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Vocal repertoire and bioacoustic analyses in *Physalaemus cuvieri* (Anura, Leptodactylidae) from southern Brazil

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We investigated the influence of air and water temperature, relative humidity, morphological characteristics and distance between males on call parameters of *Physalaemus cuvieri*. We also compared advertisement and courtship calls recorded for the species. Field observations were carried out between September 2011 and March 2012, in nine water bodies in the north west of Paraná state, southern Brazil. Males of *P. cuvieri* emitted advertisement and courtship calls in different social contexts, and all acoustic parameters except dominant frequency differed between types of call. Call duration, minimum frequency and sound pressure level (SPL) of advertisement calls were classified as static properties and other parameters were classified as intermediate properties. All acoustic parameters varied more between males than within males. We observed a negative relationship between air temperature and call duration, and a positive relationship between relative humidity and SPL and dominant frequency. Snout-vent length was negatively correlated with minimum frequency. The distance between individuals was negatively correlated with call duration, maximum frequency and frequency range, and positively correlated with dominant frequency. Changes in acoustic parameters depending on environmental, morphological and social parameters are important to expand the information about the evolution of sexual selection and aggressive interactions.

Key words: advertisement call, aggressive interactions, coefficient of variation, courtship call, vocalisations

INTRODUCTION

In anuran amphibians, the most conspicuous mechanisms of communication comprise acoustic signals (Haddad, 1995; Gerhardt & Huber, 2002; Wells, 2007). Bioacoustic studies relate to ecology, evolution and animal behaviour (Ryan, 2001), and the study of advertisement calls is an important tool used to determine species (Duellman & Trueb, 1994). Vocalisations play a key role in territorial delimitation (Ryan, 2001; Costa et al., 2010; Reichert, 2010), female attraction (Roesli & Reyer, 2000; Taylor et al., 2007), maintenance of spacing between males (Bastos & Haddad, 2002; Morais et al., 2012), as well as species recognition and reproductive isolation (Littlejohn, 1977; Wells, 1977b; Cocroft & Ryan, 1995; Haddad, 1995; Bourne & York, 2001; Martins & Jim, 2003).

The advertisement call is the best documented call type in anurans (Larson, 2004; Bastos et al., 2011a). It is species-specific, and serves for attracting conspecific females and territory delimitation (Haddad, 1995). Other vocalisations are encounter calls (Scroggie & Littlejohn, 2005), agonistic calls (Bourne, 1992), territorial calls (Costa et al., 2010; Morais et al., 2012) and courtship calls (Kokubum & Giaretta, 2005). Detailed properties of acoustic signals can depend on temperature (Guimarães & Bastos, 2003; Lingnau & Bastos, 2007; Morais et al., 2012) and morphological factors such as snout-vent length and body weight (Briggs, 2010; Morais et al., 2012). Signal variation can also depend on social context such as chorus size and distance between conspecific neighbours (Wells, 1988; Bastos et al., 2011b; Lemes et al., 2012; Morais et al., 2012).

Physalaemus cuvieri (Fitzinger, 1826) is a leptodactylid species with reproductive activity between late September and March (Bastos et al., 2003). Its eggs are deposited in foam nests on water (Bastos et al., 2003; Mijares et al., 2010). Despite being widely distributed in South America (Frost, 2012; Bastos et al., 2003; Mijares et al., 2010), there is little information about the acoustic repertoire of this species (for a description of the advertisement call see Barrio, 1965; Heyer et al., 1990). The present study aims to examine the vocal repertoire of *P. cuvieri* in order to address the following questions: i) Does the advertisement call differ from the courtship call? ii) Do acoustic parameters of advertisement calls vary among populations? iii) Do morphological characteristics, air temperature, water temperature, humidity and distance between males influence acoustic parameters of the advertisement calls?

