

# Vocal behaviour and conspecific call response in *Scinax centralis*

Rogério P. Bastos<sup>1</sup>, Mariana B. Alcantara<sup>1</sup>, Alessandro R. Morais<sup>1,2</sup>, Rodrigo Lingnau<sup>3</sup> & Luciana Signorelli<sup>1,2</sup>

<sup>1</sup>Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Brazil

<sup>2</sup>Programa de Pós-Graduação em Ecologia e Evolução, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Brazil

<sup>3</sup>Universidade Tecnológica Federal do Paraná, Francisco Beltrão, Brazil

We describe the vocal repertoire of *Scinax centralis* (Anura, Hylidae), examine the influence of individual characteristics on acoustic parameters, and explore the role of sound level in aggressive interactions. Observations were carried out between January 1997 and June 2001 in a rivulet at Floresta Nacional (Flona), municipality of Silvânia, state of Goiás, Brazil. Male *S. centralis* emitted four distinct types of vocalizations: an advertisement call, two types of aggressive call and a displacement call. Early in the nightly vocalizing activity, males emitted more aggressive calls and few advertisement calls. Males called at faster rates when inter-male distances were shorter. The mean intensities of the three calls (advertisement call, long and short aggressive calls) were positively correlated with the number of individuals present in the chorus, as well as snout–vent length (SVL) and mass of the calling male. The mean dominant frequency was negatively correlated with SVL and mass. Males increased the number of advertisement or aggressive calls during playback compared to pre-playback periods. Mean call intensity significantly increased with playback SPL. Like other species, *Scinax centralis* presents a complex vocal repertoire, with males emitting four types of vocalizations depending on social interactions.

**Key words:** aggressive interactions, Anura, Hylidae, sound level, vocalizations

## INTRODUCTION

A peculiarity of the anuran breeding system is the formation of aggregations with the participation of many individuals (e.g. Wells, 1977). Within these aggregations, one of the complications of attracting a mate for a calling male is acoustic interference by its conspecifics (Brenowitz & Rose, 1994; Bee & Perril, 1996; Bastos & Haddad, 2002). To minimize this problem, males may either maintain nonrandom inter-male distance (Brenowitz, 1989; Bastos & Haddad, 1999; Murphy & Floyd, 2005) or adjust their vocal behaviour in response to other individuals (Rose & Brenowitz, 1991; Marshall et al., 2003). This adjustment could involve a shift from the advertisement call to the aggressive call (Stewart & Bishop, 1994; Grafe et al., 2000) or an increase in call intensity (Rose & Brenowitz, 1997; López et al., 1988; Marshall et al., 2003), rate (Brenowitz, 1989; Bee & Perril, 1996; Bosch & Márquez, 1996; Luddecke, 2002; Tárrano, 2002), duration (Bee & Perril, 1996), frequency (Bee & Bowling, 2002), or complexity (Rand & Ryan, 1981; Wells & Greer, 1981; Schwartz & Wells, 1985).

*Scinax centralis* is a hylid that is known to inhabit two localities in the State of Goiás, Central Brazil (Pombal & Bastos, 1996). Females are larger and heavier than males (Alcantara et al., 2007). In choruses, males vocalize on branches of dense vegetation that grows adjacent to streams, and the operational sex ratio is highly male-biased (Alcantara et al., 2007). The presence of individuals is positively correlated with the air temperature on the two previous days and negatively correlated with rainfall on the day of observation (Alcantara et al., 2007).

In this study, we investigated the vocal repertoire of *Scinax centralis* to answer the following questions: 1) how do individual characteristics and temperature influence acoustic parameters and 2) how does sound intensity interfere in aggressive interactions?

## MATERIALS AND METHODS

We studied *S. centralis* in a rivulet at Floresta Nacional (Flona), municipality of Silvânia, state of Goiás, Brazil. We conducted observations either fortnightly or monthly from January 1997 to April 1998, monitoring the rivulet for between two and ten nights each visit, totalling 278 hours across 41 visits. The playback experiments were carried out between January and June 2001. Field observations were conducted from 1730 until 2400 or 0200, depending on the activity of the treefrogs.

Nocturnal observations were performed with a 6V spotlight, covered with sheets of thin red plastic when necessary. We measured the air temperature to the nearest 0.1 °C with a digital thermohygrometer. We employed focal-animal, sequence and all-occurrence sampling (Lehner, 1996). Focal animal sampling was conducted at intervals of one to five minutes, during which we recorded the types of vocalizations, the context in which they were emitted (territorial dispute or female attraction), air temperature, call rate and perch height.

We walked at regular time intervals (1 h) along a segment of the rivulet about 30 m in length to record the following: 1) number of calling males, 2) height of the calling sites, 3) vocalization types and 4) number of calls emitted.

**Table 1.** Acoustic parameters of the different types of vocalizations of *Scinax centralis* from the municipality of Silvânia, Goiás, Brazil. Data are presented as mean ± SD (min–max).

