

Habitat use, reproductive traits and social interactions in a stream-dweller treefrog endemic to the Brazilian Cerrado

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Abstract. The richest anuran fauna is found in the Neotropics, but the natural history of most species is unknown. *Bokermannohyla ibitiguara* is a stream-dweller treefrog endemic to the Brazilian Cerrado and classified as “Data Deficient” by the IUCN. Herein we describe the species’ reproductive biology. Fieldwork was conducted from August 2010 to July 2011. Reproductive activity occurred from October to June and was positively correlated with air temperature, humidity, and monthly rainfall. Individuals were observed only in gallery forests at the margins of streams and males used various kinds of substrates as calling sites. Males did not aggregate in specific parts of the streams and spatial distance between males was higher in the dry season. Males and females did not differ in length, but females without mature oocytes were lighter than males. The reproductive investment (gonad mass/body mass) of males was 0.29% and that of females was 20.26%. Female ovaries contained a mean of 202 ± 75 mature oocytes with a mean diameter of 1.96 ± 0.16 mm. We describe, for the first time for the genus, a complex courtship behaviour and also male-male fight and satellite behaviour. The Cerrado is probably the most threatened savanna in the world, having been intensively modified over the last decades. Endemic species associated to gallery forests, such as *B. ibitiguara*, are highly vulnerable to habitat alterations. Thus, our study provides important data on the species’ biology, which might be useful for conservation practices, but also to investigate taxonomic and phylogenetic relationships in this genus.

Keywords: *Bokermannohyla ibitiguara*, calling sites, courtship behaviour, Hylidae, temporal distribution.

Introduction

Currently, 5966 amphibian anurans are known in the world (Frost, 2011), with the highest diversity found in the American tropics (Duellman, 1988). The greatest anuran richness, 946 species, is found in Brazil (Segalla et al., 2012), with approximately 60% of endemism (Vasconcelos and Rossa-Feres, 2005). Despite the great diversity in the Neotropics, approximately 35% of the amphibians are endangered due to habitat loss or fragmentation, as well as a result of habitat split (Becker et al., 2007; Loyola et al., 2008), and its huge fauna is still poorly known (Haddad and Prado, 2005; Toledo and Batista, 2012). This combination of facts makes the study of species’ natural history and ecology

urgent, in order to support conservation practices.

The natural history of species is important not only for conservation purposes but also in phylogenetic and evolutionary contexts. For instance, studies on anuran social interactions may help understand sexual selection mechanisms (e.g. Wells, 1977a, 1977b; Montanarin, Kaefer and Lima, 2011). Social interactions in anurans include courtship behaviours of varying complexity, involving acoustic and tactile communication (e.g. Zina and Haddad, 2007), and aggressive behaviour, with vocal duels and physical combats between males (e.g. Martins, Pombal-Jr and Haddad, 1998). Although our knowledge of anuran social systems has greatly improved over the last decades (e.g. Wells, 1977a; Kirkpatrick and Ryan, 1991; Ryan, 1997; Ursprung et al., 2011), our understanding is limited by the lack of detailed studies on tropical species, which account for much of the morphological, taxonomic, behavioural, and ecological diversity in this group (Zamudio and Chan, 2008).

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The genus *Bokermannohyla* (Faivovich et al., 2005), within the family Hylidae, includes 29 species, distributed in central, south and southeastern Brazil (Frost, 2011). Together with the genera *Hyloscirtus*, *Miersiohyla*, *Hypsiboas* and *Aplastodiscus* they form the Cophomantini tribe, a well-supported clade (Faivovich et al., 2005; D'Heursel and Haddad, 2007). *Bokermannohyla ibitiguara* (Cardoso, 1983) is a stream-dweller treefrog, endemic to the Cerrado in Southeastern Brazil. The species is currently placed in the *B. pseudopseudis* group, with *B. alvarengai*, *B. pseudopseudis*, *B. saxicola*, *B. oxente*, and *B. itapoty* (Faivovich et al., 2005; Frost, 2011). General information on its natural history can be found in the original description (Cardoso, 1983). It is a medium-size species, the male advertisement call is composed of primary and secondary notes, and adults inhabit rocky environments along small streams (Cardoso, 1983). Population status is unknown and reproductive behaviour had never been studied in detail, reasons used to include *B. ibitiguara* in the Data Deficient category by the IUCN (Caramaschi and Eterovick, 2004).