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Table 1. Municipalities in the northwest of Paraná state (south of Brazil) and geographic coordinates of each point where the recordings of *Physalaemus cuvieri* males were made, with number of recorded males (*n* recorded), of advertisement calls analysed (five calls for each male, *n* advertisement) and courtship calls analysed (up to three calls for each male, *n* courtship). Numbers in parentheses in the last column represent the numbers of males that emitted courtship calls.

Local	Municipality	Geographical coordinates	*n* recorded	*n* advertisement	*n* courtship
PTN1	Maringá	23° 20’ 38’’ S, 51° 52’ 6’’ W	17	85	0 (0)
PTN2	Sussuí	23° 43’ 7” S, 52° 13’ 34” W	13	65	5 (3)
PTN3	Sussuí	23° 43’ 33” S, 52° 13’ 8” W	12	60	2 (2)
PTN4	Mandaguari	23° 23’ 26’’ S, 51° 42’ 41’’ W	12	60	1 (1)
PTN5	Mandaguari	23° 33’ 4’’ S, 51° 42’ 53’’ W	11	55	3 (3)
PTN6	Porto Rico	22° 46’ 19’’ S, 53° 15’ 25’’ W	16	80	2 (2)
PTN7	Iguatemi	23° 21’ 17’’ S, 52° 4’ 24’’ W	13	65	2 (2)
PTN8	Maringá	23° 16’ 19’’ S, 51° 49’ 10’’ W	16	80	4 (2)
PTN9	Maringá	23° 21’ 21’’ S, 51° 54’ 16’’ W	12	60	0 (0)

MATERIALS AND METHODS

We studied individuals of *P. cuvieri* in nine water bodies located in the north-west of Paraná state, south of Brazil (Table 1). Observations were carried out between September 2011 and March 2012. Fieldwork was conducted from 1900 until 0000 hours. Vocalisations of 122 males were recorded with a DAT SONY TCD100 recorder (48 kHz sampling rates and 16 bits) and a YOGA HT-81 directional microphone placed at 50 cm from the calling frog. To avoid recording the same male more than once, 110 of 122 males were collected immediately after the recording. We measured the sound pressure level (SPL) in decibels for all males with a Minipa® digital decibel meter (Type II; time weighting: fast; A-weighted), placed about 50 cm from the calling male. After each recording session, we measured snout-vent length (SVL) with a digital calliper (Starret® 799, accurate to 0.05 mm) and weighed each individual with a digital scale (Pocket scale Diamond® A04, accurate to 0.01 g). Air temperature and relative humidity were recorded with a digital thermo-hygrometer, and water temperature was recorded with a digital thermometer with an internal and external sensor (Digital-ThermoPart Number®, accurate to 0.1 °C).

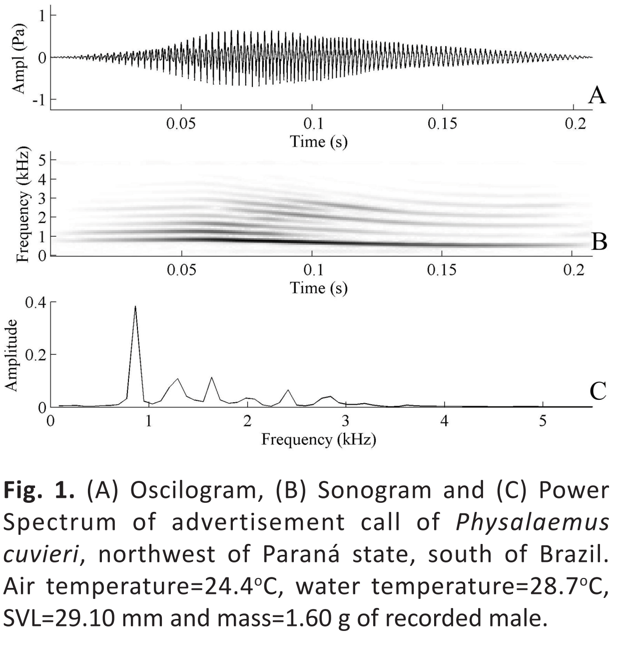

Fig. 1. (A) Oscilogram, (B) Sonogram and (C) Power Spectrum of advertisement call of *Physalaemus cuvieri*, northwest of Paraná state, south of Brazil. Air temperature=24.4°C, water temperature=28.7°C, SVL=29.10 mm and mass=1.60 g of recorded male.