Characteristics	Advertisement call	Long aggressive call	Short aggressive call	Displacement call
Call duration (ms)	589±134 (390–909)	298±120 (110–597)	38.9±6.2 (30–46)	1,608±330 (1,401–1,988)
Number of notes	6.5±2 (1–10)	1	1	7±1 (6 or 7)
Note duration (ms)	31.4±1.8 (20–35.5)	298±120 (110–597)	38.9±6.2 (30–46)	119±199 (46–750)
Number of pulses per call	65.4±15.9 (44–102)	47.9±12.6 (24–74)	9.6±3.5 (3–14)	33±9 (27–40)
Pulse duration (ms)	3.3±0.4 (1–4.4)	3.8±0.3 (1–5)	3.7±0.56 (2–7.5)	8.1±3.2 (2–17)
Mean dominant frequency (kHz)	4.16±0.37 (3.49–4.89)	4.05±0.2 (3.78–4.47)	4.07±0.18 (3.78–4.57)	4.33±0.04 (4.3–4.4)
Intensity (dB)	62.1±9.1 (59.0–78.8)	60.8±5.4 (58.2–76.1)	60.2±5.50 (58.7–74.5)	–
Number of males recorded	23	19	22	4

We measured the sound intensity of three to five calls with a Minipa digital decibelimeter (fast setting) at 50 cm from the treefrog. All sound level measurements are expressed as dB SPL, with reference to  $2 \times 10^{-5}$  Pa. We recorded calls of 23 males with a Nagra E tape recorder and a Sennheiser ME80 directional microphone or a DAT TASCAM DAP1 and Sennheiser ME66 at 30–50 cm. After each recording or playback experiment session, we captured the male, measured its body length (snout–vent length, SVL) to the nearest 0.5 mm with a caliper and its mass to the nearest 0.05 g with a Pesola® scale, marked it by the toe clipping method (Martof, 1953), and released it at the same location it was captured.

The vocalizations were edited at a sampling frequency of 22kHz and a 16 bit resolution with a PC-Pentium computer and analysed with Avisoft-SONAGRAPH light and Cool Edit 96 software. Frequency information was obtained through Fast Fourier Transformation (FFT), (Width 1024 points). The audiospectograms were made with overlap 75%, Window Flat Top, Frame 100% and FFT-length 256. The bioacoustic terminology is in agreement with Duellman & Trueb (1986), Gerhardt (1998) and Wells (2007).

Playback experiments were conducted over 10 days, two to four hours after sunset. We visually located each calling male to be tested and the equipment (speaker and recorder) was prepared around 50 cm from the treefrog. The stimulus used in all playbacks consisted of a 1 min sequence of 10 advertisement calls recorded from a male (SVL = 18.4 mm; mass = 0.40 g) belonging to the study population.

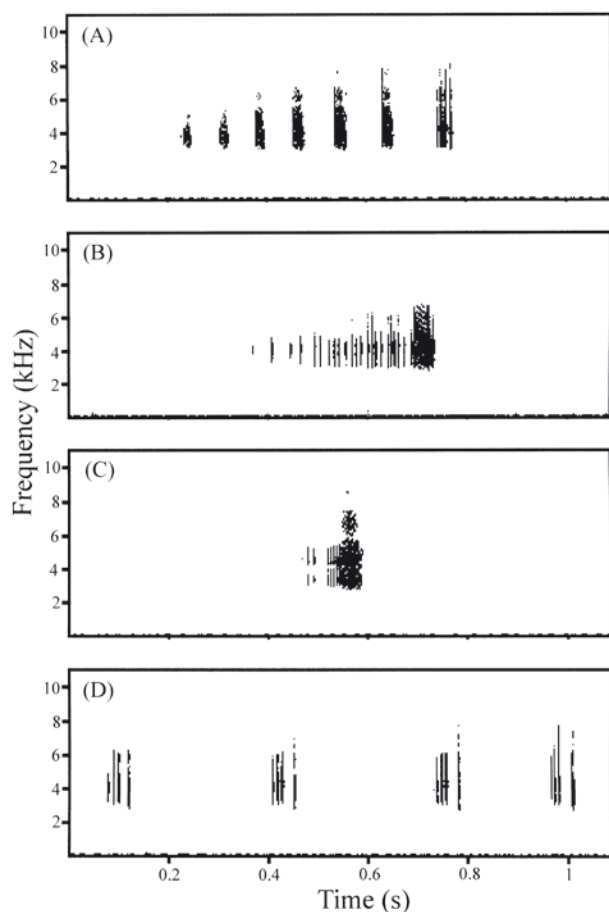
Playbacks of advertisement calls were made at modal amplitudes of 62 dB, 68 dB and 74dB, 50 cm from the speaker. In this population, the average sound level was 62.1 dB (present study) at 50 cm from the calling male.

Ten treefrogs were exposed to the three call amplitudes. An increase of 6 dB in call amplitude corresponds to a reduction in the distance to the tested male from the sound source by half. Thus, the calls were played in increasing amplitude, simulating an intruding male progressively approaching the focal male (from 50 to 25 cm, and from 25 to 12.5 cm).