Herein, we describe the reproductive biology of *B. ibitiguara*, including habitat use patterns, breeding period, and social behaviours, such as a complex courtship and male-male fight, both described for the first time for the genus *Bokermannohyla*. Moreover, following the recommendation of Pimenta et al. (2005), that researchers should concentrate efforts to study Data Deficient species to obtain information on their population status, we believe that the results reported here will be extremely useful for conservation practices, but also to solve taxonomic and phylogenetic questions.

Materials and methods

Study area

The study site is located within the Cerrado morphoclimatic domain. The Cerrado is the largest, most species-rich and, probably, most threatened tropical savanna in the world (Silva and Bates, 2002), thus it is one of the 25 most threat-

ened hotspots on Earth (Myers et al., 2000). The topography is mountainous, with flat or rounded hills, reaching up to 1500 m in elevation, with deep valleys and many streams (Dietz, 1984). The region was originally covered by the Cerrado vegetation, grassland fields at higher elevations, gallery forests in the valleys along streams, and patches of semideciduous forest (Dietz, 1984). Currently, much of the region has been modified into pastures. The climate is markedly seasonal, with a hot and rainy summer (October to March) and a dry winter (April to September), with total annual precipitation between 1300–1700 mm (Queirolo and Motta-Junior, 2007).

Fieldwork was conducted at private farms in the municipality of Sacramento (19°51'S; 47°26'W), Minas Gerais state, Southeastern Brazil. Three streams were sampled: (i) permanent stream 1 (20°16'21.9''S; 47°04'24.5''W; 677 m elevation); (ii) temporary stream (20°13'09.9''S; 47°06'21''W; 880 m elevation), and (iii) permanent stream 2 (20°12'20.1''S; 47°07'53.6''W, 839 m elevation).

Data collection

Seventeen field expeditions yielded 190 hours of observations throughout a whole year (August 2010 to July 2011). Two field expeditions per month were made in the rainy season, except for March ($n = 11$ expeditions; 160 hours) and one per month in the dry season ($n = 6$ expeditions; 30 hours), lasting about 5 hours per night. For permanent streams 1 and 2, we sampled about 50 m in extension, with a total of 80 and 75 hours of observations, respectively. For the temporary stream, we sampled about 30 m, with a total of 35 hours of observations.

Individuals were found by active search at breeding sites guided by male vocalizations and were observed with flashlights. To reduce the interference of luminosity on the frogs' behaviour, red lights were used (e.g. Miranda et al., 2008), avoiding, whenever possible, to point the light focus directly toward the individuals. To examine some reproductive traits (see below), 21 adult males and eight females were hand-captured, anesthetized with lidocaine 10%, fixed in formalin 10%, and preserved in alcohol 70% (McDiarmid, 1994). The 29 specimens were deposited at the CFBH (Célio F. B. Haddad) amphibian collection, Universidade Estadual Paulista, Rio Claro, São Paulo state, Brazil (males: CFBH31743 to CFBH31763; females: CFBH31764 to CFBH31771).

Male calling sites

We evaluated male abundance in each type of substrate, such as leaf, trunk, branch, water, hidden places, and ground. We measured horizontal distance from the water (DFW), height above water (HAW) and height above ground (HAG). Distance to the nearest neighbor (DNN) ranged from less than 1 m to approximately 10 m, and was registered categorically: less than 1 m; 1 to 5 m; 5 to 10 m and over 10 m. We performed a Chi-squared test for the frequencies of less than 5 m and more than 5 m, comparing the DNN between the rainy season (Oct-Mar) and dry season (Apr-Sep). We used 5 m as a threshold because it represents the approximate mid-point of the range. During the study period, we found only nine females, thus we could not evaluate habitat use nor distance between them.