We analysed five advertisement calls and up to three courtship calls for each individual. Courtship calls were emitted when a male was close to a female, and after emission of courtship calls all males were observed in amplexus with females. Recordings were processed with a SONY VAIO-based digital signal analysis system, edited with 22 kHz input frequency and 16-bit resolution. The frequency was obtained through Fast Fourier Transformation (FFT, 1024 points). For analysis of call duration (CD), minimum frequency (MF), maximum frequency (MAXF) and frequency range (FR) we used the software Avisoft-SAS Lab Lite®, and for the analysis of spectral parameters of dominant frequencies (DF) we used the software Cool Edit 2000®. Minimum and maximum frequencies were obtained by the minimum and maximum values observed in oscillograms constructed in Avisoft-SAS Lab Lite® for each

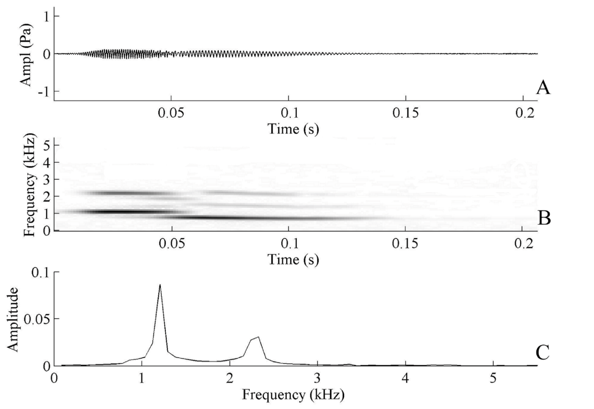

Fig. 2. (A) Oscilogram, (B) Sonogram and (C) Power Spectrum of courtship call of *Physalaemus cuvieri*, northwest of Paraná state, south of Brazil. Air temperature=24°C, water temperature=23.6°C, SVL=26.84 mm and mass=1.63 g of recorded male.

call. The frequency range was obtained by subtracting the minimum frequency from the maximum frequency. Coefficients of variation between males ($CV_{between}$) and within each male (CV_{within}) were calculate to determine static and dynamic properties (*sensu* Gerhardt, 1991). Coefficients of variation for sound pressure level (SPL) were calculated with mean values of SPLs, because the conversion of SPLs into linear scale creates dubious values.

Oscillograms, sonograms and the spectral range of calls were measured with SoundRuler® software, following terminologies from Gerhardt (1998) and Gerhardt & Huber (2002). Vouchers are housed at Coleção Zoológica da Universidade Federal de Goiás (ZUFG), section of adult amphibians (6529, 6537, 6540, 6545, 6551, 6583, 6594, and 6596) and section of sound files (1471–1479).

To test for differences between acoustic parameters of advertisement and courtship calls we applied one-way ANOVAs (Zar, 1999) with acoustic traits as dependent variables. The non-parametric Kruskal-Wallis test was employed when acoustic parameters did not meet the normality assumption. We used multiple regression analyses to test the influence of abiotic characteristics, air temperature (°C), relative air humidity (%) and water temperature (°C), biotic characteristics relative to body size (achieved by multiplying the SVL by the body weight) and distance between males on acoustic parameters of the advertisement call. To reduce multicollinearity we opted to use body size, because SVL and body weight are correlated. All statistical analyses were run with the software Statistica v.7.0 (StatSoft Inc., 2004), using the significance level of p=0.05.