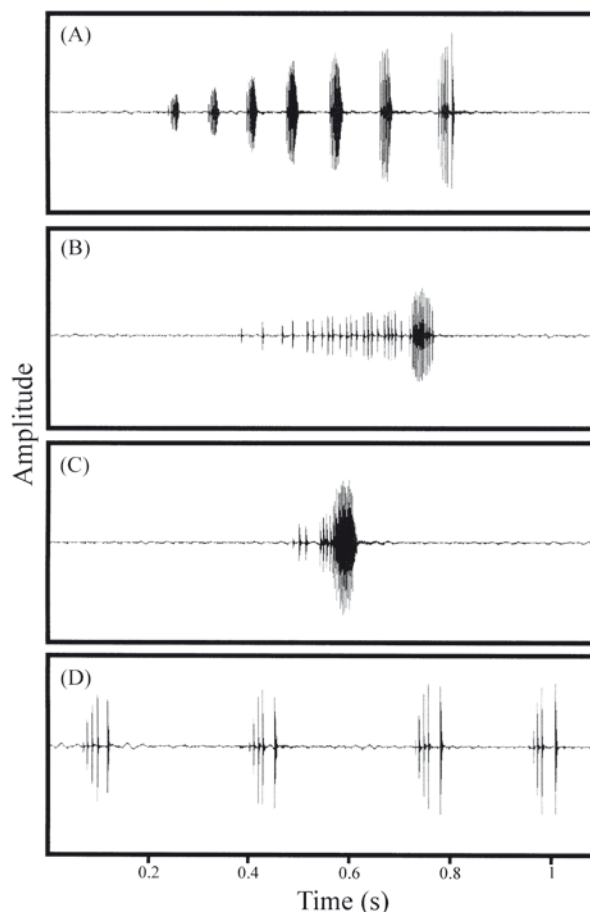
After preparing the site for playbacks, we waited for at least 10 minutes until the focal male resumed calling behaviour. We counted the number of calls emitted by the treefrog during a 1 min preliminary baseline period (pre-playback period). Advertisement and aggressive calls were counted separately because they differed in temporal structure. However, the different types of aggressive calls were counted together.

Following the 1 min baseline period, playback of the test stimulus was initiated. The number of calls emitted by the focal male was counted during the 1 min playback period. Following the end of the playback, the number of calls produced by the focal male for 1 min was also recorded. Playbacks were separated by 5–8 mins, and started when the focal treefrog began his next period of calling. We performed a set of control playbacks with five treefrogs. The protocol was the same as described above, except that signal amplitude remained at 62 dB for each of the three successive playbacks.

Prior to any statistical analysis, we tested homogeneity of variances and normality of data. We used Student’s t-test or the Pearson correlation coefficient (Zar, 1996) for analyses and to compare the relationship among following: 1) intensity of calls and number of individuals, 2) call rate and distance to the nearest calling male and 3) SVL/weight of the calling males and acoustic characteristics (duration, rate, dominant frequency and intensity of call).



**Fig. 1.** Sonograms of advertisement calls (A), long aggressive calls (B), short aggressive calls (C) and displacement calls (D) of *Scinax centralis*.



**Fig. 2.** Oscillograms of advertisement calls (A), long aggressive calls (B), short aggressive calls (C) and displacement calls (D) of *Scinax centralis*.

To compare the response of individuals to conspecific calls, we calculated the mean number and mean intensity of advertisement and aggressive calls given at each sound level. The different types of aggressive calls were considered as only one vocalization. Then we calculated an ANOVA (Zar, 1996). The level of significance was 0.05. Under Bonferroni correction, multiple F tests were tested at  $\alpha=0.016$  (0.05/3) (Rice, 1989). Voucher specimens and vocalizations were deposited in the Coleção Zoológica da Universidade Federal de Goiás (ZUFG).