Temporal distribution and temporal breeding pattern

The numbers of calling males and active females were registered every night. Rainfall (monthly accumulated rainfall) and air humidity (mean monthly air humidity) were obtained from the meteorological station of the municipality of Sacramento, from the National Institute of Meteorology (INMET), distant ca. 60 km from the study sites. Air and water temperatures were registered at each stream every night with an analogical thermometer, from which we calculated mean monthly air and water temperatures. Water temperature was measured at about 10 cm depth. To verify abiotic effects on species activity, we performed a multiple correlation analysis, using Kendall's rank correlation coefficient (Zar, 1999).

Body size and reproductive traits

Body mass and snout-vent length (SVL) of 57 males were measured in the field with a dynamometer (0.1 g) and analogical calipers (0.05 mm), respectively. Furthermore, body mass of eight females and SVL of nine females were also measured in the field. Measures of 10 males collected in a preliminary field trip were included in some of the analyses (see below). Males were recognized by the presence of secondary sexual traits: developed prepollex, hypertrophied forearm, and yellowish vocal sac. To verify the occurrence of sexual size dimorphism (SSD), SVL and body mass of males and females were log-transformed, checked for normality with Shapiro-Wilk test, and mean values were compared through a Student's *t*-test (Zar, 1999).

The reproductive mode of the species was defined according to Haddad and Prado (2005). Since we did not find any clutches in the field, mature oocytes in the ovaries of gravid females ($n = 6$ females) were analyzed to obtain information on mean mature oocyte diameter, mean ovary mass and mean number of mature oocytes per female. Diameter of approximately 10 oocytes per female was measured under a Leica stereomicroscope with a photo capturing software (Leica Application Suite).

The reproductive investment (RI) was calculated for the preserved specimens (males and females), as the percentage of gonad mass/body mass (Prado and Haddad, 2005). Body and gonad mass were measured in a digital balance (0.001 g). Although body mass of some individuals had already been measured in the field with a dynamometer, we measured them more accurately in the lab prior to RI calculation. Males collected in a previous field trip, in January 2010, were also used ($n = 10$).

Social interaction observations

To study social interactions, we used the methods of focal-animal sampling, all occurrences sampling, and sequence sampling (Altmann, 1974). Animals were recognized through natural skin marks (spots, scars, etc.; Bradfield, 2004). Males and females were differentiated in the field by the secondary sexual traits described above.

Results*Male calling sites and chorus structure*

Males of *B. ibitiguara* were observed calling only inside the gallery forests, along the streams covered by the canopy. They were found calling (i) from tree or shrub leaves (56.6%; $n = 129$), (ii) on trunks (21.9%; $n = 50$), (iii) from branches (10.1%; $n = 23$), (iv) inside hidden places – among roots and leaves, under rocks or fallen trunks – (7.5%; $n = 17$), (v) on the ground (2.2%; $n = 5$), and (vi) partially submersed in the water (1.8%; $n = 4$). When males called perched, they could be either above the water or above the ground: mean HAW was 1.13 ± 0.89 m (range 0–2.93 m; $n = 67$) and mean HAG was 0.99 ± 0.74 m (range 0–2.93 m; $n = 136$). In the last case, mean DFW was 0.67 ± 0.64 m (range 0.05–3.54 m; $n = 117$).

Calling males did not aggregate at specific sites, but rather they were distributed sparsely along the streams. Only 4.3% of males participating in the chorus were less than 1 m from the nearest calling male, 45.7% were distant between 1 and 5 m, 19.7% between 5 and 10 m, and 30.3% were farther than 10 m from the nearest calling male. Comparing the frequencies between seasons, males tend to be closer (<5 m) to each other in the rainy season, and more distant (>5 m) in the dry season (Chi-square $\chi^2_1 = 10.21$, $P < 0.05$).

Temporal distribution and temporal breeding pattern

Bokermannohyla ibitiguara exhibited a prolonged breeding pattern (sensu Wells, 1977a). Considering the three water bodies sampled, calling males of *B. ibitiguara* were observed from October to June, ranging from three individuals in June to 20 in February. Adult females were found in November ($n = 2$), January ($n = 3$), February ($n = 3$) and April ($n = 1$), at most one per night.