RESULTS

The mean distance between calling males was 3.24±2.74 m (0.05–15 m, n=111 males). Mean SVL and weight of recorded males were 29.17±1.57 mm (25.18–34.00 mm, n=110 males) and 2.09±0.37 g (1.38–3g, n=110 males), respectively. Mean values of air temperature, humidity and water temperature were 21.82±3.5°C (14.6–39.9°C, n=122), 63.99±26.79% (21–98%, n=122) and 25.32±2.83°C (18–34°C, n=122) immediately after recordings, respectively.

We analysed 629 calls of *P.cuvieri.* The advertisement call (Fig. 1) was most common, and is characterised by descending frequency modulation. Advertisement calls have higher call duration, maximum frequency and range frequency, and lower minimum frequency than courtship calls (Fig. 2, Table 2). The mean dominant frequency of the two types of call was similar. Following Gerhardt (1991), call duration, minimum frequency and SPL of advertisement calls were classified as static, whereas maximum frequency, range frequency and dominant frequency were classified as intermediate call properties. All acoustic properties varied more between than within males, with $CV_{between}/CV_{within}$ ratios above two (Table 2).

Table 2. Mean, standard deviation (SD) and coefficient of variation (CV) of call parameters in *Physalaemus cuvieri* in the northwest of Paraná state (south of Brazil). Values of call parameters are expressed as mean±SD. Values measured in dBs were average. Coefficient of variation and sound pressure level of courtship calls were not obtained because the low number of emissions for each individual.

Vocalisations	Acoustic parameters	mean±SD	$CV_{between}$	CV_{within}	CV ratio
Advertisement call	Call duration (ms)	0.25±0.03	11.94	4.78	2.50
	Minimum frequency (Hz)	282.94±49.64	17.54	1.25	14.03
	Maximum frequency (Hz)	3582.41±820.45	22.92	5.19	4.42
	Frequency range (Hz)	3294.25±832.77	25.30	5.94	4.26
	Dominant frequency (Hz)	730.94±135.41	18.52	6.04	3.07
	Sound pressure level at approx. 50 cm (dB)	69.10±3.14	4.55	2.11	2.16
Courtship call	Call duration (ms)	0.19±0.07	-	-	-
	Minimum frequency (Hz)	476.32±57.85	-	-	-
	Maximum frequency (Hz)	2306.84±407.28	-	-	-
	Frequency range (Hz)	1830.53±415.91	-	-	-
	Dominant frequency (Hz)	739.18±109.12	-	-	-

Table 3. Acoustic parameters of *Physalaemus* species recorded in Brazil. CD- Call duration (ms), DF- Dominant frequency (kHz), CS- Call structure (H-harmonic; P-pulsed). Harmonic structure has waveform periodicities that are integral multiple of the fundamental frequency and pulsed structure has pulses at irregular intervals. Information not registered in the reference (?).