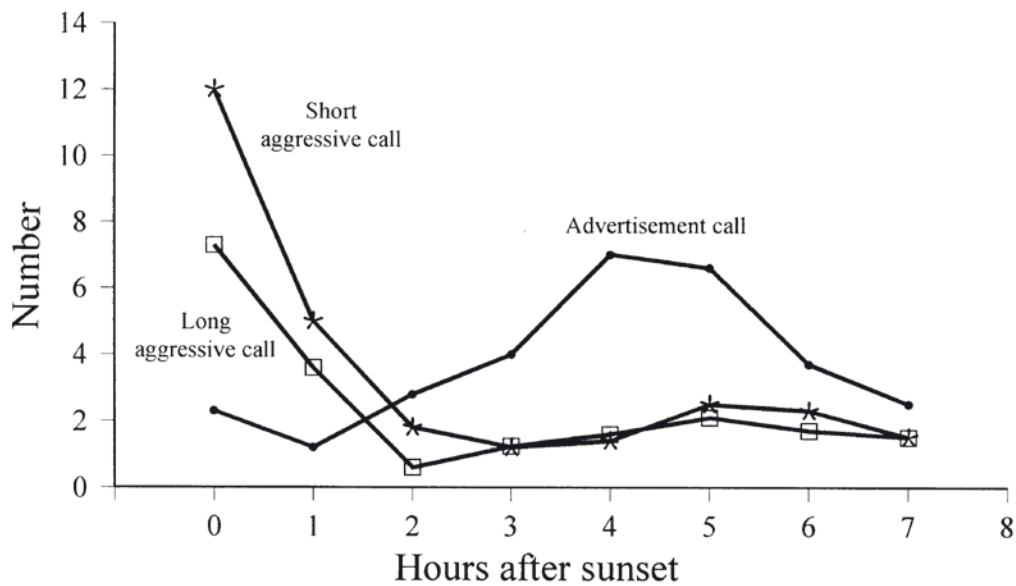
## RESULTS

Male *S. centralis* started calling activity an average of 18 minutes after sunset (SD=3.4 min;  $n=9$  nights). The nightly starting time for calling activity was positively correlated with time of sunset ( $r=0.90$ ;  $n=9$  nights;  $P<0.05$ ), but not with air temperature at dusk ( $r=0.58$ ;  $n=9$  nights;  $P>0.10$ ). Calling activity peaked at about four hours after sunset and began to decrease about six hours after dusk. At the beginning of the breeding season (December), reproductive activity extended up to about 0400, whereas at the end of the season (April) individuals stopped calling around 0130. Males used fallen branches emerging from the water or branches on the marginal vegetation up to

90 cm in height for calling ( $\bar{X}=27.71\pm19.99$ cm;  $n=129$  individuals). We did not observe any individual vocalizing in the water.

Male *S. centralis* emitted four distinct types of vocalizations (*sensu* Wells, 2007) with different structures and functions (Table 1): advertisement call (Figs 1a, 2a), two types of aggressive calls (Fig. 1b,c; Fig. 2b,c), and a displacement call (Figs 1d, 2d). The advertisement call is the primary vocalization because solitary males (in an average radius of 10.0 m) emitted only this call. Aggressive call type 1 (long aggressive call) was emitted when an intruder was noticed. When the last part of this call is emitted separately, we refer to it as aggressive call type 2 (short aggressive call). The short and long aggressive calls could be considered as components of an escalated system of aggressiveness. The displacement call was emitted by jumping males during displacement.

Early in the nightly activity, males emitted short and long aggressive calls, which decreased one hour after sunset (Fig. 3). Males emitted few advertisement calls at the beginning of choruses. The distance to the closest calling male was negatively correlated with emission rates of advertisement calls ( $r=-0.49$ ;  $P=0.02$ ;  $n=22$ ), long aggressive calls ( $r=-0.54$ ;  $P=0.02$ ;  $n=17$ ) and short aggressive calls ( $r=-0.55$ ;  $P=0.03$ ;  $n=16$ ).



**Fig. 3.** Mean number of advertisement and aggressive calls emitted by male *Scinax centralis* at different times.

The mean intensity of calls was positively correlated with the number of individuals present in the chorus (Table 2), as well as with SVL and body mass of the calling male for all the call types; call duration and call rate were unrelated to SVL and body mass (Table 3). There was a negative and significant correlation between mean dominant frequency of the three calls and the vocalizing male mass and SVL (Table 3).

In the control experiment, where the sound level remained at 62 dB in three successive playbacks, we did not observe any differences in call intensity and rate of the advertisement and aggressive calls during playback (Table 4). Therefore, the repeated presentation of stimuli is not cumulative, and any differences observed in the playback experiment resulted from the increase in sound level. In the playback experiment, males increased the number of advertisement or aggressive calls in relation to the pre-playback period (Fig. 4). On average, males emitted 421% more aggressive calls and 198% more advertisement calls compared to the pre-playback period. During the post-playback period, the number of aggressive calls increased with the sound level. The number of calls (advertisement or aggressive calls) emitted during

the playback period did not vary significantly with signal amplitude (Table 5; Fig. 4).

The intensity and number of calls emitted did not differ significantly during the three pre-playback periods (Table 5). The tested males increased the sound level of advertisement and aggressive calls during the playback period in relation to the pre-playback period for the three intensities (62, 68 and 74 dB; Table 5). In the post-playback period, the sound level was lower than in the playback period. However, there was a significant increase in mean advertisement call intensity during the playback period (Table 5).

DISCUSSION

*Scinax centralis*, similarly to other neotropical anurans, presents a complex vocal repertoire that is related to different social contexts (Bastos & Haddad, 1995; Martins et al., 1998, 2002; Guimarães & Bastos, 2003; Toledo & Haddad, 2005). The vocal repertoire of *S. centralis* is composed of the following four vocalizations (*sensu* Wells, 2007): an advertisement call, two types of aggressive call and a displacement call. The vocalizations have a pulsed structure, a widespread characteristic in the *S. catharinae* clade (Pombal et al., 1995; Bastos & Haddad, 2002).

