

Territoriality, agonistic behaviour, and vocalization in *Pseudis bolbodactylus* A. LUTZ, 1925 (Anura: Hylidae) from Central Brazil

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Abstract. We describe the social behaviour related to breeding in *Pseudis bolbodactylus* from Central Brazil. We analyzed the territoriality, spatial distribution, calling sites, call types, and present notes on the breeding activity of the species. Males of *P. bolbodactylus* did not search actively for females, being territorial and defending their call sites against invaders by acoustic and agonistic interactions. Each male had a floating territory, which was occupied and defended in distinct areas at different nights. Territorial call, encounter call, and agonistic behaviour are herein described for the first time for *P. bolbodactylus*.

Key words. Amphibia: *Pseudis bolbodactylus*, reproduction, breeding activity, inter-male interactions and calling sites, Neotropics.

Introduction

One of the most studied aspects of the anuran social behaviour is related to reproductive strategies (e.g. communication, territoriality, reproductive success), presenting an extensive literature (e.g. DUELLMAN & TRUEB 1986, JUNGFER 1996, BEVIER 1997, ORLOV 1997, MEASEY & TINSLEY 1997, VAIRA 2001, GUIMARÃES & BASTOS 2003, RODRIGUES et al. 2003, GIARETTA & MENIN 2004, MENIN et al. 2004, WOGEL et al. 2004). Reproductive strategies can be interpreted as being a blend of physiological, morphological and behavioural attributes that under specific environmental conditions produce an optimal number of descendents (DUELLMAN & TRUEB 1986).

During the breeding season, males of many anuran species defend territories or call sites in choruses (WELLS 1977, BURMEISTER et al. 1999). According to DUELLMAN & TRUEB (1986), a territory can be defined as an area coincident with, or within, the home range that is defended against intruders. The defense of a particular site is advantageous if it promotes access and resources to an indi-

vidual that are needed for its own survival or reproduction. Agonistic behaviour, one consequence of the defense of a specific site, has been observed in males of many species of anurans (WELLS 1977). Many of these interactions occur during courtship, and include specific vocalizations that play an important role in territory defense.

According to SAVAGE & CARVALHO (1953) *Pseudis* is of masculine gender, giving us ground to refer the species as *P. bolbodactylus*. Nevertheless, many recent authors treat it as feminine (e.g. CARAMASCHI & CRUZ 1998, BRANDÃO et al. 2003, FROST 2004, MELCHORS et al. 2004, TEIXEIRA et al. 2004, FROST et al. 2006). *Pseudis bolbodactylus* A. LUTZ, 1925 is an exclusively aquatic species that occurs in the States of Bahia, Minas Gerais, northern Espírito Santo and Goiás, Brazil (CARAMASCHI & CRUZ 1998, FROST 2004). Information on the natural history of this species is scarce, with only one study describing the advertisement call (GUIMARÃES et al. 2001), and two others on diet, habitat use, and antipredator behaviour for one population from Central Brazil (BRANDÃO et al. 2003) and diet and some ecological data

for one population from southeastern Brazil (TEIXEIRA et al. 2004).

The goal of this study was to describe aspects of the reproductive behaviour of *P. bolbodactylus*, mainly those related to territoriality (agonistic behaviour, calling sites and types, spatial distribution, inter-male spacing, displacement), for a population from Central Brazil.

Materials and methods

This study was conducted between May 2003 and May 2004 in a permanent pool (17°21'31.6"S; 49°05'59.5"W) with a surface area of about 470 m², in the municipality of Piracanjuba, state of Goiás, Central Brazil. The pool has abusive vegetation around its external border, and emergent vegetation around its internal border. Its mean depth is around 60 cm. We observed for approximately 115 hours over the course of 35 nights. Observations started at around 17.00 hrs, and extended for a variable period of time, depending on the level of chorus activity.

During sixteen nonconsecutive nights between December and May, the pool was subdivided into imaginary quadrants (ca. 32 m² each), in which the positions of all the males were marked, making possible to calculate the density and the individual distance to the nearest neighbor. These data were used for the analysis of spatial dispersion, following CLARK & EVANS (1954): $R = r_a/r_c$; where R = degree in which an observed distribution deviates from the random expectation; r_a = mean of observed distances between the individuals in the choruses ($r_a = \sum r/n$, where r = distance between the individuals and n = the number of individuals present in the chorus); and r_c = mean distance that would be expected if the population were distributed randomly ($r_c = 1/2\sqrt{\rho}$, where ρ = density of the individuals). The significance of the difference between the values of r_a and r_c was tested by the deviation from the normal curve: $c = (r_a - r_c)/\sigma r_c$; where c is the stand-

ardized variation of the normal curve, and σr_c represents a standard error of the mean distance between the neighbors in a population with random distribution with the same density observed in the analyzed population.

