Advertisement call of *Scinax littoralis* and *S. angrensis* (Amphibia: Anura: Hylidae), with notes on the reproductive activity of *S. littoralis*

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Abstract. Scinax littoralis and S. angrensis are poorly known Atlantic forest endemic species from the Scinax catharinae group, which is known from southern and southeastern Brazil. Herein, we describe the advertisement calls of these two species and compare them to other species within the S. catharinae group. Additionally, we provide information on breeding sites, and calling activity in S. littoralis. Advertisement calls of S. angrensis and S. littoralis are composed of multi-pulsed notes with multiple frequency bands and frequency modulation. Scinax littoralis has a higher minimum and maximum frequency, and lower dominant frequency than S. angrensis, while Scinax littoralis has a longer call. Scinax littoralis appears to be a habitat generalist, occurring from secondary to mature forests, and breeding both in temporary and in permanent ponds. Male S. littoralis were usually observed calling perched on shrub stems, and displayed satellite behavior when the male density was high.

Keywords. Bioacoustics, breeding activity, satellite behavior, vocalization, treefrog.

INTRODUCTION

Vocalization is the most widespread means of communication for frogs, especially for mate attraction (Ryan, 2001). Call types are usually categorized into mating or advertisement, territorial, release, distress, and warning calls (Bogert, 1960), but for several species, one signal type may communicate many things to conspecifics (Wells, 2007). The advertisement call is mainly a reproductive signal, but may also provide information about spe-

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cies recognition or territory defense (Ryan, 2001; Wells, 2007). Because frogs have species-specific calls, the study of acoustic signals can be useful for researchers: field research dependent on auditory surveys (e.g., line transects, Zimmerman, 1993), or research focusing on behavior (Bee et al., 1999), natural history (Lima et al., 2010) or taxonomic goals (e.g., Cocroft and Ryan, 1995; Pombal et al., 1995; Toledo et al., 2007) can all capitalize on differences in calls among species to gain information relevant to a specific study.

Both *Scinax littoralis* and *S. angrensis* belong to *S. catharinae* group, which is within the *S. catharinae* clade (Faivovich, 2002). Both species are endemic to the Brazilian Atlantic forest and are morphologically similar (cryptic species) and apparently allopatric. However, their life history and ecology remain poorly known. The distribution of *S. littoralis* ranges from southern portion of the state of São Paulo (Pombal and Gordo, 1991) to the state of Paraná (Conte et al., 2009) and *S. angrensis* may be found from the state of Rio de Janeiro (Carvalho-e-Silva et al., 2008) to the northeastern portion of the state of São Paulo (Araújo et al., 2009). The reproductive season of *S. littoralis* is prolonged, with breeding occurring throughout the year (Narvaes et al., 2009). Males of this species usually call from high perches over permanent ponds (Narvaes et al., 2009). Females display two distinct reproductive modes: eggs may be deposited in ponds or in bromeliad leaf axils, and females have been observed depositing eggs in temporary ponds (Toledo et al., 2012). *Scinax angrensis* males have been recorded calling around temporary and permanent ponds and around stream zones (Carvalho-e-Silva et al., 2008). One reproductive mode was observed: females lay eggs in ponds (Hartmann et al., 2010).

Herein, we describe the advertisement calls of both *S. littoralis* and *S. angrensis* and provide novel data on the reproductive and calling behavior of *S. littoralis*. These calls are compared to other closely related species, which may provide insight into relationships within the group.

MATERIAL AND METHODS

Call description

The advertisement call of *S. littoralis* was recorded in Candonga Village (25°35'26"S, 48°48'47"W, 230 m a.s.l.), in the municipality of Morretes (Fig. 1), state of Paraná, in November 2010, at 2230h – 0100h (air temperature = 23 °C). The advertisement calls of this species were recorded with a TASCAM DR-08 digital recorder with external microphone Seinnheser ME66. The advertisement call of *S. angrensis* was recorded in the Serra do Mar State Park (23°21'53"S, 44°49'27"W, 50 m a.s.l.), municipality of Ubatuba (Fig. 1), state of São Paulo, in January 1994, at 2000h-2130h (air temperature = 23.5°C). The advertisement calls of this species were recorded with a NAGRA-E tape recorder with an external microphone Seinnheser ME66.