Male *S. centralis* are influenced by the calling activity of their neighbours, as observed in other anuran species (Given, 1987; Bastos & Haddad, 2002). The calling pattern exhibited by male *S. centralis*, with a high incidence of aggressive calls at the beginning of a chorus, is similar to other species studied (Wells, 1978; Given, 1987). This strategy may allow males to establish territories before females arrive, reducing acoustic interference from neighbours (Bastos & Haddad, 2002; Given, 1987; Toledo & Haddad, 2005).

**Table 2.** Correlation between mean intensity of calls (dB) and number of individuals present in the chorus. *n*=number of calling males.

Vocalization	<i>r</i>	<i>P</i>	<i>n</i>
Advertisement call	0.512	<0.001	39
Short aggressive call	0.629	0.012	15
Long aggressive call	0.806	<0.001	12

**Table 3.** Correlation of SVL and body mass of calling male *Scinax centralis* with the variables of advertisement calls, long aggressive calls and short aggressive calls. *n* = number of calling males.

	Call variable	SVL			Mass		
		<i>r</i>	<i>n</i>	<i>P</i>	<i>r</i>	<i>n</i>	<i>P</i>
Advertisement call	Call duration	0.033	22	0.88	0.108	22	0.63
	Call rate	−0.09	43	0.55	0.118	43	0.45
	Dominant frequency	−0.62	22	0.002	−0.57	22	0.005
	Intensity	0.51	21	0.001	0.39	21	0.039
Long aggressive call	Call duration	0.474	20	0.034	0.179	20	0.451
	Call rate	0.244	30	0.193	0.307	30	0.099
	Dominant frequency	−0.68	19	0.001	−0.62	16	0.005
	Intensity	0.614	16	0.011	0.528	16	0.035
Short aggressive call	Call duration	0.406	13	0.169	−0.057	13	0.852
	Call rate	0.063	27	0.756	0.132	27	0.513
	Dominant frequency	−0.574	22	0.005	−0.529	22	0.011
	Intensity	0.48	19	0.036	0.54	19	0.016

The two aggressive calls could be considered as components of a graded aggressive signalling system, because the end of one vocalization is similar to the entire call of the other vocalization (see also Wells & Schwartz, 1984; Wells, 1989). Since the displacement calls are emitted during locomotion by males, they could have a territorial function. As the advertisement call was the only vocalization emitted by solitary males, it is the primary vocalization of *S. centralis* with functions in specific/individual recognition, territoriality and attraction of females.

That call intensity was positively correlated with SVL and mass was expected, because a large body size correspond with a large larynx (Márquez et al., 2005). Höglund

& Robertson (1988) stated that despite the call intensity being dependent on the distance from the sound source, larger males produce louder sounds that probably attract more distant females, and thus potentially attract a larger number of them. However, such a correlation is not always found (López & Narins, 1991; Esteban et al., 2002), and according to Márquez et al. (2005) environmental variables and social contexts also play an important role. We detected no relationship between some temporal parameters of the call and the male’s body size, similarly to other species for which call rate, intensity and duration are not related to male body size (e.g. *Pseudacris crucifer*, Forester et al., 1988). Giacoma et al. (1997) reiterated that the link between male size and temporal parameters is not

**Table 4.** Analyses of variance (ANOVA) between pre-, play- and post-periods in the control experiment for *Scinax centralis*.

	Intensity (dB)			<i>F</i>	<i>P</i>	Calls/min			<i>F</i>	<i>P</i>
	62	62	62			62	62	62		
a) Advertisement call										
Pre-playback	60.6	59.3	60.2	0.391	0.679	3.80	3.80	3.20	0.06	0.946
Playback	63.6	62.4	64.6	2.94	0.068	4.20	5.00	5.00	0.162	0.851
Post-playback	58	61.4	59.1	1.24	0.323	1.00	1.20	1.60	0.412	0.678
b) Aggressive call (short + long)										
Pre-playback	54.0	54.4	55.5	0.530	0.640	2.00	1.40	3.20	0.615	0.557
Playback	57.8	58.3	58.2	0.058	0.943	4.40	6.40	7.20	0.937	0.419
Post-playback	55.1	54.2	53.9	0.889	0.889	8.20	7.80	8.60	0.013	0.987



**Table 5.** Analyses of variance (ANOVA) between pre-, play- and post-periods at the three sound levels (62, 68 and 74) for *Scinax centralis*.