During the nights of observation took place ($n = 35$), the following information were recorded: number of males and females, climatic conditions (wind, rain, thunders), luminosity (clear night, dark night), temperature and relative humidity of the air (with a Minipa® MT-241 digital thermohygrometer), and water temperature at a maximum depth of 5 cm (with a mercury thermometer with a precision of 0.5 C).

Specimens were collected with dip nets and by hand; furthermore, they were weighted on a Pesola® scale (precision 0.05g) and measured (snout-vent length, SVL) with a Mytutoyo® digital calliper (precision 0.1 mm). Specimens collected were marked by toe clipping (MARTOF 1953), and released in the place of capture.

Vocalizations were recorded with a Sony® DAT TCD-D100 recorder, and a Sony® ECM-MS907 directional microphone. Immediately after recording, males were collected and the following data were obtained: air temperature, water temperature, recording time, and relative humidity. The vocalizations were edited at a sampling frequency of 22 kHz and 16 bite resolution with a PC-Pentium computer, and analyzed with Avisoft Sonograph Light (version 2.75 for Windows) and Cool Edit 96 (version 1.0, Syntrillium Software Corporation) software. Oscillograms and sound spectrograms were produced with 256 points overlap of 100% in flat top.

The terms related to the bioacoustic parameters followed DUELLMAN & TRUEB (1986) and GERHARDT (1998). Correlations between the number of calling males and the environmental factors, and between the number of calling males and density, were tested using the Pearson's correlation coefficient. The level of significance considered was $P < 0.05$ (ZAR 1996).

Results

Considerations about breeding activity, inter-male spacing and calling sites

Breeding activity of *Pseudis bolbodactylus* was evidenced by the presence of calling males and occurred from September to May, a period coincident with the rainy season in the Cerrado biome (OLIVEIRA & MARQUIS 2002). The correlation between the water temperature registered at the beginning of the night (19.00 hrs) and the number of males in reproductive activity was positive and significant ($r = 0.413$; $P = 0.020$; $N = 28$). There was no significant correlation between the number of males at the reproductive site and the air temperature ($r = 0.140$; $P = 0.450$; $N = 31$), or relative humidity of the air ($r = 0.020$; $P = 0.890$; $N = 31$). Snout-vent length (SVL) of males varied from 40 to 50 mm (45.6 ± 2.9 mm; $N = 15$) and mass varied from 11 to 20 g (15.8 ± 2.9 g; $N = 15$).

Adult males have a single vocal sac and, during the breeding season, the gular region turns yellow, evidencing sexual dimorphism and ontogenetic variation, because this colour pattern was never seen in females or in juveniles. Pairs in amplexus were had never been observed. On 15 December 2003, one male (SVL = 43.5 mm; mass = 15 g) and one female (SVL = 50 mm; mass = 19 g) were captured and placed in the same plastic bag with the intention of stimulating mating. The male amplexed the female and the spawn was obtained. The spawn was characterized by bipolar black and cream eggs, which were held together by a gelatinous layer that adhered to particles in suspension in the water. The clutch (230 eggs) was divided in small clumps. The tadpoles hatched after three days.

Females arrived at the reproductive site at around 20.00 hrs ($N = 2$). On 26 February 2004 an amplexant pair was observed *in loco* at around 20.30 hrs. Tadpoles were found throughout the entire reproductive season (September to May). Recently metamorphosed froglets were observed in December.

Distance between males varied from 0.15

to 12 m (3.03 ± 3.2 m, $N = 83$). In 100% of the examined choruses, males occupied the calling sites following a random pattern. As calling sites, the males occupied areas next to (ca. 15 cm) the aquatic marginal (94.5%) and emergent, floating (5.5%) vegetation. Mean density of males in the pool was 0.01 males/m² (= one male per 100 square meters) (range = 0.004 - 0.021; $N = 20$ nights on which observations were made). Eight males were recaptured from one to five times, totaling 18 recaptures. Two of the eight recaptured males were still in the initial territory. The maximum displacement observed was of 10 m.

Vocalizations and agonistic behaviour

Males occupied the territories and initiated isolated vocalizations at about 1 h 15 min before sunset ($N = 8$ days). There was no significant correlation between the beginning of the vocalizations and the time of sunset ($r = 0.44$; $P = 0.231$; $N = 9$), nor with the air temperature ($r = 0.36$; $P = 0.337$; $N = 9$) and relative humidity of the air ($r = 0.60$; $P = 0.08$; $N = 9$). Vocalizations ceased in wind, rain, or thunders, restarting after them. Apparently, calling activity of males was more intense during clear nights.

