

Bioacoustics of four *Scinax* species and a review of acoustic traits in the *Scinax catharinae* species group (Amphibia: Anura: Hylidae)

FÁBIO HEPP^{1,2}, ANA CAROLINA CALIJORNE LOURENÇO³ & JOSÉ P. POMBAL JR¹

¹) Universidade Federal do Rio de Janeiro, Departamento de Vertebrados, Museu Nacional, Quinta da Boa Vista, 20940-040 Rio de Janeiro, Brazil

²) Carnegie Museum of Natural History, Section of Amphibians and Reptiles, 4400 Forbes Avenue, Pittsburgh, PA 15213, USA

³) Universidade Estadual Paulista Júlio de Mesquita Filho, Instituto de Biociências, Departamento de Zoologia, Jacarezáριο, Av. 24-A, n 1515, Bela Vista, Cx P 199, 13506-900 Rio Claro, SP, Brazil

Corresponding author: FÁBIO HEPP, e-mail: fabiohepp@gmail.com

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Abstract. Herein, we present new data on the acoustic repertoires of *Scinax heyeri*, *S. humilis*, *S. longilineus*, and *S. trapi-cheiroi*, all of which are species belonging to the *S. catharinae* species group. Based on the acoustic features of the calling signals of the group's representatives, we recognize two acoustic patterns: long call (four species) and short call (13 species). We found two- and three-note types for species with long and short calls, respectively. This acoustic diversity of notes is recurrent in the literature about the acoustic repertoire of the *S. catharinae* group and may be directly related to a functional diversity. The species *S. humilis* has a unique call that does not match any of the acoustic patterns described, and the calls of *S. agilis* resemble calls of another species group, the *Scinax ruber* group. Additionally, we review the call nomenclature of the group and standardize it according to homology criteria: acoustic similarity, relative position, and connection by intermediate taxa between the call structures analysed. The interspecific acoustic differences and similarities found here suggest that bioacoustic features may help solve taxonomic issues and aid in the construction of phylogenetic hypotheses within the *S. catharinae* group.

Key words. Bioacoustics, taxonomy, Dendropsophini, vocalization, Atlantic Forest, Cerrado.

Introduction

Acoustic communication mediates mating, aggressive behaviour, antagonistic encounters, and advertises the position of an individual to others (WILCZYNSKI & CHU 2001, GERHARDT & HUBER 2002, WELLS 2007). In anurans, several studies have shown the importance of acoustic signals to species-specific recognition, especially seen in the calls with mating function (e.g., HADDAD & POMBAL 1998, CANEDO & POMBAL 2007, HEPP et al. 2015). Given the complex taxonomy of the *Scinax catharinae* species group, acoustic features have helped to clarify species identities (e.g., GAREY et al. 2012, MENDES et al. 2013). Moreover, acoustic traits have been used for estimating phylogenetic relationships in support of molecular and morphological data (ROBILLARD et al. 2006, GOICOECHEA et al. 2010).

The *Scinax catharinae* species group (sensu FAIVOVICH et al. 2005) currently comprises 33 species (LOURENÇO et al. 2014), and despite the calls of 21 species of the group having been described (Table 1), its vocal communication is still poorly studied. It was only recently that authors have described and compared in detail the acoustic data in the

S. catharinae group (e.g., LOURENÇO et al. 2009, POMBAL et al. 2010, GAREY et al. 2012, MENDES et al. 2013). One reason for this delay might be the high acoustic complexity of calls in this group, which complicates the comparison of acoustic data between species (see POMBAL & BASTOS 1996). In order to adequately compare biological structures, primary homologies need to be well established and characters properly codified (WAGNER 1989). To do so with acoustic structures, detailed vocalization descriptions and comparisons are necessary for deeper comprehension of the acoustic features and consequently better application of homology criteria (see WENZEL 1992).