		Intensity (dB)				Calls/min					
		62	68	74	<i>F</i>	<i>P</i>	62	68	74	<i>F</i>	<i>P</i>
a) Advertisement call											
	Pre-playback	62.4	62.4	62.8	0.105	0.900	1.70	2.10	2.00	0.378	0.689
	Playback	65.7	68.9	70.8	20.9	0.0001	3.80	3.40	4.20	0.204	0.817
	Post-playback	65.3	62.8	64.2	2.66	0.093	1.00	1.20	0.70	0.643	0.534
b) Aggressive call (short + long)											
	Pre-playback	55.9	52.8	55.1	0.886	0.427	3.40	2.90	1.70	0.847	0.439
	Playback	59.2	63.0	62.4	1.68	0.200	8.90	13.40	9.20	1.60	0.220
	Post-playback	57.3	55.9	57.1	0.317	0.731	5.08	10.40	11.30	3.02	0.005

as clear as for spectral parameters, although the temporal characteristics of the call co-vary with size and air temperature. Because the dominant frequency is negatively correlated with SVL and body mass (Bee & Perril, 1996; Bastos et al., 2003; Toledo & Haddad, 2005; Giasson & Haddad, 2006), it could be informative for assessing the opponent’s size, avoiding physical combat and maintaining uniform spatial distributions. In *S. centralis*, our data indicate that advertisement and aggressive calls contain information regarding the combat ability of the vocalizing male, demonstrated by a negative correlation between dominant frequency and SVL as well as body mass.

We did not observe a significant difference in the number of advertisement and aggressive calls during the pre-playback periods of the series of three amplitudes (62, 68 and 74dB). As in other studies (e.g. Brenowitz, 1989), this indicates that individuals did not remain aroused from

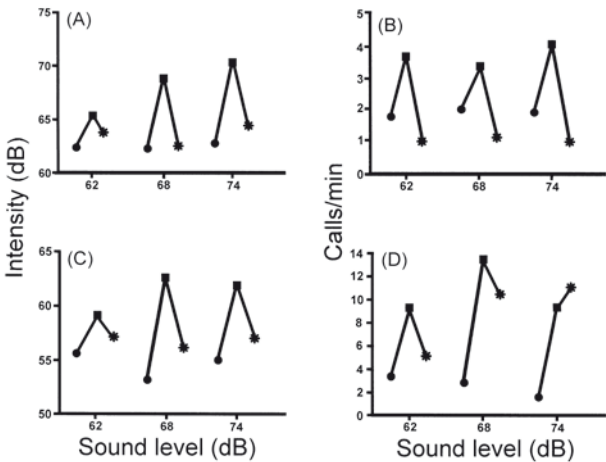
previous exposure to lower amplitude signals, emphasizing that the differences observed in calling activity were associated with an increase in the sound level.

In *Eleutherodactylus coqui*, males produce more aggressive calls and reduce the number of advertisement calls as the sound level increases (Stewart & Bishop, 1994). In *S. centralis*, the number of advertisement or aggressive calls emitted during the playback period did not significantly change, despite an increase in signal amplitude. However, the number of aggressive calls emitted during post-playback periods increased considerably as amplitude increased. A similar effect of the playback amplitude on calling behaviour has been observed in other studies (Wells & Schwartz, 1984; López et al., 1988; Rose & Brenowitz, 1991).

With increasing signal amplitude in playback experiments, male *S. centralis* emitted louder advertisement calls. More discernible calls may increase the reproductive success of calling males (Forester et al., 1988). Modifying its call rate or increasing the intensity of the call as the background noise in the reproductive aggregation increases, allows a male to become more audible, decreasing interference by neighbouring males (Ayre et al., 1984; Brenowitz, 1989; Wilczynski & Brenowitz, 1988; Boatright-Horowitz et al., 2000; Bee et al., 2001; Penna et al., 2005).

ACKNOWLEDGEMENTS

We thank C.P.A. Prado, P.A. Abrunhosa, T.F.L.V.B. Rangel and H. Wogel for critical reading of the manuscript, and D.M. Silva, S. Quail and B.D. Hawkins for help with the English. J. Vaz e Nunes and C.M. Vieira helped in the field work. The Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis allowed us access to the study area. The Centro Nacional de Pesquisa e Conservação de Répteis e Anfíbios (ICMBio/RAN) gave us a licence for capture/transportation. Financial support was provided by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Fundação de Apoio à Pesquisa-UFG (FUNAPE). CNPq and CAPES provided fellowships.



**Fig. 4.** Variation in intensity and call rate of advertisement calls (A, B) and aggressive calls (C, D), emitted by male *Scinax centralis* in the pre- (●), play- (■) and post- (✱) periods among the three sound levels (62, 68 and 74 dB).