Physalaemus	CD	DF	CS	Reference
P. angrensis	0.52	1.12-2.11	P	Weber et al., 2005a
P. albifrons	0.2	1.0–2.0	H	Bokermann, 1966b
P. albonotatus	1.4 –1.5	2.1–4.0	H	Barrio, 1965
P. aguirrei	0.21–0.25	3.1	H	Pimenta & Cruz, 2004
P. atlanticus	1.11–1.47	0.91–1.43	?	Weber et al., 2005a
P. barrioi	1.24	2.66–2.85	H	Provete et al., 2012
P. biligonigerus	0.7–1.0	?	H	Barrio, 1965
P. bokkermani	0.17–0.25	1.8–5.3	?	Thomé et al., 2007
P. camacam	0.38–0.87	0.66–1.69	P	Pimenta & Cruz, 2004
P. crombiei	0.37–0.41	1.06–1.45	P	Heyer & Wolf, 1989
P. cuvieri	0.17–0.32	0.47–1.25	H	Present study
P. ephippifer	0.24–0.31	0.85–1.03	H	Bokermann, 1966a
P. erikae	0.56	0.34–4.8	H	Cruz & Pimenta, 2004
P. erythros	0.04–0.07	1.03–1.52	P	Baêta et al., 2007a
P. evangelistae	1.0–1.2	2.0–4.0	H	Bokkerman, 1967
P. feioi	2.5–5.6	2.31–2.75	P	Cassini et al., 2010
P. gracilis	0.9–1.0	4.0–5.0	H	Barrio, 1965
P. henselii	1.37–2.11	3.7–5.97	P	Maneyro et al., 2008
P. irroratus	0.25–0.96	1.38–1.81	H	Cruz et al., 2007
P. jordanensis	1.4–1.6	?	H/P	Bokermann, 1967
P. kroyeri	0.7–0.9	?	H	Bokermann, 1966b
P. lateristriga	2.3–5.5	0.75–2.8	P	Cassini et al., 2010
P. lisei	0.71–2.14	1.27	H	Morais & Kwet, 2012
P. maculiventris	0.2–0.75	0.7–3.7	P	Heyer et al., 1990
P. marmoratus	1.06–1.1	0.27–0.61	H	Giaretta & Menin, 2004
P. maximus	1.09–2.31	0.69–1.81	H	Baêta et al., 2007b
P. moreirae	0.5–0.7	0.6–1.6	H/P	Heyer et al., 1990
P. nanus	0.16–0.19	1.81–1.88	H/P	Weber et al., 2005a
P. obtectus	0.05–0.10	1.1–1.5	H	Bokkerman, 1966a
P. olfersii	2.6–5.1	1.38–2.59	P	Cassini et al., 2010
P. orophilus	3.1–5.2	3.0–3.39	P	Cassini et al., 2010
P. riograndensis	0.8–0.9	1.2–6.0	H	Barrio, 1965
P. rupestris	2.43–3.56	1.6–2.8	P	Nascimento et al., 2001
P. signifer	0.3	0.7–2.5	H	Bokkerman, 1966a
P. soaresi	1.34–2.4	3.0	?	Weber et al., 2005b
P. spiniger	0.22–0.30	1.16–1.67	P	Weber et al., 2005a

The courtship call was recorded for only 15 males and was emitted when a female was less than 20 cm from a calling male. This call has descending frequency modulation, and is lower in frequency than that of the advertisement call (Table 2). A maximum of three calls were emitted by each male. We were unable to obtain data on SPL and coefficients of variation due to the low sample size. Only the dominant frequency was not significantly different between the types of call recorded ($F_{(1,139)}$=0.06; p=0.80, Fig. 3E), whereas all other measured variables differed from each other (call duration: $H_{(1,141)}$=20.95; p<0.01, minimum frequency: $F_{(1,139)}$=238.38; p<0.01, maximum frequency: $H_{(1,141)}$=42.02; p<0.01, frequency range: $H_{(1,141)}$=44.60; p<0.01). We also used call duration, call structure (harmonic or pulsed) and dominant frequency to differentiate the advertisement call of *P. cuvieri* from other species of the genus found in Brazil (Table 3). Harmonic structure represents calls with