Here we describe the acoustic structures of *Scinax heyeri* (PEIXOTO & WEYGOLDT, 1986), *S. humilis* (A. LUTZ & B. LUTZ, 1954), *S. longilineus* (B. LUTZ, 1968), and *S. trapi-cheiroi* (A. LUTZ & B. LUTZ, 1954), all of which belong to the *S. catharinae* group (LOURENÇO et al. 2014, FROST 2015). These species occur in the Atlantic Forest, southeastern Brazil, with the exception of *S. longilineus*, which occupies the Cerrado and transitional areas connecting these biomes (LOURENÇO et al. 2013). *Scinax heyeri* is found at its type locality (municipality of Santa Teresa, state of Es-

Bioacoustics of the *Scinax catharinae* group

Table 1. Species of the *Scinax catharinae* group that have had their calls described, respective references, original terms, call type classified here, and identification numbers used in Table 2. The names of the acoustic structures in the literature ('References' column) and the terms applied here in the acoustic patterns comparison (see Discussion) are presented in the 'Original names' and 'Comparison names' columns, respectively. Identification numbers in 'ID' column associate the acoustic structures with the parameter values presented in Table 2.

Species	References	Original call name	Call type	Original note name	IN		
<i>S. agilis</i> (CRUZ & PEIXOTO, 1983)	NUNES et al. (2007)	Advertisement call	A	Note a	1		
				Note b	2		
<i>S. albicans</i> (BOKERMANN, 1967)	HEYER (1980)	Advertisement call	A		3		
<i>S. angrensis</i> (LUTZ, 1973)	GAREY et al. (2012)	Advertisement call	A		4		
<i>S. argyreornatus</i> (MIRANDA-RIBEIRO, 1926)	POMBAL et al. (1995)	Short call	A		5		
		Long call	B		6		
<i>S. aromothyella</i> FAIVOVICH, 2005	PEREYRA et al. 2012	Advertisement call	A	Short note	7		
				B	Trilled note	8	
<i>S. berthae</i> (BARRIO, 1962)	BARRIO (1962)	Non-pulsed call	A		9		
				Pulsed call	B	10	
	PEREYRA et al. 2012	Advertisement call	A	Short note	11		
				B	Trilled note	12	
<i>S. canastrensis</i> (CARDOSO & HADDAD, 1982)	CARDOSO & HADDAD (1982)	Nupcial call	A		13		
		Encounter call	B		14		
<i>S. catharinae</i> (BOULENGER, 1888)	HEYER (1980)	Advertisement call	A		15		
<i>S. centralis</i> POMBAL & BASTOS, 1996	POMBAL & BASTOS (1996)	Call A	A		16		
		Call B	B		17		
		Advertisement call	A		18		
		Long aggressive call	B		19		
		Short aggressive call	B		20		
		Displacement call	B		21		
		Call B	B		33		
<i>S. heyeri</i> (PEIXOTO & WEYGOLDT, 1986)	PEIXOTO & WEYGOLDT (1987)	Mating call	A		22		
		Rasping sounds	B		23		
		Present study	Call A	A		24	
			Call B	B		25	
			Call C	C		26	
<i>S. hiemalis</i> (HADDAD & POMBAL, 1987)	HADDAD & POMBAL (1987)		A	Complex note	27		
			B	Transitory note	28		
			A		29		
<i>S. humilis</i> (A. LUTZ & B. LUTZ, 1954)	BEVIER et al. 2008	Advertisement call	A		30		
<i>S. littoralis</i> (POMBAL & GORDO, 1991)	Present study	Call A	A		31		
<i>S. longilineus</i> (LUTZ, 1968)	GAREY et al. (2012)	Advertisement call	A		32		
<i>S. luizotavioi</i> (CARAMASCHI & KISTEUMACHER, 1989)	Present study	Call A	A		34		
<i>S. machadoi</i> (BOKERMANN & SAZIMA, 1973)	LOURENÇO et al. (2009)	Advertisement call (type locality)	A		35		
		Advertisement call (Ouro Preto)	A		36		
<i>S. ranki</i> (ANDRADE & CARDOSO, 1987)	BOKERMANN & SAZIMA (1973)	Nupcial call	A		37		
		ANDRADE & CARDOSO (1987)	Common call	A		38	
			ANDRADE & CARDOSO (1991)	Sequence 1	B	note a	39
				Sequence 2	B	secondary note	40
				Sequence 3	A	note b	41
<i>S. rizibilis</i> (BOKERMANN, 1964)	BOKERMANN (1964)	Introductory notes	A		42		
		'Laugh'	B		43		
		POMBAL et al. (1995)	Advertisement call	A+B		44	
		BEVIER et al. (2008)	Advertisement call	A+B		45	
				multi-note	46		
				short	47		
				creak	48		
<i>S. strigilatus</i> (SPIX, 1824)	MENDES et al. (2013)	Advertisement call			49		
<i>S. skaios</i> POMBAL, CARVALHO, CANELAS & BASTOS, 2010	POMBAL et al. (2010)	Advertisement / long call	A		50		
		Isolated call / short call	B		51		
<i>S. trapicheiroi</i> (A. LUTZ & B. LUTZ, 1954)	Present study	Call A	A		52		

