



Geographic variation in advertisement calls among populations of *Dendropsophus cruzi* (Anura: Hylidae)

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Anuran advertisement calls receive much attention because of their importance in mating behaviour and the recognition of conspecifics. Herein, we studied geographic variation in the advertisement call of *Dendropsophus cruzi* from central Brazil, to test the hypothesis that between-population differences in call parameters can be explained by geographical distance. We recorded 129 individuals from 10 populations of *D. cruzi* in Goiás State, Brazil, measuring call parameters of five calls of each individual. We found that dominant frequency is useful to distinguish populations, and that geographic distance is not a predictor of overall call differences. However, clinal geographical patterns were found for call duration, dominant frequency, call rate and snout-vent length (SVL). We suggest that differences in calls among populations can be due to local selective pressures.

Key words: Anuran, dominant frequency, geographical patterns, isolation by distance

INTRODUCTION

Acoustic signals are widespread among anuran species (Giaretta et al., 1993; Gerhardt, 1994a; Gerhardt & Huber, 2002; Wells, 2007). The most common vocalisation is the advertisement call, which is used for species recognition, territory defense, and to attract females (Wells, 1977; Tárrano & Guyer, 2001; Amézquita et al., 2006; Bastos et al., 2011). As such, the advertisement call is under multiple selective pressures (Ryan & Rand, 2003; Boul et al., 2007). For example, female mate choice is expected reduce variability in advertisement calls, stabilising the patterns found in the male repertoire (Lesbarreres & Lode, 2002). However, sexual selection also predicts that males will produce individually discernible calls to enhance their own reproductive success (Gerhardt & Davis, 1988; Cocroft & Ryan, 1995).

The evolution of intraspecific signal diversity is limited by the importance of species recognition. Nevertheless, the communication repertoire of a species may vary geographically (Wilczynski & Ryan, 1999; Bernal et al., 2005; Smith & Hunter, 2005; Pröhl et al., 2006). Several hypotheses have been proposed to explain

geographic variation in anuran calls, such as differences in environmental conditions (Castellano et al., 2000; Smith et al., 2003), sexual selection (Gerhardt, 1994b), variation in environmental sound transmission (Bernal et al., 2005), pleiotropic changes with geographic variation in body size (Boul & Ryan, 2004), and isolation by distance (Telles et al., 2006; Silva et al., 2008). In widely distributed populations, isolation arising from distance can lead to gradual clines in call properties (Castellano et al., 2000; Bernal et al., 2005). Therefore, call characteristics that vary in their degree of stereotyping can also have different patterns of geographic variation (Castellano et al., 2002). Comparisons of inter- and intraspecific advertisement calls reveal both geographic and phylogenetic influences on call variation (Cocroft & Ryan, 1995; Smith & Hunter, 2005).

Dendropsophus cruzi is a small hylid found in the Brazilian savannah (Cerrado-Pombal & Bastos, 1998). Males vocalise in open areas and have a prolonged breeding seasons *sensu* Wells (1977, see also Bastos et al., 2003). The advertisement call is composed by a single pulsed note (0.007–0.009 s at 4–7 kHz, Pombal & Bastos, 1998). Herein, we examine geographic variation in the advertisement call of ten populations of *D. cruzi*

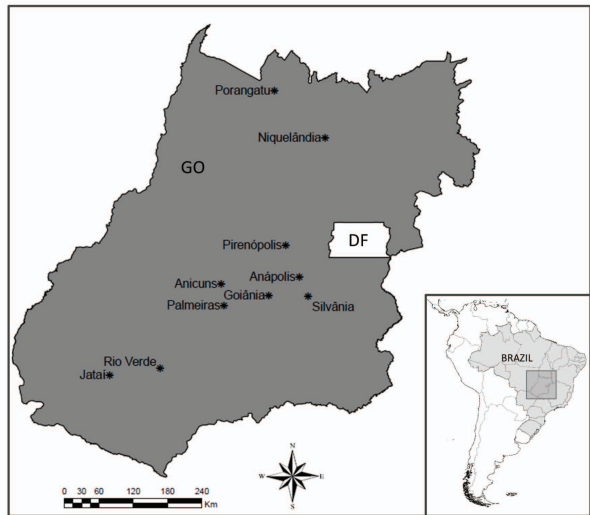


Fig. 1. Map showing municipalities where populations of *Dendropsophus cruzi* were sampled in central Brazil.

to answer the following questions: (i) Do call parameters differ between populations? (ii) Is geographic distance between populations a predictor of call differences?