## REFERENCES

- Alcantara, M.B., Lima L. & Bastos, R.P. (2007). Breeding activity of *Scinax centralis* (Anura, Hylidae) in central Brazil. *Iheringia, Série Zoologia* 97, 406–410.
- Ayre, D.J., Coster, P., Bailey, W.J. & Roberts, J.D. (1984). Calling tactics in *Crinia georgiana* (Anura: Myobatrachidae): alternation and variation in call duration. *Australian Journal of Zoology* 32, 463–470.
- Bastos, R.P., Bueno, M.A., Dutra, S.L. & Lima, L.P. (2003). Padrões de vocalização de anúncio em cinco espécies de Hylidae (Amphibia: Anura) do Brasil Central. *Comunicações do Museu de Ciências e Tecnologia da PUCRS, Série Zoologia* 16, 39–51.
- Bastos, R.P. & Haddad, C.F.B. (1995). Vocalizações e interações acústicas em *Hyla elegans* (Anura, Hylidae) durante a atividade reprodutiva. *Naturalia* 20, 165–176.
- Bastos, R.P. & Haddad, C.F.B. (1999). Atividade reprodutiva de *Scinax rizibilis* (Bokermann) (Anura, Hylidae) na Floresta Atlântica, sudeste do Brasil. *Revista Brasileira de Zoologia* 16, 409–421.
- Bastos, R.P. & Haddad, C.F.B. (2002). Acoustic and aggressive interactions in *Scinax rizibilis* (Anura, Hylidae) during the reproductive activity in southeastern Brazil. *Amphibia–Reptilia* 23, 97–104.
- Bee, M.A. & Bowling, A.C. (2002). Socially mediated pitch alteration by territorial male bullfrogs, *Rana catesbeiana*. *Journal of Herpetology* 36, 140–143.
- Bee, M.A., Kozich, C.E., Blackwell, K.J. & Gerhardt, H.C. (2001). Individual variation in advertisement calls of territorial male green frogs, *Rana clamitans*: implications for individual discrimination. *Ethology* 107, 65–84.
- Bee, M.A. & Perril, S.A. (1996). Responses to conspecific advertisement calls in the green frog (*Rana clamitans*) and their role in male–male communication. *Behaviour* 133, 283–301.
- Boatright-Horowitz, S.L., Horowitz, S.S. & Simmons, A.M. (2000). Patterns of vocal interactions in a bullfrog (*Rana catesbeiana*) chorus: preferential responding to far neighbors. *Ethology* 106, 701–712.
- Bosch, J. & Márquez, R. (1996). Acoustic competition in male midwife toads *Alytes obstetricians* and *Alytes cisternasii*: response to neighbor size and calling rate. Implications for female choice. *Ethology* 102, 841–855.
- Brenowitz, E.A. (1989). Neighbor call amplitude influences aggressive behavior and inter-male spacing in choruses of the Pacific treefrog (*Hyla regilla*). *Ethology* 83, 69–79.
- Brenowitz, E.A. & Rose, G. (1994). Behavioral plasticity mediates aggression in choruses of the Pacific treefrog. *Animal Behaviour* 47, 633–641.
- Duellman, W.E. & Trueb, L. (1986). *Biology of Amphibians*. New York: McGraw-Hill.
- Esteban, M., Sánchez-Herráiz, S., Barbadillo, L.J., Castanet, J. & Márquez, R. (2002). Effects of age, size and temperature on the advertisement calls of two Spanish populations of *Pelodytes punctatus*. *Amphibia–Reptilia* 23, 249–258.
- Forester, D.C., Lykens, D.V. & Harrison, K. (1988). The significance of persistent vocalization by the spring peeper *Pseudacris crucifer* (Anura: Hylidae). *Behaviour* 108, 197–208.
- Gerhardt, H.C. (1998). Acoustic signals of animals: recording, field measurements, analysis and description. In *Animal Acoustic Communication: Sound Analysis and Research Methods*. Hopp, S.L., Owren, M.J. & Evans, C.S. (eds). New York: Springer-Verlag.
- Giacoma, C., Zugolaro, C. & Beani, L. (1997). The advertisement calls of the green toad (*Bufo viridis*): variability and role in mate choice. *Herpetologica* 53, 454–464.
- Giasson, L.O.M. & Haddad, C.F.B. (2006). Social interactions in *Hypsiboas albomarginatus* (Anura: Hylidae) and the significance of acoustic and visual signals. *Journal of Herpetology* 40, 171–180.
- Given, M.F. (1987). Vocalizations and acoustic interactions of the carpenter frog, *Rana virgatipes*. *Herpetologica* 43, 467–481.
- Grafe, T.U., Steffen, J.O. & Stoll, C. (2000). Vocal repertoire and effect of advertisement call intensity on calling behavior in the West African tree frog, *Leptopelis viridis*. *Amphibia–Reptilia* 21, 13–23.
- Guimarães, L.D. & Bastos, R.P. (2003). Vocalizações e interações acústicas em *Hyla raniceps* (Anura, Hylidae) durante a atividade reprodutiva. *Iheringia, Série Zoologia* 90, 97–104.
- Höglund, J. & Robertson, J.G.M. (1988). Chorusing behaviour, a density-dependent alternative mating strategy in male common toads (*Bufo bufo*). *Ethology* 70, 324–332.
- Lehner, P.N. (1996). *Handbook of Ethological Methods*, 2<sup>nd</sup> edn. New York: Cambridge University Press.
- López, P.T. & Narins, P.M. (1991). Mate choice in the neotropical frog, *Eleutherodactylus coqui*. *Animal Behaviour* 41, 757–772.
- López, P.T., Narins, P.M., Lewis, E.R. & Moore, S.W. (1988). Acoustically induced call modification in the white-lipped frog, *Leptodactylus albilabris*. *Animal Behaviour* 36, 1295–1308.
- Luddecke, H. (2002). Male and female responses to call playbacks in the Andean frog *Colostethus subpunctatus*. *Amphibia–Reptilia* 23, 141–150.
- Márquez, R., Moreira, C., Amaral, J.P.S., Pargana, J.M. & Crespo, E.G. (2005). Sound pressure level of advertisement calls of *Hyla meridionalis* and *Hyla arborea*. *Amphibia–Reptilia* 26, 391–395.
- Marshall, V.T., Humfeld, S.C. & Bee, M.A. (2003). Plasticity of aggressive signalling and its evolution in male spring peepers, *Pseudacris crucifer*. *Animal Behaviour* 65, 1223–1234.
- Martins, M., Pombal Jr, J.P. & Haddad, C.F.B. (1998). Escalated aggressive behaviour and facultative parental care in the nest building gladiator frog, *Hyla faber*. *Amphibia–Reptilia* 19, 65–73.
- Martof, B.S. (1953). Territoriality in the green frog, *Rana clamitans*. *Ecology* 34, 195–174.
- Murphy, C.G. & Floyd, S.B. (2005). The effect of call amplitude on male spacing in choruses of barking treefrogs (*Hyla gratiosa*). *Animal Behaviour* 69, 419–426.
- Penna, M., Narins, P.M. & Feng, A.S. (2005). Thresholds for evoked vocal responses of *Eusophus emiliopugini* (Amphibia, Leptodactylidae). *Herpetologica* 61, 1–8.
- Pombal, Jr. J.P. & Bastos, R.P. (1996). Nova espécie de *Scinax* Wagler, 1830 do Brasil Central (Amphibia, Anura, Hylidae). *Boletim do Museu Nacional, N.S., Zoologia*, 371, 1–11.
- Pombal, Jr., J.P., Bastos, R.P. & Haddad, C.F.B. (1995).