Maximum number of calling males per month correlated significantly with air temperature (Kendall's rank coefficient $\tau = 0.52$, $P <$

0.05; $n = 11$), relative air humidity ($\tau = 0.69$, $P < 0.05$; $n = 11$), and total monthly rainfall ($\tau = 0.52$, $P < 0.05$; $n = 11$).

Body size and reproductive traits

Average SVL and mass of males and females are shown in table 1. Females without eggs were significantly lighter than males (Student's t -test $t_{73} = 3.09$, $P < 0.05$), but they did not differ in SVL ($t_{74} = -0.12$, $P = 0.91$).

During observation of courtship 1 and 2 (see below), it was possible to recognize two likely oviposition sites: (1) a basin covered by leaves and a fallen trunk, with 10 cm in diameter and 5.5 cm deep, and (2) a cavity on the stream's bank, with 20 cm between the opening and the end of the cavity. The first site is probably a natural basin. As we were unable to find clutches in the field, as they are commonly laid in hidden sites, we determined mean number of mature oocytes and oocyte diameter examining gravid females (table 1). Oocytes were black on the animal pole and beige on the vegetative pole. One female spawned one single egg while kept in a plastic bag, and its diameter was 1.99 mm inside an individual jelly capsule with a diameter of 3.4 mm. Males invested approximately 0.3% of their body mass in gonads and females 20.3% (table 1).

Courtship behaviour, male territoriality and satellite males

We observed three sequences of courtship behaviour: courtship 1 and 2 with the same female, on 18 January, 2011 (air temperature = 21°C), and courtship 3 on 28 February, 2011 (air temperature = 22°C). The courtship is relatively complex, including male advertisement calls to attract the female, one or two slaps performed by the male on the female's body, and female inspection of the nest. The basic events of *B. ibitiguara* courtship are summarized in fig. 1. However, we observed some differences among the three courtships that are described in table 2.

During courtship 2, a satellite male followed the pair quietly. Although he was noticed by the pair, the courtship occurred normally. After the courtship, the pair followed by the satellite male entered the oviposition site, inside a cavity amidst the rocks. The resident male kept calling for about five more minutes, then he stopped calling for another 5 min. We assume that oviposition occurred during this time. Afterwards, both the resident male and female left the oviposition site, and the satellite male remained inside. After a while, the satellite male began to call inside the cavity and the resident male approached and called toward the satellite male. Subsequently, the resident male entered the cavity and different sounds were emitted,

Table 1. Body size and reproductive traits for individuals of *Bokermannohyla ibitiguara* in the studied population. Gravid females were weighed without oocytes for female body mass. Results are shown as mean \pm SD (range; number of observations).

	Females	Males
SVL (mm)	39.96 \pm 2.72 (36.7-43.9; $n = 9$)	39.90 \pm 3.75 (32.6-48.4; $n = 67$)
Body mass (g)	3.27 \pm 1.02 (1.79-4.58; $n = 8$)	4.45 \pm 1.23 (2.65-7.86; $n = 67$)
Gonad mass (g)	0.97 \pm 0.36 (0.65-1.62; $n = 6$)	0.011 \pm 0.003 (0.006-0.017; $n = 21$)
RI (% gonad mass/body mass)	20.26 \pm 4.53 (13.98-26.73; $n = 6$)	0.29 \pm 0.10 (0.15-0.55; $n = 21$)
Oocyte diameter (mm)	1.96 \pm 0.16 (1.69-2.41; $n = 61$)	–
n oocytes per ovary	202 \pm 75 (128-347; $n = 6$)	–