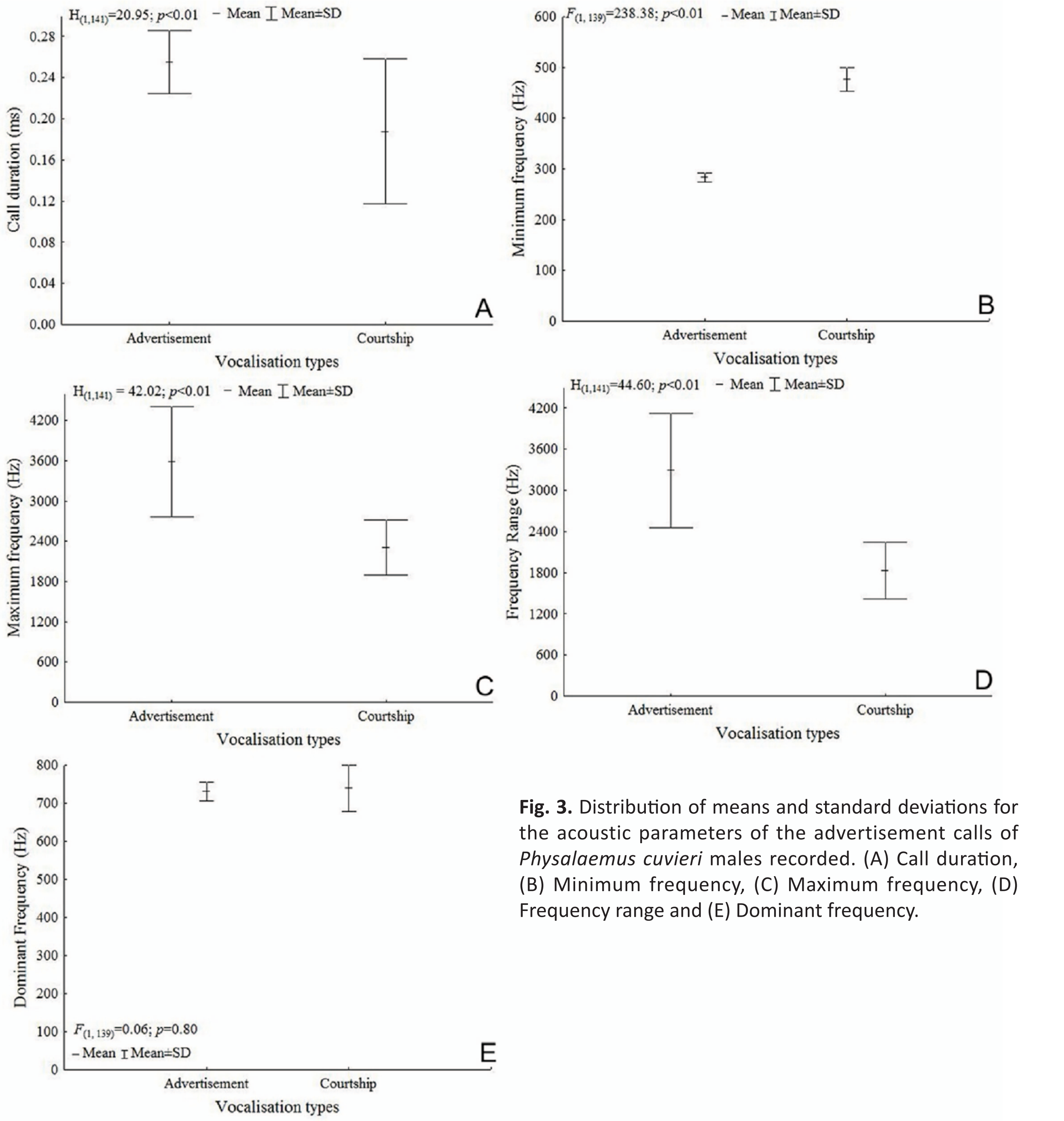

Fig. 3. Distribution of means and standard deviations for the acoustic parameters of the advertisement calls of *Physalaemus cuvieri* males recorded. (A) Call duration, (B) Minimum frequency, (C) Maximum frequency, (D) Frequency range and (E) Dominant frequency.

waveform periodicities that are integral multiple of the fundamental frequency and pulsed structure produces pulses at irregular intervals (Gerhardt, 1998).