Calls were digitalized and analyzed in Raven Pro 1.3 (Cornell Bioacoustics Research Program) at 16 bits, 44 kHz, a FFT frame length of 512 samples, and Hann window type. The brightness was adjusted to 68%, the contrast was adjusted to 80%, and overlap was adjusted to 50%. The terminology used in these descriptions follows Toledo and Haddad (2005a). For *S. littoralis*, 21 advertisement calls of three males were analyzed (n = 75 notes), and for *S. angrensis* 17 calls of two individuals were analyzed (n = 43 notes). We analyzed the number of notes per call, number of frequency bands, call duration, note duration, number of pulses per note, pulse rate, minimum, maxi-

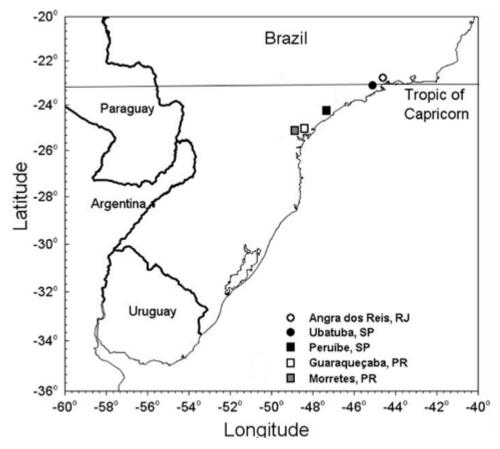


Fig. 1. Map of Southern Brazil showing the municipalities of species type-localities and study sites. White circle: *Scinax angrensis* type-locality; black circle: *S. angrensis* study-site; black square: *Scinax littoralis* type-locality; white and gray square: *S. littoralis* study-sites.

mum and dominant frequency, inter-note interval and call rate. To analyze the difference in internote intervals between S. littoralis advertisement calls, and to determine if there were differences in call parameters among S. littoralis and S. angrensis we used a Student's t-test. All variables were also tested for normality and variance homogeneity statistical analysis. Data are presented as mean \pm standard deviation.

The advertisement calls of *Scinax littoralis* (FNJV 12855-12862) and *S. angrensis* (FNJV 12863) were deposited in Fonoteca Neotropical "Jacques Vielliard", Instituto de Biologia, Universidade Estadual de Campinas, Campinas, state of São Paulo, Brazil. Voucher specimens of *S. littoralis* were deposited in the Coleção Herpetológica of the Museu de Zoologia Universidade de São Paulo, São Paulo, Brazil (MZUSP 137947-48). We collected individuals from the same population of *S. angrensis*, however, we did not collect the specimens from which the advertisement calls were recorded. The specimens of the population of *S. angrensis* from Serra do Mar State Park, nucleus Picinguaba, were deposited in the amphibian collection of Célio F. B. Haddad, Departamento de Zoologia, Instituto de Biociência, São Paulo State University, Rio Claro, Brazil (CFBH 7912-7916).

Reproductive activity of S. littoralis

The reproductive behavior of *S. littoralis* was studied at Reserva Natural Salto Morato (RNSM; $25^{\circ}09^{\circ}S$; $48^{\circ}16^{\circ}-48^{\circ}20^{\circ}W$), in the municipality of Guaraqueçaba (Fig. 1), on the north coast of the state of Paraná, southern Brazil. RNSM is composed of a mosaic of landscapes due to its land use history. The protected area cover comprises ~2.500 ha of Atlantic forest, with altitude ranging from 25 to 930 m a.s.l. In this region, the climate according to the Köppen-Geiger classification (Peel et al., 2007) is of the type Cfa: temperate climate with no dry season, and an average annual temperatures of around 21 °C. Annual rainfall is elevated; with more than 2,000 mm y^{-1} and mean relative humidity is 85% (Maack, 2002).

We sampled nine lentic water bodies, one per night, using the visual and acoustic survey at breeding sites technique (Scott and Woodward, 1994). Data were collected between September 2006 and April 2007. Surveys generally began at 1900 h and were finished at midnight. We searched for frogs at swamps, temporary and permanent ponds in early secondary forest, late secondary forest and mature forest (see Gatti, 2000), three water bodies in each successional forest stage. The water bodies were located between 20 to 200 m a.s.l. For each male found calling, we measured the perch height and the horizontal distance to the margin of pond. In each survey area, the number of calling males was estimated by counting all individuals in each surveyed area by walking around the perimeter of each breeding site (Vasconcelos and Rossa-Feres, 2005). Males were observed for approximately one hour per night using animal focal sampling (Altmann, 1974).