pírito Santo, Brazil) and surrounding areas (ALMEIDA et al. 2011), *S. humilis* in coastal lowlands from the south of Espírito Santo to the north of São Paulo state (IZECKSOHN & CARVALHO-E-SILVA 2001), and *S. trapicheiroi* in the coastal mountain range of the state of Rio de Janeiro (LUTZ 1973). The goal of this study is to improve our comprehension of the vocal traits of the *Scinax catharinae* group by describing the calls of the four above-mentioned species, applying homology criteria (see WENZEL 1992) to the acoustic structures, and reviewing the characters of all calls known from the species within this group.

Material and methods

Vocalizations of *Scinax heyeri*, *S. humilis*, and *S. longilineus* were recorded with a Marantz PMD-660 digital recorder and a Sennheiser ME-66 microphone, at a sampling rate of 44,100 Hz and sample size of 16 bits. Vocalizations were recorded with a Tascam DA-P1 digital audio tape (DAT) recorder and a Sennheiser ME-66 microphone, at a sampling rate of 22,050 Hz and sample size of 16 bits, and with an Olympus LS-10 digital recorder and a Sennheiser ME-67 microphone, at a sampling rate of 48,000 Hz and sample size of 24 bits. *Scinax heyeri* was recorded on 12 December 2012 in the Reserva Biológica Santa Lúcia, municipality of Santa Teresa, state of Espírito Santo (air temp. 25°C); *S. humilis* on 3 and 4 June 2012 in Ponta Negra, municipality of Maricá, state of Rio de Janeiro (air temp. 29°C); *S. longilineus* on 7 August 2011 at the Estação Ecológica do Tripuí, córrego Volta Grande, municipality of Ouro Preto, state of Minas Gerais (air temp. 15°C); *S. trapicheiroi* on 12 October 2004 in Feema, Vista Chinesa, Tijuca Forest, municipality of Rio de Janeiro (air temp. 15°C) and on 10 August 2014 in the municipality of Mendes, both in the state of Rio de Janeiro (air temp. 16°C).

Sound analyses were conducted using Raven Pro 1.4 (64-bit version) from the Cornell Laboratory of Ornithology (Bioacoustics Research Program 2011). The quantitative parameters measured were: call duration; number of notes per call; note duration; note intervals; note periods (measured from the beginning of one note to the beginning of the following one, thus encompassing the note duration and the inter-note interval [see GERHARDT 1998]); note rate (number of notes divided by call duration); pulse rate; sideband distances (WATKINS 1967); dominant frequency (carrier frequency); and fundamental frequency. The parameters 'note intervals' and 'note periods' are highly dependent on each other. The former parameter has been widely used in studies of this group and seems to be important for species comparisons. 'Note period' has been used only recently with the aim of reducing the influence of reverberation on the measurement by considering only the beginning of the acoustic structures (e.g., WEBER et al. 2005, HEPP & CARVALHO-E-SILVA 2011, HEPP & CANEDO 2013). Numerical parameters are each given as range followed by Mean \pm SD, Mode and N in parenthesis ($x \pm$ SD; Mo; n). All recordings were low-cut filtered at 500 Hz.