The minimum distance between the studied populations is 3.8 km, and the maximum distance is 182 km. Maximum frequency ($H_{(8,\ 122)}$=11.45; *p*<0.18), frequency range ($H_{(8,\ 122)}$=11.91; *p*<0.15), dominant frequency ($H_{(8,\ 122)}$=14.19; *p*<0.08) and SPL ($H_{(8,\ 122)}$=7.37; *p*<0.49) of advertisement calls did not differ among the nine sampled populations. Significant differences occurred for call duration ($F_{(8,113)}$=4.28; *p*<0.01) and minimum frequency ($H_{(8,\ 122)}$=33.94; *p*<0.01). Minimum frequency showed no relationship with abiotic characters, and the other acoustic parameters were not related to body size (Table 4). Relative humidity was positively correlated with SPL and dominant frequency, and air temperature was negatively correlated with call duration (Table 4). The minimum frequency was negatively correlated with body size. The distance between individuals, represented as social context, was negatively correlated with call duration, maximum frequency, and frequency range, whereas positive correlations were observed for dominant frequency (Table 4).

DISCUSSION

The vocal repertoire of anurans consists of different types of calls emitted in distinct social contexts (Guimarães & Bastos, 2003; Bastos et al., 2011b; Morais et al., 2012). The present study describes the courtship call of *P. cuvieri* emitted when a female is close to a calling male. According to Wells (1977a, 1988), altering the acoustic

Table 4. Multiple regressions of body size, abiotic characteristics, social context and acoustic parameters of *Physalaemus cuvieri* during the breeding season. Significant values are in *italics*, $p<0.05$. CD-Call duration (ms); MF-Minimum frequency (Hz); MAXF-Maximum frequency (Hz), FR-Frequency range (Hz); DF-Dominant frequency (Hz); SPL- Sound pressure level (dB); β context – Distance between males (m). β represent β values of multiple regression.

Acoustic parameters	β context	β air temperature	β humidity	β water temperature	β body size	$r^2_{aj.}$	*F*
CD	*<-0.01*	*<-0.01*	<-0.01	<0.01	<0.01	0.22	6.55
MF	1.72	1.20	0.33	-0.09	*-0.80*	0.04	1.85
MAXF	*-107.08*	-0.55	-3.88	-6.00	4.02	0.10	3.05
FR	*-105.40*	-1.94	-4.11	-8.15	4.90	0.09	2.97
DF	*8.52*	4.74	*1.07*	2.67	1.36	0.12	3.54
SPL	-0.15	-0.05	*0.03*	0.08	<0.01	0.10	2.30

behaviour in the presence of females makes individual males more distinct from a chorus.

Courtship calls are usually longer than advertisement calls (Rosen & Lemon, 1974; Klump & Gerhardt, 1987; Hartmann et al., 2004; Owen et al., 2006). It is not known whether a switch from advertisement to courtship calls increases the stimulation of female for mating, or enhances conspecific recognition (Hartmann et al., 2004). Males of *P. cuvieri* respond to the presence of females with a shortening of the advertisement call, as well as increased minimum frequency, reduced maximum frequency and reduced range amplitude.

The advertisement call was the most common vocalisation emitted by *P. cuvieri* males during the breeding season. Advertisement calls are important for specific recognition between neighbours (Narins & Feng, 2007), for attracting females, and territorial delimitation (Haddad, 1995). Although some neotropical anurans have complex advertisement calls (e.g., Bastos et al., 2011a; 2011b, Morais et al., 2012), most species belonging to the genus *Physalaemus* emit repeated notes (Pimenta & Cruz, 2004; Provete et al., 2012) similar to *P. cuvieri*. The advertisement calls observed in the present study were similar to earlier descriptions by Barrio (1965), Heyer et al. (1990) and Silva et al. (2008).

According to Márquez & Eekhout (2006), data on within-individual variation can provide information about which acoustic parameters are more variable, whereas data on between individual variation suggest which call characteristics may be involved in inter-individual recognition, sexual selection and species recognition. Temporal parameters of advertisement calls play a significant role in species recognition among leptodactylids, particularly in *Physalaemus* (Márquez et al., 1995). On the other hand, spectral properties of the call such as minimum frequency appear to have high potential for sexual selection.

