.737$; $P=0.9929$).

Discussion

We have analysed the spatial pattern of advertisement call variation among populations of *H. cordobae* across the entire geographic distribution range of this species. Our results

Table 4 Segregation among individuals of six population of *H. cordobae*

Function	1	Classification table							
		Actual group	n	1	2	3	4	5	6
Eigenvalue	2.22431	1	11	0 (0.00 %)	1 (50 %)	1 (50 %)	0 (0.00 %)	0 (0.00 %)	0 (0.00 %)
Relative %	71.19	2	2	7 (63.64 %)	1 (9.09 %)	1 (9.09 %)	1 (9.09 %)	0 (0.00 %)	1 (9.09 %)
Canonical correlation	0.83058	3	7	2 (28.57 %)	0 (0.00 %)	5 (71.43 %)	0 (0.00 %)	0 (0.00 %)	0 (0.00 %)
Wilk's lambda	0.142319	4	15	1 (6.67 %)	4 (26.67 %)	3 (20 %)	5 (33.33 %)	0 (0.00 %)	2 (13.33 %)
χ^2	98.4590	5	16	0 (0.00 %)	0 (0.00 %)	0 (0.00 %)	0 (0.00 %)	14 (87.50 %)	2 (12.50 %)
df	55	6	9	1 (11.11 %)	0 (0.00 %)	0 (0.00 %)	0 (0.00 %)	1 (11.11 %)	7 (77.78 %)
P	0.0003								

Populations: *1* Los Linderos, *2* Pampa de Achala, *3* Los Tabaquillos, *4* La Carolina, *5* Las Guindas, *6* Achiras

demonstrated that populations of *H. cordobae* vary in advertisement calls. ANOVA revealed statistically significant differences among populations in all spectral calls parameters, and in two temporal parameters. Multivariate analysis using discriminant functions showed highly significant differences among populations, and we found a clinal trend in spectral parameters.

Clinal variation in call characteristics has been described for several anuran species (Narins and Smith 1986; Ryan and Wilczynski 1991; Ryan et al. 1996; Castellano and Giacoma 2000; Wycherley et al. 2002; Smith et al. 2003a, b; Bernal et al. 2005; Smith and Hunter 2005; Bionda et al. 2006; Pröhl et al. 2007). In particular, Baraquet et al. (2007) analysed advertisement calls of *H. pulchellus*, a sister species of *H. cordobae*, and reported differences between the two studied populations confirming the presence of geographic variation. Our results suggest that a similar pattern of geographic variation is found in *H. cordobae*. Most of the differences that we found among populations in the advertisement calls can be explained by a geographic cline: we found a clinal trend from south to north of decreasing call dominant frequency and note dominant frequency in *H. cordobae*. In other anuran species, clinal variation in spectral properties of calls has been attributed to concomittant clinal variation in body size along the same geographical axis (Bernal et al. 2005; Pröhl et al. 2007). However, analysis of geographic variation in body length of adult males from the same localities and individuals of *H. cordobae* considered in the present study, were significantly associated with latitude, but this correlation was negative (Baraquet et al. 2012).

Regressions between acoustic spectral parameters and altitudinal levels of the six populations of *H. cordobae* showed negative relationships between call frequencies and altitude (lower frequencies at higher altitudes). Among-population variation in advertisement call may be correlated with geographic variation in body size (Narins and Smith 1986; Ryan and Wilczynski 1991). Previous studies of many anuran species have reported that the size of the calling males is highly negatively correlated with the dominant frequencies of their advertisement calls (Ryan 1985; Platz 1988; Schneider and Steinwarz 1990; Ryan and Wilczynski 1991; Cocroft and Ryan 1995; Sullivan et al. 1996; Burmeister et al. 1999; Bee et al. 2000; Bosch et al. 2000; Bee and Gerhardt 2001; Bee 2002; Bernal et al. 2004; Scroggie and Littlejohn 2005). This negative correlation may exist because the frequencies of acoustic signals in anurans are partially determined by the shape and mass of the laryngeal apparatus; an increase in the size of the vocal cords, cartilage and resonating box in larger males tends to lead to calls with lower dominant frequencies (Duellman and Trueb 1994; McClelland et al. 1996; Wells

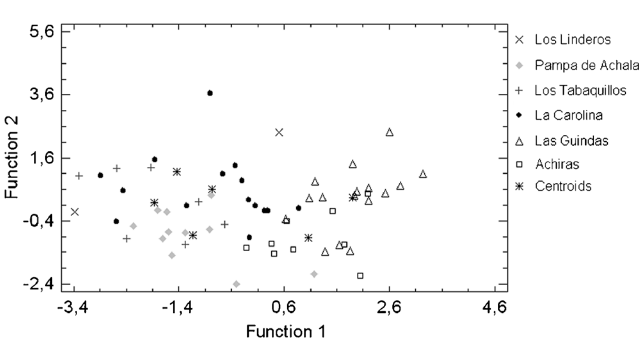

Fig. 4 Acoustic segregation among individual of *H. cordobae* from the six populations studied. Discriminant function analysis

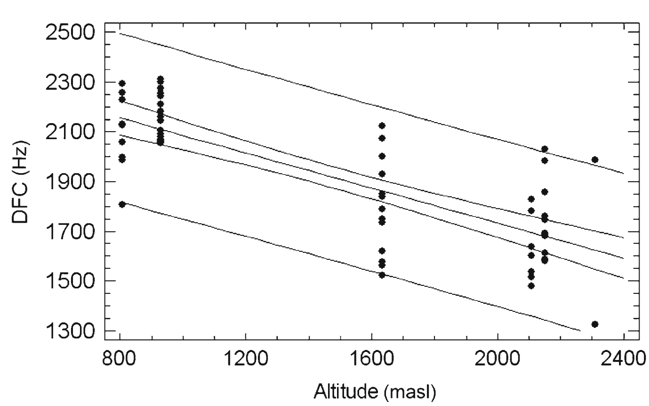

Fig. 5 Simple regressions between call dominant frequency and altitudes of six population studied of *H. cordobae*

2007). Altitudinal variation of the body length is a common pattern in amphibians, with individuals from higher altitudes tending to be larger in body size, consistent with Bergmann's rule (Narins and Smith 1986; Castellano and Giacoma 2000; Wells 2007; Băncilă et al. 2009, 2010; Baraquet et al. 2012; Plăiaşu et al. 2010; Liu et al. 2012; Lou et al. 2012).

In the previous study of geographic variation in body length of adult males of *H. cordobae* from the same individuals considered in our study, demonstrated a significant positive correlation between altitude and body size (Baraquet et al. 2012). Populations of higher altitudinal level showed higher snout–vent length and lower frequencies. Therefore, the altitudinal variation of frequencies observed in the advertisement calls of *H. cordobae* may be attributable to the variation in body length among the six populations.

In addition, the Mantel tests showed no significant relationships between linear geographic distances and bioacoustic distances, or between altitudinal distances and bioacoustic distances. This supports the fact that call variations are due to, and not to the distances between pairs of localities.

In conclusion, our work on *H. cordobae* across the known distribution of this species showed differences between the studied populations, confirming the presence of geographic variation in the call. However, this evidence should be supplemented with studies of other characters such as molecular characters and environmental conditions; and studies to determine which acoustic variables are stronger in the process of species recognition and female choice to assess the significance of the observed geographic variation.

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