MATERIALS AND METHODS

We studied the advertisement calls of males of *D. cruzi* in ponds from ten municipalities in the state of Goiás, Brazil (Anápolis, Anicuns, Goiânia, Jataí, Niquelândia, Palmeiras, Pirenópolis, Porangatu, Rio Verde, and Silvânia, Fig. 1; Table 1). Localities where advertisement calls were recorded are typically open areas, and we did not record any information on surrounding vegetation. The climate in the Cerrado domain is tropical, with dry seasons between April and September and rainy seasons from October to March, coinciding with the breeding season of *D. cruzi* (Peel et al., 2007).

We recorded advertisement calls during 2000–2001, 2006–2007 and 2009–2010. Observations started after sunset (1800 hours) when individuals began their vocal activity. Calls were recorded using a Marantz PMD660 (digital) or PMD222 (analog) tape recorder coupled with a directional Sennheiser (ME66) microphone. The recording files were edited using the following settings: frequency at 22 kHz, resolution at 16 bits and FTT at 1,024 points. We analysed temporal call parameters (call rate, call duration, pulse number and pulse duration) using Avisoft-SAS Lab Light software, while the spectral parameters (i.e. dominant frequency) were analysed using Cool Edit software. The bioacoustic terms used in

the analyses followed Wells (2007). We used the package Seewave v. 1.6.4 (Sueur et al., 2008) from the statistical software R (R Development Core Team, 2014) to obtain sonograms, oscillograms and spectrograms setting window name (Fourier transform window) as Hanning, window length as 256 samples, and an overlap of 90%.

Each individual was recorded for about two minutes, and five advertisement calls were randomly selected for analysis. The number of individuals recorded in each population ranged between 7 and 15 (Table 1). We quantified call rate (calls/min), call duration (s), pulse number (pulses/call), pulse duration (s) and dominant frequency (Hz). After each recording session, we captured all males and measured SVL to the nearest 0.05 mm with a caliper and mass to the nearest 0.01 g with digital scales. We used xylocaine 5% to euthanise voucher specimens which were fixed in 10% formalin, preserved in 70% ethanol and housed at Zoological collection of the Universidade Federal de Goiás (ZUFG 923–935; ZUFG1400; ZUFG 1755–57; ZUFG 2036–37; ZUFG 2617; ZUFG 2910; ZUFG 3344–49; ZUFG 2574–2561).

We considered the mean (based on five calls) of call parameters for each individual. To consider temperature as an influence in call properties, we followed the approach of Kaefer & Lima (2012) by calculating a linear regression of each call parameter against temperature, using their coefficients in the equation $Y_{adj} = y - (b * T_{Local}) + (b * T_{Mean})$, where Y_{adj} is the adjusted value of the parameter, b is the regression coefficient, T_{Local} is the temperature at the location of the record and T_{Mean} is the mean temperature of all records (24.3°C, SD=2.75, range=17.7–31.8). We further regressed these temperature-adjusted values against SVL, considering the score values for Principal Component Analyses (PCA) to determine if the structure of advertisement calls varied among populations. We used the components of the PCA to perform a Linear Function Analysis (LFA). Wilks’ lambda distribution was used to determine whether differences among populations were statistically significant.

To evaluate if call parameters exhibit clinal geographic variation we used multiple regressions with temperature-adjusted and SVL-regressed call traits as dependent variables, and latitude and longitude as independent variables. Additionally, we used Mantel tests to evaluate the extent of covariation between geographic distance and variation in the structure of advertisement calls. We performed this analysis with the original values, using temperature and SVL as covariates. A geographic dissimilarity matrix was constructed using Euclidean distances between longitude and latitude,

Table 1. Results of Principal Component Analysis (PCA) for advertisement call variation of *Dendropsophus cruzi* from Central Brazil. Significant results are shown in *italic*.

Call parameters	PC1	PC2	PC3	PC4	PC5
Call duration	-0.523	0.427	0.096	-0.515	-0.517
Number of pulses	-0.679	-0.117	0.142	-0.087	0.704
Pulse duration	0.433	<i>0.636</i>	-0.056	-0.409	0.485
Dominant frequency	-0.221	<i>0.629</i>	-0.051	<i>0.743</i>	-0.006
Call rate	-0.163	-0.044	-0.982	-0.078	0.023

Table 2. Results of Linear Discriminant Analysis for advertisement call variation of *Dendropsophus cruzi* from Central Brazil. This analysis was performed with the canonical axis from the PCA. CPE: cumulative percentage of explanation. Significant results are shown in *italic*.