Differences in perch height and distance to ponds margin among the forest succession stages were analysed using ANOVA. Differences among treatments were determined using the Tukey-Kramer HSD test.

RESULTS

Call description

The advertisement call of S. angrensis is composed by 1-7 multi-pulsed notes that present multiple frequency bands and an irregular frequency modulation (Table 1). The mean duration of the advertisement call is 0.42 ± 0.1 s, the mean note duration is 0.025 ± 0.012 s (first note = 0.025 ± 0.009 s, second note = 0.034 ± 0.011 s, third note = 0.015 ± 0.011 s, fourth note = 0.023 ± 0.024 s, fifth note = 0.034 s, sixth note = 0.005 s, and seventh note = 0.009 s), with 17.88 \pm 5.18 pulses per note (first note = 12.6 \pm 0.009, second note = 14.4 \pm 5.6, third note = 8.7 \pm 8.9, fourth note = 10.5 \pm 12, fifth note = 15, sixth note = 4, and seventh note = 6 pulses per note). The inter-note interval was 50.13 ± 15.74 ms (23-76, n = 23). Notes have 2-4 frequency bands (Fig. 2). The minimum frequency of the fundamental band is 1.67 \pm 0.23 kHz, the maximum frequency of the highest band is 4.51 \pm 0.69 kHz, while the dominant frequency is 3.13 ± 0.37 kHz, which is the second band (first note = 3.29 ± 0.33 kHz, second note = 3.39 ± 0.23 kHz, third note = 3.17 ± 0.45 kHz, fourth note $= 3.01 \pm 0.24$ kHz, fifth note = 2.76 kHz, sixth note = 2.41 kHz, and seventh note = 3.49kHz). The pulse rate is 575 ± 7.5 pulses/s, and pulse rate was higher in the middle of the notes. The call rate was 16 calls/min, and note rate was 0.072 note/s. The last note tends to be shorter than the others when the call is composed of three or more notes.

The advertisement call of *S. littoralis* consists of 3-4 multi-pulsed notes, with 3-10 simultaneously frequency bands (Table 1). The mean duration of the advertisement call is

Table 1. Call parameters of the Scinax catharinae species group. Nn: number of notes/call; Duration: duration of the advertisement call; Pulses/note: number of pulses per note; Pulses/s: rate of pulses per second; Fmax: maximum frequency; Fmin: minimum frequency; Fdom: dominant frequency; Struc: structure of call, presence of pulses = P and/or presence of harmonics = H; Nfb = number of frequency bands. Data are shown as: mean ± standard deviation (range, n).

	Nn	Duration (s)	Pulses/note	Pulses/s	Fmax (kHz)	Fmin (kHz)	Fdom (kHz) Struc Nfb	Struc	Nfb	Reference
Scinax angrensis	(1-7)	0.42 ± 0.1 (0.17-0.7, n = 43)	17.88 ± 5.18 (7-28, n = 33) (17.88 ± 5.18 434.65 ± 63.28 (7-28, n = 33) (289.47-542.86, n = 33)	4.51 ± 0.69 (3.12-5.75; n = 75)	1.67 ± 0.23 (1.11-2.13; n = 75)	3.13 ± 0.37 (2.15-3.7, n = 42)	P/H	2-8	Present study
S. littoralis	(3-4)	0.55 ± 0.12 (0.21-0.79; n = 75)	23.68 ± 2.73 (8-30, n = 37)	23.68 ± 2.73 462.49 ± (8-30, n = 37) 129.43 (314.29-1000, n = 37)	4.65 ± 0.79 (2.87-5.57, n = 42)	2.2 ± 0.31 (1.47-2.79, n = 42)	2.65 ± 0.29 (1.89-3.53; n = 75)	P/H	3-10	Present study
S. agilis (note "a")	7	0.39 ± 0.76 (0.38-0.40, n = 12)	85.67 ± 5.07 (74-96, n = 12)	1	1		7.66 ± 0.18 (7.45-7.92, n = 12)	Ь	0	Nunes et al., 2007
S. agilis (note "b")	7	2.5 ± 5.3 (1.06-3.2, n = 104)	2.5 ± 5.3 7.15 ± 1.22 $(1.06-3.2, n = (5-11, n = 104)$ $104)$				7.02 ± 0.48 (5.6-7.88, n = 104)	Ъ	0	
S. albicans	1	0.7	•	1	4.2	2.8	(3.3-4.1)	P/H	1	Pombal et al., 1995*
S. argyreornatus	(5-280)	(0.8-25)	(2-25)	1	9.0	3.6	(5.0-6.3)	Ь	0	Pombal et al., 1995
S. canastrensis	(2-9)	1	1	ı	5.6	1.4	1	Ь	0	Cardoso and Haddad, 1982
S. catharinae	,	> 2	1	1	3.1	2.2	1	P/H	ı	Pombal et al., 1995∗
S. centralis	7	0.37 ± 0.06 (n = 4)		ı	6.2	2.8	(3.2-4.6)	Ь	0	Pombal and Bastos, 1996
S. hiemalis	7	1	1	ı	7.0	2.0	(2.2-4.3)	P/H	(2-4)	(2-4) Haddad and Pombal, 1987
S. machadoi	(6-7)	0.05	1	ı	5.2	0.15	3.5	Ħ		Bokermann and Sazima, 1973
S. ranki	(4-5)	1	•	ı	5.5	1.5	1	Ь	0	Andrade and Cardoso, 1987
S. rizibilis	(7-23)	(1.29-2.74)	(15-72)	1	5.5	2.0	(2.8-4.0)	Ь	0	Pombal et al., 1995
S. skaios	(42-73)	(4.42-7.9)	9.2 ± 3.33 (5-16, n=10)	ı	1	1	(2.21-2.24)	Ь	0	Pombal et al., 2010