Information of sound pressure level has applications for playback levels in behavioural studies (Gerhardt, 1975), in individual spacing in the chorus (Penna & Solís, 1998; Bastos et al., 2011b, Lemes et al., 2012), and for calibration of acoustic monitoring protocols (Llusia et al., 2011). Values of sound pressure level obtained for *P. cuvieri* are lower than for other neotropical anurans (Guimarães & Bastos, 2003; Bastos et al., 2011b; Morais et al., 2012), consistent with the low minimum distances between calling males and the formation of communal nests (Barreto & Andrade, 1995; Bastos et al., 2003). This suggests that females are attracted to males from rather short distances.

The advertisement call of *P. cuvieri* was previously described as harmonic (Barrio, 1965; Heyer et al., 1990; Silva et al., 2008). According to Gerhardt (1998) and Martins & Jim (2003), harmonic calls present integral multiples of the fundamental frequency. Most calls of species closely related to *P. cuvieri* are harmonic (Pimenta & Cruz, 2004; Provete et al., 2012). However, false harmonics are regularly observed (Gerhardt, 1998), making direct comparisons between studies more difficult.

Some measured acoustic parameters were correlated with air temperature, relative air humidity and body size, although this is not always confirmed in other studies (e.g., Guimarães & Bastos, 2003; Lingnau & Bastos, 2007). Our study is in line with Bastos et al. (2011b), who found no evidence that morphological traits influence temporal characteristics of the advertisement call. However, body size was negatively correlated with minimum frequency, a relationship which has previously been found with respect to dominant frequency (e.g., Guimarães & Bastos, 2003; Castellano et al., 2002; Silva et al., 2008; Briggs, 2010; Morais et al., 2012). Minimum frequency can be used as a predictor of male size, amongst others in order to reduce physical fights between individuals (Smith & Roberts, 2003; Byrne, 2008; Richardson et al., 2008; Briggs, 2010; Bastos et al., 2011b).

The ectothermic nature of anurans results in negative relationships between air temperature and acoustic parameters (Wells, 2007; Lingnau & Bastos, 2007; Rodríguez et al., 2010; Morais et al., 2012). Our observation that relative air humidity is correlated with dominant frequency and SPL has however only rarely been reported previously (Wagner, 1989; Castellano et al., 2002; Guimarães & Bastos, 2003; Larson, 2004), and suggests potential confounding factors to the relationship between body size and acoustic characteristics (Lingnau & Bastos, 2007).

The acoustic behaviour of *P. cuvieri* is affected by the social context of individuals, a pattern which has previously been reported in other anurans (e.g., Bastos & Haddad, 2002; Bastos et al., 2011b; Morais et al., 2012; Lemes et al., 2012). Some anurans emit territorial calls (e.g., Wagner, 1989), or enhance the complexity of the advertisement call when conspecific males are nearby (e.g., Wells, 1988; Morais et al., 2012). For *P. cuvieri*, spacing between males appears to be maintained by changes in the advertisement call, such as increase in call duration, maximum frequency, frequency range, and decrease in dominant frequency. Bastos & Haddad (2002), Bastos et al. (2011b) and Morais et al. (2012) have observed increases in call repetition rates when conspecific males were close to the calling male. Although physical encounters have been observed in *P. cuvieri* (Barreto & Andrade, 1995), changes in acoustic behaviour to maintain the spacing between males may decrease their occurrence (Briggs, 2010; Bastos et al., 2011b). The antiphony in *P. cuvieri* calling males, a behaviour first registered by Barreto & Andrade (1995), can also be linked to the spacing between males, since it reduces acoustic interferences between individuals (Passmore & Telford, 1981). This acoustic behaviour was also observed for the congener *P. signifer* (Wogel et al., 2002).

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