PCA axis	LD1	LD2	LD3	LD4	LD5
PC1	0.399	0.429	0.565	-0.076	-0.143
PC2	<i>-1.410</i>	0.376	0.030	-0.440	0.282
PC3	0.205	0.862	-0.550	0.402	0.009
PC4	<i>-1.381</i>	-0.098	0.311	0.735	-0.412
PC5	-0.616	0.202	-1.294	-1.791	-3.388
CPE	0.838	0.925	0.972	0.994	0.999

and a dissimilarity matrix for acoustic parameters was constructed using average values for all individuals in each location using Bray-Curtis distances, calculating a distance matrix for mean temperature and SVL for each population. The statistical analyses were done using the statistical software R (R Development Core Team, 2014).

RESULTS

We analysed 645 calls of 129 *D. cruzi* males from ten populations. Mean and standard deviations of each acoustic parameter in each population are described in Table 1 of the Online Appendix. The advertisement call of *D. cruzi* males is composed by one single pulsed note with an average duration of 0.01 ± 0.003 s (range: 0.004–0.027 s, Fig. 2). We observed 2.6 ± 1.1 pulses/call (range: 1–8 pulses/call), with a pulse duration of 0.004 ± 0.002 s (range: 0.001–0.015 s). The average dominant frequency was 5.94 ± 0.92 kHz (range: 4.38–8.19), and the average call rate was 73.6 ± 21.5 calls/min (range: 28–136).

The linear discriminant analysis revealed significant differences among populations (Wilks' lambda=0.12; $F_{(45, 518)}=6.95$; $p<0.001$).

Populations were largely characterised by the first LDA axis, which explained 83% of variation in the data and was composed predominantly of PCA axis 2 (represented by pulse duration and dominant frequency) and PCA axis 4 (predominantly represented by dominant frequency; Tables 1 and 2).

Dominant frequency, duration and repetition rate were negatively related to latitude, and we observed that SVL decreased northwest of the Goiás State; the number of pulses and pulse duration were not affected by latitude and longitude (Table 3, Online Appendix Figure 1). Using Mantel tests, we did not observe any relationship between geographic distance among populations and the structure of advertisement calls ($p>0.11$).

DISCUSSION

In the present paper we re-described the advertisement call of *D. cruzi* males based on 129 individuals, increasing the range of parameter values for this species (see Bueno et al., 2003). We observed geographic differences in advertisement calls, with dominant frequency