Five types of vocalizations were observed (*sensu* DUELLMAN & TRUEB 1986) in *Pseudis bolbodactylus*: advertisement call, territorial call, encounter call, release call, and distress call. The most common was the advertisement call. During the silent periods of the advertisement call, males emitted a different and shorter vocalization, interpreted as a territorial call. The encounter call was recorded only once during the agonistic interaction of two males. On 26 December 2003, the emission of the release call was observed when one male accidentally grasped another male. On some occasions males emitted another type of vocalization while being handled for measuring and weighing, which was interpreted as a distress call. The release call and the distress call were not recorded.

The advertisement call (Fig. 1) showed pulsed structure (N = 10 calls by different males) formed by one note with a mean total duration of 183 ± 17.62 ms (N = 10 calls).

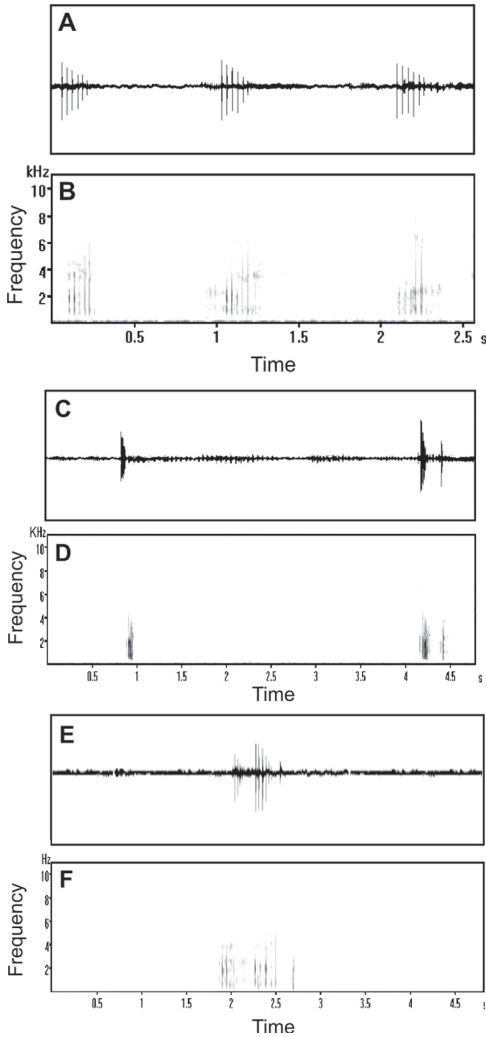


Fig. 1. Oscillograms and sound spectrograms of three advertisement calls (A and B) (23 December 2003, 25 °C), two different (type I and type II) territorial calls (C and D) (26 December 2003, 25 °C), and one encounter call (E and F) (26 December 2003, 25 °C) of *Pseudis bolbodactylus* recorded in Piracanjuba, Central Brazil.

Mean number of pulses in each call was 6.6 ± 0.9 (N = 10 calls), with a mean duration of 5.4 ± 2.46 ms each (N = 50 pulses). Mean interval between calls was 1.50 ± 1.30 s (N = 10 calls), and mean rate of repetition was 14 ± 8.48 calls per minute (N = 2 males). Mean dominant frequency was 1936.8 ± 138.7 Hz (N = 10 calls), ranging from 1828.0 to 2305.0 Hz.

Two types of territorial calls were recorded (Fig. 1). The first territorial call (type I) was formed by one note and one pulse, with a mean duration of 50.25 ± 26.88 ms (N = 5 calls by different males). The second territorial call (type II), rarer than the first one, was formed by two notes. It had a duration of 243 ms (N = 1), being formed by two pulses. The interval between the notes of the type II call was 63 ms, and mean duration of each note was 46.5 ms. The territorial calls (type I and type II) were emitted at a mean interval of 3.71 ± 0.92 s and an average repetition call rate of seven calls per minute. Mean dominant frequency was 1892 ± 379.31 Hz (N = 5 calls), ranging from 1590 to 2544 Hz.

The encounter call analyzed (Fig. 1) was composed of three pulsed notes, with a total duration of 512 ms. The first note was formed by four pulses and had a duration of 110 ms. The second note was formed by seven pulses and had a duration of 181 ms. The last note was formed by one pulse, with a duration of 31 ms. Mean interval between notes was 90.5 ms and call dominant frequency was 1961 Hz.