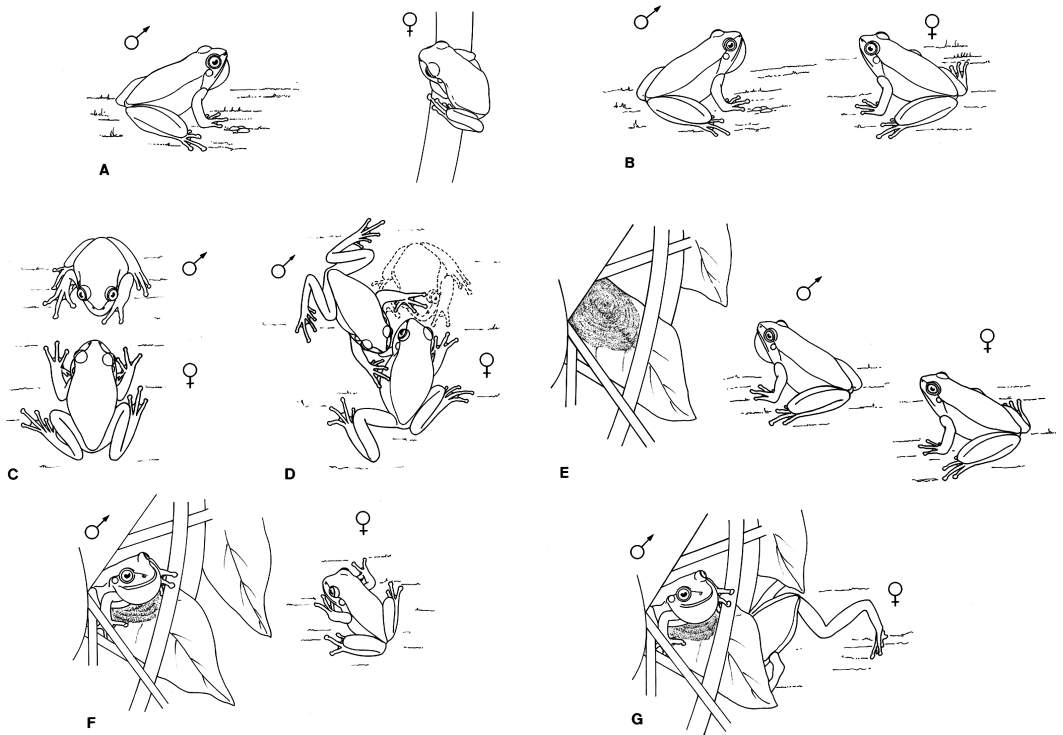


Figure 1. Courtship in *Bokermannohyla ibitiguara*. (A) ♂ calling and ♀ observing him; (B) ♀ approaches the ♂ gradually; (C) ♂ and ♀ stand face to face, and (D) the ♂ slaps the ♀ on her side, once or twice, with or without walking between them. (E) ♂ starts to approach his nest; (F) the ♂ enters the nest and keeps calling to attract the ♀, which (G) enters, probably to inspect the nest. During the whole process, the male called regularly, except for moments C and D. We observed the male emitting courtship call (not recorded) between moments B and C, when the female approached and faced the male.

Table 2. Characteristics of the three sequences of courtship behaviour of *B. ibitiguara* observed in this study.

	Courtship 1	Courtship 2	Courtship 3
Distance between calling male at first sight and nest	About 40 cm	About 150 cm	Unknown
Presence of satellite male	No	Yes	No
Beginning time and duration	20 h 30; approximately 60 minutes	22 h 10; approximately 30 minutes	21 h; approximately 30 minutes
Number of male slaps towards the female	1	2	2
Female inspection of oviposition site	Yes	Unknown	No
Amplexus	No	Probably; not possible to observe	No
Other observations	Female entered oviposition site twice, remaining outside for 5 minutes	At the beginning, the female bumped into the male, making him jump to a lower leaf, from where he kept calling	–