* Data of other authors presented by Pombal et al. 1995.

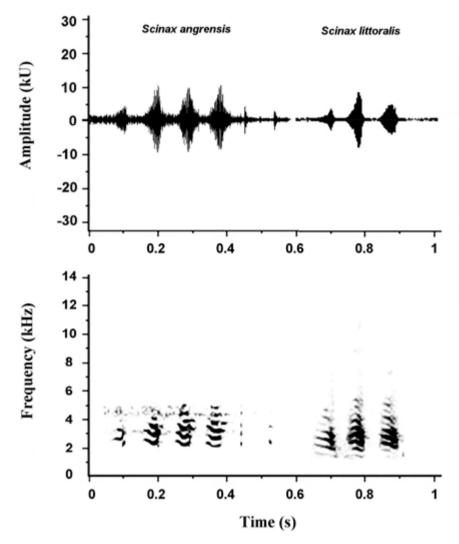


Fig. 2. Waveform (above) and spectrogram (below) of the advertisement calls of *S. angrensis* (air temperature = 23.5 °C), and *Scinax littoralis* (air temperature = 23 °C).

 0.55 ± 0.12 s, the mean note duration is 0.050 ± 0.013 s (first note = 0.054 ± 0.011 s, second note = 0.053 ± 0.001 s, third note = 0.047 ± 0.016 s, and fourth note = 0.023 ± 0.001 s), with 23.68 ± 2.73 pulses per note (first note = 21.9 ± 4.17 , second note = 22.43 ± 2.11 , third note = 18.53 ± 6.81 , fourth note = 7 ± 1 pulses per note). The minimum frequency of the fundamental band is 2.20 ± 0.31 kHz, the maximum frequency of the highest frequency band is 4.65 ± 0.79 kHz, whereas the dominant frequency is 2.65 ± 0.29 kHz, which is the third band (first note = 2.58 ± 0.26 kHz, second note = 2.72 ± 0.20 kHz, third note = 2.67 ± 0.20 kHz, and fourth note = 2.47 ± 0.19 kHz). The first two notes were simi-

lar in irregular frequency modulation. The third note varied: in some cases, it was modulated like the first two notes, while in others it was of relatively constant frequency. The pulse amplitude increased across the note. The interval between the first and second notes was 41.69 ± 9.43 ms (24-66; n=51), and the interval between the third and fourth note was 43.22 ± 8.33 ms (27-63; n=23). The call rate was 6.37 ± 2.73 call/min (4.8-9.52; n=3), and note rate was 0.082 note/s.