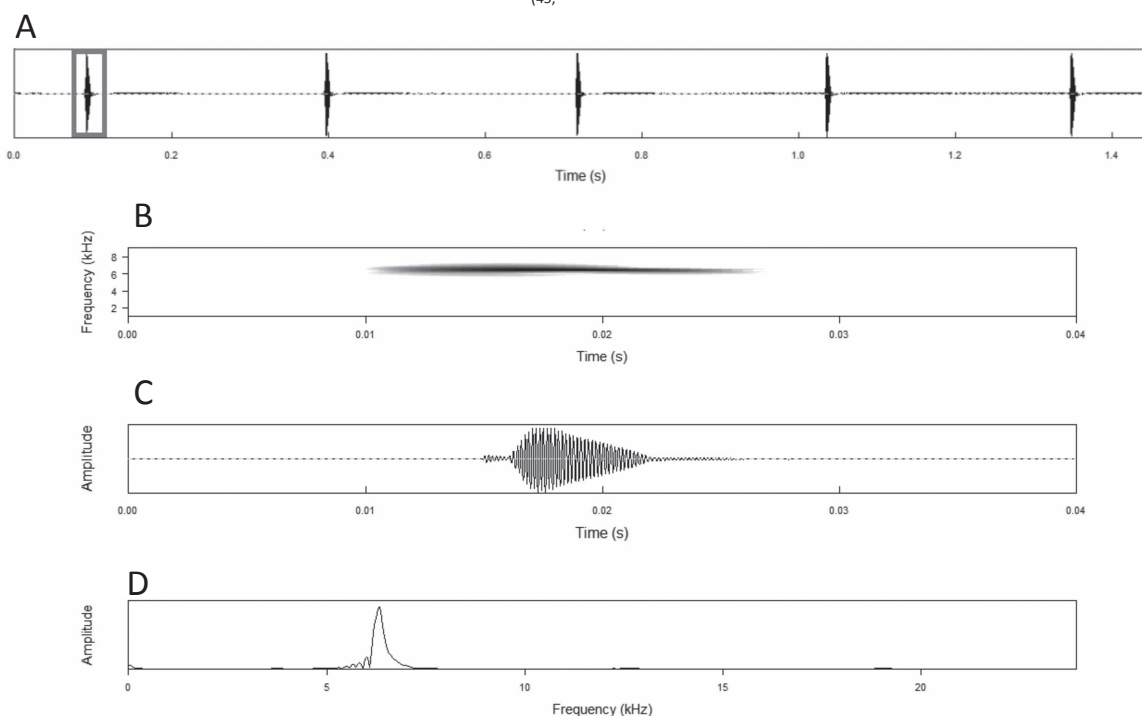


Fig. 2. Oscillogram and sonogram of advertisement call of, Rio Verde municipality, Goiás State, Brazil. (Air temperature=21.5°C; SVL=19.85 mm; Mass=0.53 g).

Table 3. Multiple regression between call parameters of the advertisement call of *Dendropsophus cruzi* and latitude and longitude. Significant results are shown in *italic*.

Acoustic parameters	R_{partial}	p	R^2_{model}	$F_{(2,126)}$	p
Call duration			<i>0.06</i>	<i>4.06</i>	<i>0.01</i>
Latitude	0.0005	0.01			
Longitude	-0.007	0.02			
Number of pulses			0.02	1.48	0.2
Latitude	0.09	0.1			
Longitude	-0.1	0.2			
Pulses duration			0.005	0.34	0.7
Latitude	0.0006	0.57			
Longitude	-0.001	0.44			
Dominant frequency			<i>0.28</i>	<i>25</i>	<i><0.001</i>
Latitude	<i>318.1</i>	<i><0.001</i>			
Longitude	<i>-334.5</i>	<i><0.001</i>			
Call rate			<i>0.16</i>	<i>12.2</i>	<i><0.001</i>
Latitude	<i>3.74</i>	<i>0.002</i>			
Longitude	<i>4.75</i>	<i>0.01</i>			
SVL			<i>0.1</i>	<i>7.8</i>	<i><0.001</i>
Latitude	-0.3	<i>0.001</i>			
Longitude	<i>0.3</i>	<i>0.002</i>			

being the most important parameter to distinguish between populations. In anurans, vocalisations have a fundamental role in species recognition, for which the dominant frequency often plays a more important role than temporal call traits (Castellano et al., 2002; Smith & Hunter, 2005; Morais et al., 2012). Because the efficiency of signal transmission is dependent on the environment, different vegetation and microclimate could represent differential selective pressures influencing which call features can cause divergence between populations (Castellano et al., 2000; Macedonia & Clark, 2003).

Clinal geographical patterns in anuran call parameters are commonly found (Ashton, 2002; Lüddecke & Sánchez, 2002; Laugen et al., 2003; Weight et al., 2005; Pröhl et al., 2007; Baraquet et al., 2015), and could result from forces that act directly on body size (McClelland et al., 1996; Wollermann & Wiley, 2002). Our results that revealed an inverse relationship between dominant frequency and SVL support this observation. The increase in the dominant frequency to the north of Goiás State could be related to populations in this area experiencing higher temperatures and a marked seasonality in food availability (Olalla-Tárraga et al., 2009). Clinal variation in SVL could reflect differential growth rates imposed by temperature (Alvarez & Nicieza, 2002; Ashton, 2002; Laugen et al., 2005). In areas with a shorter period of food availability, a reduction in length of the larval period can further lead to reproduction at smaller sizes (Leips & Travis, 1994; Nicieza, 2000; Ohmer et al., 2009). We observed that duration and repetition rate of the advertisement call

increased from south to north. Anurans may alter the temporal parameters of their call to make them more attractive to females (Gerhardt et al., 2000; Smith & Roberts, 2003; Kim et al., 2004; Guerra & Ron, 2008), and we suggest that individuals from northern populations might be able to modify temporal call parameters for improved reproductive success.

Geographic distance did not explain the variability in acoustic parameters suggesting that gene flow alone is insufficient to explain the observed variation. Phenotypes are products of genomes and the environment (Schluter, 2000), and local selective pressures have likely contributed to the observed variation in call parameters. Future studies are needed to assess the influence of environmental parameters on the spatial structure of advertisement calls of *D. cruzi*.

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