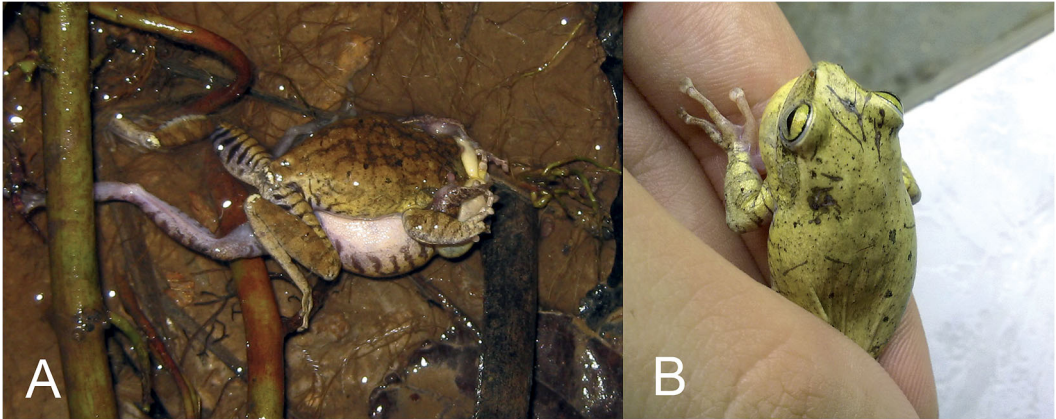


Figure 2. Male-male fight in *B. ibitiguara* and the scars on the back of a male after the fight. (A) Note that both males use their prepollical spines to cause injury, mainly in the eyes and tympanum area of the opponent. (B) The defeated male shows several scars, mainly on its head. This figure is published in colour in the online version.

probably fight calls (R.C. Nali, unpubl. data). After that, both males jumped out of the cavity and fought in the water stream (fig. 2A). They remained clasped chest to chest, using their prepollical spines to injure the opponent's head region (e.g. eyes and the tympanum). The fight lasted about 18 min, but for the final 6 min, the satellite male simply subdued the resident male, until they released one another. The satellite male won the fight and remained calling inside the cavity. He was larger (SVL = 41.6 mm) and heavier (body mass = 5.44 g) than the resident male (38.75 mm, 4.5 g). Many scars were visible on the resident's head (fig. 2B).

Satellite behaviour was observed many times during the study ($n = 20$ satellite males), where non-calling males remained next to males that were calling. In two occasions we observed even two satellite males next to one single calling male. Average distance between satellite and calling male was 54 ± 29 cm (range 15–100 cm; $n = 13$). Mean SVL of satellite males was 39.2 mm ($n = 9$) and mean mass was 4.32 g ($n = 8$); mean SVL of calling males was 39.3 mm ($n = 8$) and mean mass was 4.50 g ($n = 7$). Satellite and calling males did not differ significantly neither in SVL ($t_{15} = 2.13$, $P = 0.95$) nor in mass ($t_{13} = 2.16$, $P = 0.76$).

Discussion

During this study, adults of *B. ibitiguara* were always found in gallery forests, associated with the streams. Considering species in the *B. pseudopseudis* group, which occur predominantly in open formations, *B. oxente* and *B. itapoty* also have association with riparian vegetation (Lugli and Haddad, 2006a, 2006b), but *B. alvarengai* and *B. saxicola* seem to breed in streams without vegetation as well (Eterovick and Sazima, 2000). At our study site, even with the riparian vegetation being fragmented in many portions and presenting roads nearby, males were able to use a great variety of microhabitats as calling sites, suggesting that *B. ibitiguara* is, to some extent, resistant to human alterations. However, as the species is strongly associated with gallery forests and streams, it is necessary to preserve these habitats properly.

Bokermannohyla ibitiguara males used a greater variety of microhabitats as calling sites compared to *B. nanuzae* and *B. saxicola*, all species in the *B. pseudopseudis* group (Eterovick et al., 2010). Furthermore, these two species were observed at shorter distances from the water (average 0.18 and 0.32 m, respectively; Eterovick et al., 2010) than *B. ibitiguara* (average 0.67 m; this study). Individuals of *Bokermannohyla* sp. (gr. *circumdata*) were ob-

served perched at higher sites compared to *B. ibitiguara*, with an average height varying from 1.38 to 2.67 m (Eterovick et al., 2010). Microhabitat use by adult anurans may be correlated with phylogeny, but is also a plastic trait strongly influenced by ecological factors, such as habitat heterogeneity, microhabitat availability, climatic conditions, and competition and predation pressures (Eterovick et al., 2010).