- Vocalizações de algumas espécies do gênero *Scinax* (Anura, Hylidae) do sudeste do Brasil e comentários taxonômicos. *Naturalia* 20, 213–225.
- Rand, A.S. & Ryan, M.J. (1981). The adaptative significance of a complex vocal repertoire in a neotropical frog. *Zeitschrift für Tierpsychologie* 57, 209–214.
- Rice, W.R. (1989). Analyzing tables of statistical tests. *Evolution* 43, 223–225.
- Rose, G.J. & Brenowitz, E.A. (1991). Aggressive thresholds of male Pacific treefrogs for advertisement calls vary with amplitude of neighbor's calls. *Ethology* 89, 244–252.
- Rose, G.J. & Brenowitz, E.A. (1997). Plasticity of aggressive thresholds in *Hyla regilla*: discrete accommodation to encounter calls. *Animal Behaviour* 53, 353–361.
- Schwartz, J.J. & Wells, K.D. (1985). Intra- and interspecific vocal behavior of the neotropical treefrog *Hyla microcephala*. *Copeia* 1985, 27–38.
- Stewart, M.M. & Bishop, P.J. (1994). Effects of increased sound level of advertisement calls on calling male frogs, *Eleutherodactylus coqui*. *Journal of Herpetology* 28, 46–53.
- Tárano, Z. (2002). Vocal responses to conspecific call variation in the neotropical frog *Physalaemus enesefae*. *Journal of Herpetology* 36, 615–620.
- Toledo, L.F. & Haddad, C.F.B. (2005). Acoustic repertoire and calling behavior of *Scinax fuscomarginatus* (Anura, Hylidae). *Journal of Herpetology* 39, 455–464.
- Wells, K.D. (1977). The social behaviour of anuran amphibians. *Animal Behaviour* 25, 666–693.
- Wells, K.D. (1978). Territoriality in the green frog (*Rana clamitans*): vocalizations and agonistic interactions. *Animal Behaviour* 26, 1051–1063.
- Wells, K.D. (1989). Vocal communication in a neotropical treefrog, *Hyla ebraccata*: responses of males to graded aggressive calls. *Copeia* 1989, 461–466.
- Wells, K.D. (2007). *The Ecology and Behavior of Amphibians*. Chicago: University of Chicago Press.
- Wells, K.D. & Greer, B. (1981). Vocal responses to conspecific calls in a neotropical hylid frog, *Hyla ebraccata*. *Copeia* 1981, 615–624.
- Wells, K.D. & Schwartz, J.J. (1984). Vocal communication in a neotropical treefrog, *Hyla ebraccata*: advertisement calls. *Animal Behaviour* 32, 405–420.
- Wilczynski, W. & Brenowitz, E.A. (1988). Acoustic cues mediate inter-male spacing in a neotropical frog. *Animal Behaviour* 36, 1054–1063.
- Zar, H. (1996). *Biostatistical Analysis*. Englewood Cliffs: Prentice Hall.

Accepted: 20 October 2010