The advertisement call of *S. angrensis* and *S. littoralis* present similarities in the structure but some parameters differed. *Scinax littoralis* has a greater call length (t = 5.97; P = 0.0001, df = 120), note length (t = 9.49; P = 0.0001; df = 120), and number pulses per note (t = 7.20; P = 0.0001; df = 120), than *S. angrensis*. However, *S. angrensis* has a higher dominant frequency (t = 4.88; P = 0.0001; df = 120), and lower minimum frequency (t = -10.86; P = 0.0001; df = 120), maximum frequency (t = 2.32; P = 0.022; df = 120), in relation to *S. littoralis*. These species did not differ in relation to notes per call (t = -0.06; t = 0.949; t = 0.949; t = 0.069; t = 0.069

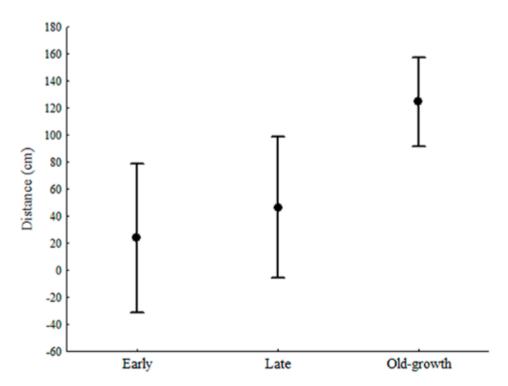


Fig. 3. Horizontal distance from the water of the perches used for calling by males *Scinax littoralis* in three vegetation succession stage sites in the Reserva Natural Salto do Morato, municipality of Guaraqueçaba, state of Paraná, Brazil. Positive values indicate that a calling site was located outside of the breeding pool; negative values indicate that a calling site was located within a pool; zero value is the margin of the pool. Dots indicate the means and bars indicate standard deviation. Early = early secondary forest; Late = late secondary forest; Old-growth = old growth forest.

Reproductive activity of S. littoralis

Scinax littoralis were found calling in every forest type sampled and bred in both temporary and permanent ponds. Males were found calling perched on shrubs ranging from 23-220 cm above the ground (69.73 \pm 33.35 cm, n = 49) located 0-308 cm horizontally from pond edges (88.37 \pm 95.83 cm, n = 49). The height of the perch used by *S. littoralis* was the same in all forest stages ($F_{(2, 48)} = 2.37$, P = 0.106). However, perches used in the mature forest were farther from the water in comparison to the others (Fig. 3; $F_{(2, 48)} = 6.50$, P = 0.003).

Scinax littoralis calls during the night and may exhibits a satellite-male strategy (n = 5). Satellite behavior was observed at nights with density of calling males > 20 males per pond, in the late secondary forest and mature forest. Satellite males had a distance of approximately 19 ± 3 cm (n = 3) from the calling male. Satellite males were standing still near the calling male, not in low posture, however, we did not record any satellite male attempting to intercept gravid females.

DISCUSSION

Multi-pulse structure, common to both *S. littoralis* and *S. angrensis*, is widespread within the genus *Scinax* (e.g., Haddad and Pombal, 1987; Pombal et al., 1995; present study). Other call features common in *S. catharinae* group are present in the calls of these two species, such as short note lengths and harmonic structure (Pombal et al., 1995). The presence of harmonics in species of the *Scinax catharinae* group may be questionable (see Vielliard, 1993). In our results it is possible to identify different frequency bands, however, only two of it would be integer multiples of the fundamental frequency, while the other seems as additional frequency modulation. Therefore, some of these frequency bands may be sidebands (Vielliard, 1993). Despite of its origin, multiple frequency band structure in the advertisement call is common among the congeneric species (e.g., Haddad and Pombal, 1987). Anyway, despite morphological and ecological similarities between *S. littoralis* and *S. angrensis*, the differences among the call features of those species are evident, especially regarding the dominant frequency level and call rate.

Few species in the *S. catharinae* group have higher dominant frequencies than *Scinax angrensis*, such as *S. agilis* (Nunes et al., 2007), and *S. argyreornatus* (Pombal et al., 1995). These species can be distinguished from *S. angrensis* by the absence of multiple frequency bands. The advertisement call of *S. angrensis* has more notes per call than *S. albicans* (Pombal et al., 1995), *S. centralis* (Pombal and Bastos, 1996), and *S. hiemalis* (Haddad and Pombal, 1987), although *S. angrensis* has lower number of notes per call than *S. argyreornatus* (Pombal et al., 1995), *S. canastrensis* (Cardoso and Haddad, 1982), *S. machadoi* (Bokermann and Sazima, 1973), *Scinax rizibilis* (Pombal et al., 1995), and *S. skaios* (Pombal et al., 2010). *Scinax angrensis* has a higher minimum frequency than *S. machadoi* as well, *S. machadoi* has the shortest call duration documented in the group (Pombal et al., 1995). *Scinax angrensis* has a shorter call than do *S. skaios* (Pombal et al., 2010), *S. catharinae*, *S. rizibilis*, and *S. argyreornatus* (Pombal et al., 1995). *Scinax angresis* differs from *S. ranki* by harmonic structure of advertisement call. For some species in this group

(e.g., *S. catharinae*) no full description of advertisement calls exists, thus we are unable to compare their calls to others in the *S. catharinae* group (Table 1).