Calling males of *B. ibitiguara* tended to be closer to each other during the rainy season compared to the dry season. This suggests that calling males get closer to each other only when male density is higher (e.g. during the rainy season). The organization of calling males in choruses in specific parts of the water bodies has advantages, e.g. increasing female attraction efficiency and decreasing individual exposure and predation risk (e.g. Ryan, Tuttle and Taft, 1981; Wells, 2007). However, for *B. ibitiguara*, as males are extremely territorial, we suggest that keeping a distance from each other might be advantageous, avoiding costs associated with territorial conflicts (e.g. male wounds; this study).

The number of calling males was positively correlated with air humidity, air temperature, and total rainfall. This result was expected, since high temperatures, air humidity, and rainfall are known to strongly influence the reproductive activity of anurans (e.g. Cree, 1989; Eterovick and Sazima, 2000; Prado, Uetanabaro and Haddad, 2005). *Bokermannohyla ibitiguara* is a typical prolonged breeder (sensu Wells, 1977a), because (i) males called over several months (Oct-Jun), (ii) we did not observe females arriving synchronously to the reproductive site, and (iii) breeding activity did not increase significantly after heavy rains, as observed for some explosive breeders at the study site (e.g. *Scinax fuscovarius* and *Elachistocleis cesarii*; pers. obs.). Furthermore, we never observed any male actively searching or intercepting females.

Bokermannohyla ibitiguara showed no SSD in SVL, as previously observed for other species

in the *B. pseudopseudis* group: *B. oxente* (Lugli and Haddad, 2006a), *B. saxicola* (Eterovick and Sazima, 2004), and *B. alvarengai* (Lugli and Haddad, 2006b). However, *B. ibitiguara* males were significantly heavier than females without mature oocytes. SSD in many taxa result from different selective forces affecting male and female sizes (Fairbairn, 1997). In most anurans, females are larger than males (Shine, 1979) and, in general, the “fecundity advantage hypothesis” (Darwin, 1874) is invoked to explain the female-biased SSD in frogs. In *B. ibitiguara*, the fact that females exhibit a high reproductive investment (see below) and that males are extremely territorial, engaging in male-male combats, could favor larger males (e.g. Shine, 1989; Katsikaros and Shine, 1997), explaining the male-biased SSD in mass and absence of SSD in SVL in this species.

Females showed a high reproductive investment (RI = 20.26%), as already observed for other anurans, such as *Leptodactylus chaquensis* (RI = 16%) and *Physalaemus albonotatus* (RI = 16.6%; Prado and Haddad, 2005). On the other hand, the RI of males was low (average 0.29%) compared to some other frogs (e.g. *Rhacophorus arboreus*: 5.15%, Kusano, Toda and Fukuyama, 1991; *Leptodactylus chaquensis*: 4.13%, Prado and Haddad, 2003). High relative testes size in anuran males is generally associated to multi-male spawning and sperm competition risk (Emerson, 1997; Prado and Haddad, 2003). In contrast, low RI for males, as observed for *B. ibitiguara*, might occur when there is low risk of sperm competition, for example: (i) in species in which the female interacts with only one male during a complex courtship and deposit eggs in a hidden place, as observed here and previously reported for species in the genus *Leptodactylus* (Prado and Haddad, 2003), and/or (ii) in species in which males actively defend their territories, engaging in fights, reducing the probability of multi-male spawning, as observed for *B. ibitiguara*.

Although we did not observe spawning behaviour, as individuals were hidden in rock

crevices or under fallen trunks, we observed likely oviposition sites during courtships. From such observations, we suggest that *B. ibitiguara* exhibits a variation of the reproductive mode 4, depositing eggs in lotic environments, probably in natural or constructed basins in hidden places, such as rock crevices or amidst fallen leaves or trunks. Many species of the genus *Bokermannohyla* deposit their eggs in flowing waters, which is described as reproductive mode 2 (e.g. *Bokermannohyla alvarengai*, *B. nanuzae* and *B. sazimai*; Haddad and Prado, 2005). However, other species are known to deposit their eggs in standing water, as *B. luctuosa* (Haddad and Sawaya, 2000), or in natural or constructed basins in both lotic or lentic environments (modes 1 and 4, respectively; Haddad and Prado, 2005).