Agonistic interactions were observed on nine different nights. They involved changes of call and posture, chases, and physical interactions. The resident male was generally emitting advertisement calls when the intruder male approached, in a satellite posture, and stopped at a mean distance of 40 cm (N = 11 observations). The intruder male emitted territorial calls and maintained a submission posture, with the vocal sac deflated. The resident male emitted the territorial call and swam toward the intruder. Physical combat, involving butting and pushing, followed

100% of the encounters, and was always preceded by the emission of the encounter call. In all the observations, the intruder males swam away and were expelled from the residents' territory. Soon after, the resident male recommenced to emit the advertisement call. The number of combats per day was positively correlated with the density of specimens in the pool ($r = 0.976$, $P = 0.004$; $N = 9$).

Discussion

Pseudis bolbodactylus is considered as a prolonged breeder (*sensu* WELLS 1977), like other species of pseudines: *Lysapsus limellus* (PRADO & UETENABARO 2000), *Pseudis paradoxus* (DIXON et al. 1995), *P. cardosoi* (KWET 2000, KWET 2001), and *P. minutus* (MELCHIORS et al. 2004). As observed in *P. cardosoi* by KWET (2000), the spawn of *P. bolbodactylus* is characterized by bipolar eggs held together by a gelatinous layer that adheres to particles suspended in the water, providing a better camouflage against predators. In the natural environment, these gelatinous capsules fix the eggs to the floating vegetation of the pool (WV, pers. obs.).

In spite of low densities at the studied site, the analysis of the spatial distribution showed a random pattern in the aggregations. The pattern of *P. bolbodactylus* male distribution indicated that the individuals did not maintain a uniform separation among them. Some factors, like density of males and vegetation structure, can explain the spacing of the individuals in the reproductive aggregations (ROBERTSON 1984, MITCHELL & MILLER 1991). According to BRANDÃO et al. (2003), the presence of aquatic and emergent vegetation in the pool is essential for the presence by *P. bolbodactylus*. This can be explained by the high number of potential prey items (mainly insects) that is usually associated with it, and because vegetation provides additional protection against predators during the calling activity (BRANDÃO et al. 2003),

besides appropriate sites to spawn.

Males of *P. bolbodactylus* do not search actively for females, being territorial and defending their calling sites against invaders through acoustic and aggressive interactions. They do not have permanent calling sites, defending distinct areas at different nights (floating territories, *sensu* WILSON 1975). Territoriality and agonistic behaviour have been described for many families of anurans (Bufonidae: CRUMP 1988; Centrolenidae: DUELLMAN & SAVITZKY 1976; Dendrobatidae: DUELLMAN 1966; Hylidae: BASTOS & HADDAD 1995; Leptodactylidae: BRATTSTROM & YARNELL 1968; Ranidae: MARTOF 1953; Rhacophoridae: ARAK 1983). This paper is the first to describe agonistic behaviour and territoriality in pseudines.

During agonistic interactions, many species show stereotypical postures and other visual displays as a sign of threat (WELLS 1977). In *P. bolbodactylus* the resident male maintains the vocal sac inflated, although no vocalization is emitted. In contrast, the intruder male maintains its submissive posture, maintaining only the top of the head out of the water.

In anurans, the agonistic behaviour does not necessarily end or culminate in physical combat. The resident male can exhibit three different behaviours: attack the intruder, abandon the calling site, or coexist with the intruder (BURMEISTER et al. 1999). While analyzing the agonistic behaviour of *Acris crepitans* (Hylidae), BURMEISTER et al. (1999) suggested that external factors to the individuals have a fundamental role in their decision. Local density was the most important variable in the decision of the resident male, when compared to the acoustic variables and to the size of the males involved in the combat. In this study, all of the agonistic interactions observed between males of *P. bolbodactylus* ended in physical combats, and resident males always won, remaining in the calling site. Some authors have shown that the residence (POMBAL et al. 1994) and the relative

body size (GIVEN 1988, TEJEDO 1988) are determinant parameters for success in physical interactions. KREBS & DAVIES (1996) proposed two other reasons favoring victory by resident males. The first would be that resident males are better fighters; second, they have more to lose, because they are familiar with their territory and the best sites to forage and spawn.

For many species stereotypical postures and visual displays are usually sufficient to avoid fights, therefore decreasing the potential risk for injuries. Clearly, more detailed investigations must be done to elucidate why males of *P. bolbodactylus* always fight, as they live in low densities at the studied site.

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