Some species in the *S. catharinae* group have higher dominant frequencies than *Scinax littoralis*, such as *S. agilis* (Nunes et al., 2007), *S. albicans* (Pombal et al., 1995), and *S. argyreornatus* (Pombal et al., 1995). Most species have a similar range of dominant frequency (Table 1). *Scinax littoralis* can be distinguished from *S. argyreornatus*, *S. rizibilis* (Pombal et al., 1995), and *S. skaios* (Pombal et al., 2010) by the presence of multiple frequency bands, lower number of notes per call, and call length. *Scinax littoralis* has higher call duration than *S. centralis* (Pombal and Bastos, 1996), *S. catharinae*, and *S. machadoi* (Pombal et al., 1995), although *S. littoralis* has lower call duration than *S. albicans* (Pombal et al., 1995). Advertisement call of *S. ranki* has no multiple frequency bands (Andrade and Cardoso, 1987). *Scinax hiemalis* has higher maximum frequency than *S. littoralis* (Haddad and Pombal, 1987). *Scinax littoralis* also has fewer notes per call than *S. canastrensis* (Cardoso and Haddad, 1982), and *S. machadoi* (Bokermann and Sazima, 1973).

As already know for the genus (e.g., Toledo and Haddad, 2005b; Abrunhosa et al., 2006), *Scinax littoralis* either exhibits a prolonged breeding season (*sensu* Wells, 1977a). The prolonged breeding season is common among tropical amphibians (Wells, 2007), and, despite our study site is at a subtropical zone, it is still likely the pattern already observed for *S. littoralis* in the type locality (Estação Ecológica Juréia-Itatins, Narvaes et al., 2009).

Males of this species may adopt satellite strategy. Satellite males are common within the most Neotropical amphibian families (e.g., Haddad, 1991; Barreto and Andrade, 1995; Pombal and Haddad, 2005). Four hypotheses, not mutually exclusive, explain satellite behavior in amphibians: 1) satellite males are sexual parasites that try to mate with females attracted by their calling neighbor (Wells, 1977b); 2) satellite males are waiting for a change in the physical condition of the dominant male, due to the high energetic cost of calling (Bevier, 1997; Pombal and Haddad, 2005); 3) satellite males are inferior or subordinate males waiting for a calling site to be vacated by the dominant male when he enters amplexus (Wells, 1977b); 4) the satellite strategy can decrease predation risk by acoustically oriented predators (e.g., Tuttle et al., 1981). We observed satellite behavior only in high densities, as suggested by Gerhardt and Klump (1988). Since we did not observe any female interception attempt by satellite males (hypothesis 1), we suggest that the other three hypotheses are therefore more likely to happen in this species.

Although *S. littoralis* appears to be constrained to the forest habitats, breeding activity seems to be independent of the successional stage of the forest and of pond stability. Perch heights did not vary between areas, but males vocalized farther from the margin of the water in mature forest. These differences in calling site may be related to the availability of bromeliads around the margin of the spawning site (see Toledo et al., 2012): and bromeliads were most abundant in mature forest, including around the margins of breeding sites. We found low abundance of bromeliads in late secondary forest, and none in early secondary forest.

We present here data on the natural history of two endemic species of Atlantic Forest of Brazil, which is an endangered biome with lacks on the life history knowledge of most amphibian species. The calling comparisons presented here aid in easy distinction among some species of the *S. catharinae* group in further surveys or to study the ecology and the evolution of the of advertisement call for the reproduction of *Scinax* clade.