The courtship in *B. ibitiguara* is relatively complex, involving acoustic and tactile stimuli, during which the male guides the female towards the nest. This is the first description of courtship for the genus *Bokermannohyla*. A similar courtship is known for other species in the Cophomantini tribe, such as species of *Aplastodiscus* (Haddad and Sawaya, 2000; Hartmann, Hartmann and Haddad, 2004; Zina and Haddad, 2007). However, the process from female arrival until her entrance into the nest lasted much less time in *B. ibitiguara* compared to *Aplastodiscus* species: in *B. ibitiguara*, the first courtship lasted about one hour, and the other two, about 30 minutes, whereas in *Aplastodiscus* the courtship can last many hours (Haddad and Sawaya, 2000; Hartmann, Hartmann and Haddad, 2004; Zina and Haddad, 2007). Another difference is that the tactile stimulus in *B. ibitiguara*, when the male reaches the female, is similar to a slap and it is somewhat aggressive, while in *Aplastodiscus* there is only one or more soft touches. Considering aggressiveness itself, the stimulus in *B. ibitiguara* is more similar to the one reported for the eleutherodactylid *Diasporus diastema*, where the male bumps into the female, almost making her fall off the perch (Ovaska and Rand, 2001).

Nevertheless, we must be cautious with such comparisons, because most studies describing courtship behaviour for Cophomantini are based on a small number of observations (e.g. Hartmann, Hartmann and Haddad, 2004; Zina and Haddad, 2007; this study).

Female inspection of male nest has been previously reported for other species in the Cophomantini tribe (e.g. species of *Aplastodiscus*: Zina and Haddad, 2007; *Hypsiboas faber*: Martins and Haddad, 1988). In *B. ibitiguara*, it is possible that inspection can be decisive for male rejection by the female, as observed in courtship 1 (this study). However, she can also reject the male prior to nest inspection, as in courtship 3 (this study), when the male remained calling perched on a branch, there was no nest inspection, and the female moved towards another male. The inspection of nests by females suggests that males with better territories can achieve higher mating success (e.g. Wells, 1977b), which can explain why males of this species should put themselves at risk in fights. Scars were commonly found in males of *B. ibitiguara*, which could have been caused by male fights, as observed once in the present study.

Satellite male behaviour is common in anurans with prolonged breeding season (Wells, 2007). We sometimes observed that when manipulating calling males, they stopped calling and satellites nearby started calling. This suggests that males of *B. ibitiguara* show plasticity in the reproductive strategies, alternating between calling and satellite behaviour, as already observed for other hylids (Perril, Gerhardt and Daniel, 1978; Haddad, 1991; Zina and Haddad, 2006). It was also observed that satellite males were less aggressive than calling males when manipulated; calling males tended to puncture our fingers with their spines (pers. obs.). These observations fit the concept of a more submissive behaviour of satellite males compared to calling males (Emlen, 1976; Toledo and Haddad, 2005). However, during courtship 2, the satellite male was aggressive, larger and heavier,

being able to defeat and take the calling male's territory. On average, satellite males were the same size of calling males, as observed for other hylids (e.g. Lance and Wells, 1993; Toledo and Haddad, 2005; Alcantara, Lima and Bastos, 2007). Thus, satellite behaviour in *B. ibitiguara* males seems to depend on social contexts rather than on male body size.

The reproductive period of *Bokermannohyla ibitiguara* lasted several months at the study site and individuals were abundant in many streams. Moreover, the species occurs in southeastern Brazil, the most developed region of the country. However, besides the original description (Cardoso, 1983), little information had previously been published on the species' natural history. This highlights how poor our knowledge on anuran biology is in Brazil, the world's richest country in anuran species (Segalla et al., 2012). Natural history data is essential for comprehending the reproductive strategies and social interactions in anurans, which also raises questions for future studies. Therefore, researchers should concentrate efforts in studying and publishing data on basic biology, mainly for Data Deficient species (IUCN), which will be useful for studies focusing on other aspects, such as ethology, ecology, genetics, and phylogeny. Moreover, natural history data might support conservation strategies, producing more effective results.

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