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REFERENCES

- Abrunhosa, P.A., Wogel, H., Pombal Jr., J.P. (2006): Anuran temporal occupancy in a temporary pond from the Atlantic Rain Forest, South-Eastern Brazil. Herpetol. J. **16**: 115-122.
- Altmann, J. (1974): Observational study of behaviour: Sampling methods. Behaviour **49**: 227-267.
- Andrade, G.V., Cardoso, A.J. (1987): Reconhecimento do grupo *rizibilis*; descrição de uma nova espécie de *Hyla* (Amphibia, Anura). Rev. Bras. Zool. **3**: 433-440.
- Araújo, O.G.S., Toledo, L.F., Garcia, P.C.A., Haddad, C.F.B. (2009): The amphibians of São Paulo State, Brazil. Biota Neotrop. **9**: 197-209.
- Barreto, L., Andrade, G.V. (1995): Aspects of the reproductive biology of *Physalaemus cuvieri* (Anura: Leptodactylidae) in northeastern Brazil. Amphibia-Reptilia **16**: 67-76
- Bee, M.A., Perrill, S.A., Owen, P.C. (1999): Size assessment in simulated territorial encounters between male green frogs (*Rama clamitans*). Behav. Ecol. Sociobiol. **45**: 177-184.
- Bevier, C.R. (1997): Breeding activity and chorus tenure of two Neotropical hylid frogs. Herpertologica 53: 297-311.
- Bogert, C.M. (1960): The influence of sound on the behavior of amphibians and reptiles. In: Animal sounds and communication, pp. 137–320. Lanyon, W.E., Tavolga, W.N., Eds, AIBS, Washington.
- Bokermann, W.C.A., Sazima, I. (1973): Anfíbios da Serra do Cipó, Minas Gerais, Brasil. 1: Duas novas espécies de *Hyla* (Anura, Hylidae). Rev. Bras. Biol. **33**: 457-472.
- Cardoso, A.J., Haddad, C.F.B. (1982): Nova espécie de *Hyla* da Serra da Canastra (Amphibia, Anura, Hylidae). Rev. Bras. Biol. **42**: 499-503.
- Carvalho-e-Silva, A.M.T., Silva, G.R., Carvalho-e-Silva, S.P. (2008): Anuros da Reserva Rio das Pedras, Mangaratiba, RJ, Brasil. Biota Neotrop. **8**: 199-209.
- Cocroft, R.B., Ryan, M.J. (1995): Patterns of advertisement call evolution in toads and chorus frogs. Anim. Behav. **49**: 283-303.
- Conte, C.E., Garey, M.V., Lingnau, R., Silva, M.X., Armstrong, C., Hartmann, M.T. (2009): Amphibia, Anura, *Limnomedusa macroglossa*, *Dendropsophus anceps*, *D. berthalut-*

- zae, D. seniculus, Scinax littoralis: new state records, distribution extension and filling gaps. Check List 5: 202-209.
- Faivovich, J. (2002): A cladistic analysis of Scinax (Anura: Hylidae). Cladistics 18: 367-393.
- Gatti, G.A. (2000): Composição florística, fenologia e estrutura da vegetação de uma área em restauração ambiental, Guaraqueçaba, PR. Unpublished master dissertation. Universidade Federal do Paraná, Curitiba.
- Gerhardt, H.C., Klump, G.M. (1988): Masking of acoustic signals by the chorus background noise in the green tree frog: a limitation on mate choice. Anim. Behav. **36**: 1247-1249.
- Haddad, C.F.B. (1991): Satellite behavior in the neotropical treefrog *Hyla minuta*. J. Herpetol. **25**: 226-229.
- Haddad, C.F.B., Pombal, J.P. Jr. (1987): *Hyla hiemalis*, nova espécie do grupo *rizibilis* do Estado de São Paulo (Amphibia, Anura, Hylidae). Rev. Bras. Biol. 47: 127–132.
- Hartmann, M.T., Hartmann, P.A., Haddad, C.F.B. (2010): Reproductive modes and fecundity of an assemblage of anuran amphibians in the Atlantic rainforest, Brazil. Iheringia **100**: 207-215.
- Lima, A.M.X., Garey, M.V., Noleto, R.B., Verdade, V.K. (2010): Natural History of the Lutz's Frog *Cycloramphus lutzorum* Heyer, 1983 (Anura: Cycloramphidae) in the Brazilian Atlantic Forest: Description of the Advertisement Call, Tadpole, and Karyotype. J. Herpetol. **44**: 360-371.
- Maack, R. (2002): Geografia física do Estado do Paraná. Imprensa Oficial, Curitiba, Paraná.
- Narvaes, P., Bertoluci, J., Rodrigues, M.T. (2009): Composição, uso do hábitat e estações reprodutivas das espécies de anuros da floresta de restinga da Estação Ecológica Juréia-Itatins, sudeste do Brasil. Biota Neotrop. **9**: 117-123.
- Nunes, I., Santiago, R.S., Juncá, F.A. (2007): Advertisement calls of four hylid frogs from the state of Bahia, northeastern Brazil (Amphibia, Anura, Hylidae). South Am. J. Herpetol. **2**: 89-96.
- Peel, M.C., Finlayson, B.L., McMahon, T.A. (2007): Updated world map of the Köppen-Geiger climate classification. Hydrol. Earth Syst. Sc. 11: 1633-1644.
- Pombal, J.P. Jr., Bastos, R.P. (1996): Nova espécie de *Scinax* Wagler, 1830 do Brasil Central (Amphibia, Anura, Hylidae). Bol. Mus. Nac., Zool. **371**: 1–11.
- Pombal, J.P. Jr., 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**: 213-255.
- Pombal, J.P. Jr., Carvalho Jr., R.R., Canelas, M.A.S., Bastos, R.P. (2010): A new *Scinax* of the *S. catharinae* species group from Central Brazil (Amphibia: Anura: Hylidae). Zoologia 27: 795-802.
- Pombal, J.P. Jr., Gordo, M. (1991): Duas novas espécies de *Hyla* da floresta Atlântica no Estado de São Paulo (Amphibia, Anura). Mem. Inst. Butantan **53**: 135-144.
- Pombal, J.P. Jr., Haddad, C.F.B. (2005): Estratégias e modos reprodutivos de anuros (Amphibia) em uma poça permanente na Serra de Paranapiacaba, Sudeste do Brasil. Pap. Avulsos Zool. **45**: 201-213.
- Ryan, M.J. (2001): Anuran Communication. Smithsonian Institution Press, Washington D.C., Washington.

- Scott, N.J., Woodward, B.D. (1994): Standard techniques for inventory and monitoring: Surveys at breeding sites. In: Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians, pp. 118-125. Heyer, W.R., Donnelly, M.A., McDiarmid, R.W., Hayek, L.A.C., Foster, M.S., Eds, Smithsonian Institution Press, Washington.
- Toledo, L.F., Garey, M.V., Costa, T.R.N., Lourenço-de-Moraes, R., Hartmann, M.T., Haddad, C.F.B. (2012): Alternative reproductive modes of Atlantic forest frogs. J. Ethol. **30**: 331-336.
- Toledo, L.F., Haddad, C.F.B. (2005a): Acoustic repertoire and calling behavior of *Scinax fuscomarginatus* (Anura, Hylidae). J. Herpetol. **39**: 455-464.
- Toledo, L.F., Haddad, C.F.B. (2005b): Reproductive biology of *Scinax fuscomarginatus* (Anura, Hylidae) in south-eastern Brazil. J. Nat. Hist. **39**: 3029-3037.
- Toledo, L.F., Garcia, P.C.A., Lingnau, R., Haddad, C.F.B. (2007): A new species of *Sphaeno-rhynchus* (Anura: Hylidae) from Brazil. Zootaxa **1658**: 57-68.
- Tuttle, M.D., Taft, K.L., Ryan, M.J. (1981): Acoustical location of calling frogs by *Philander opossum*. Biotropica **13**: 233-234.
- Vasconcelos, T.S., Rossa-Feres, D.C. (2005): Diversidade, distribuição espacial e temporal de anfíbios anuros (Amphibia, Anura) na região noroeste do estado de São Paulo, Brasil. Biota Neotrop. 5: 137-150.
- Vielliard, J. (1993): 'Side-bands' artifact and digital sound processing. Bioacoustics 5: 159-162.
- Wells, K.D. (1977a): The social behaviour of anuran amphibians. Anim. Behav. **25**: 666-693.
- Wells, K.D. (1977b): Territoriality and male mating success in the green frog (*Rana clamitans*). Ecology **58**: 750-762.
- Wells, K.D. (2007): The ecology and behavior of amphibians. University of Chicago Press, Chicago.
- Zimmerman, B.L. (1993): Audio strip transects. In: Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians, pp. 92-97. Heyer, W.R., Donnelly, M.A., McDiarmid, R.W., Hayek, L.A.C., Foster, M.S., Eds, Smithsonian Institution, Washington.