The temporal parameters were measured directly from the waveform and frequency parameters from the audiospectrogram (with window function Hann, amplitude logarithmic, window size 512 samples, and overlap 99%). Technical terms and definitions of the acoustic structures follow GERHARDT & HUBER (2002) and LITTLEJOHN (2001). All measuring methods follow HEPP et al. (2015) except for the sideband distances where they follow WATKINS (1967) and GERHARDT (1998).

The concepts related to sidebands follow WATKINS (1967), BRADBURY & VEHRENCAMP (1998), and GERHARDT (1998). Harmonics are component frequencies of the signal that are integer multiples of the fundamental frequency (GERHARDT & HUBER 2002), while sidebands are representations of high rates of emission of acoustic structures (e.g., note, pulse, etc.) visualized in determined window sizes in the spectrogram analysis (WATKINS 1967, JACKSON 1996, BRADBURY & VEHRENCAMP 1998; GERHARDT 1998). The distance between the sidebands corresponds exactly to the repetition rate of the structure responsible for the visualization of the sidebands (WATKINS 1967, BRADBURY & VEHRENCAMP 1998, and GERHARDT 1998). Moreover, WATKINS (1967) demonstrated empirically the relation of pulse rate, sideband distances, and their relative energy, pointing out the usefulness and importance of analysing the sideband characteristics in acoustic descriptions. To illustrate the relationship between pulse rate and sideband distances we used the software Audacity 2.1.1 and modulated in amplitude a generated sound at 3,000 Hz (carrier frequency; Figs 1A–C) at different modulation rates (Figs 1D–R). To show the relationship between pulse rate and sideband distances, we ran linear regressions in the software Past 2.10 between these two parameters for the species described here.

As previous authors have, we identified more than one call type (e.g., BASTOS et al. 2011, POMBAL et al. 2011). However, we do not use terms such as 'advertisement' or 'aggressive' to classify calls to avoid speculation on their functions. Instead, we herein refer to them as call types A, B, or C, according to their different acoustic organizations (see Table 1 for a comparison with the nomenclature used in previous descriptions). This classification was based on homology criteria: acoustic similarity, relative position, and connection by intermediate taxa between the call structures analysed, with this latter criterion establishing homology by comparing relative position and similarity between the acoustic structures in the different species (REMANE 1952, WENZEL 1992). Comparative data for other species were directly obtained from recordings examined (see Appendix) or the literature listed in Table 1. The calls of a few species that were just briefly described or commented on are not included in Tables 1 and 2 (*S. argyreornatus*: BOKERMANN 1966, *S. brieri* and *S. flavoguttatus*: HEYER et al. 1990, and *S. longilineus*: ANDRADE & CARDOSO 1991). The note rate values of *S. angrensis* and *S. littoralis* (GAREY et al. 2012, see Table 2) are not used in the comparisons (see Discussion).

Eighteen nominal species of the *Scinax catharinae* group have had their calls described so far (Tables 1 and

2), of which twelve have two or more recognized types of call structure (*S. agilis*, *S. argyreornatus*, *S. aromothyela*, *S. berthae*, *S. canastrensis*, *S. centralis*, *S. heyeri*, *S. hiemalis*, *S. ranki*, *S. rizibilis*, *S. skaios*, and *S. littoralis*). All types of acoustic structure were considered and compared with the call type A described here. Call type A described here was selected as a reference for species comparisons due to the stereotyped characteristics of this call type (vs call B and C that may be too variable). Moreover, call type A is recurrently referred to as “advertisement call” in the literature (Table 1) and thus often used for comparisons (see Discussion).

Voucher specimens were collected, fixed in 10% formalin, and preserved in 70% ethyl alcohol and are housed in the amphibian collections of the Museu Nacional, Rio de Janeiro, Brazil (MNRJ), and Departamento de Zoologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (ZUFJR). Recordings were deposited in the acoustic collections of the Setor de Herpetologia, Departamento de Vertebrados, Museu Nacional (MNVOC), and Laboratório de Anfíbios e Répteis, Departamento de Zoologia, Universidade Federal do Rio de Janeiro (ZUFJR); vouchers are listed in the Appendix. Additional analysed recordings of the *S. catharinae* group

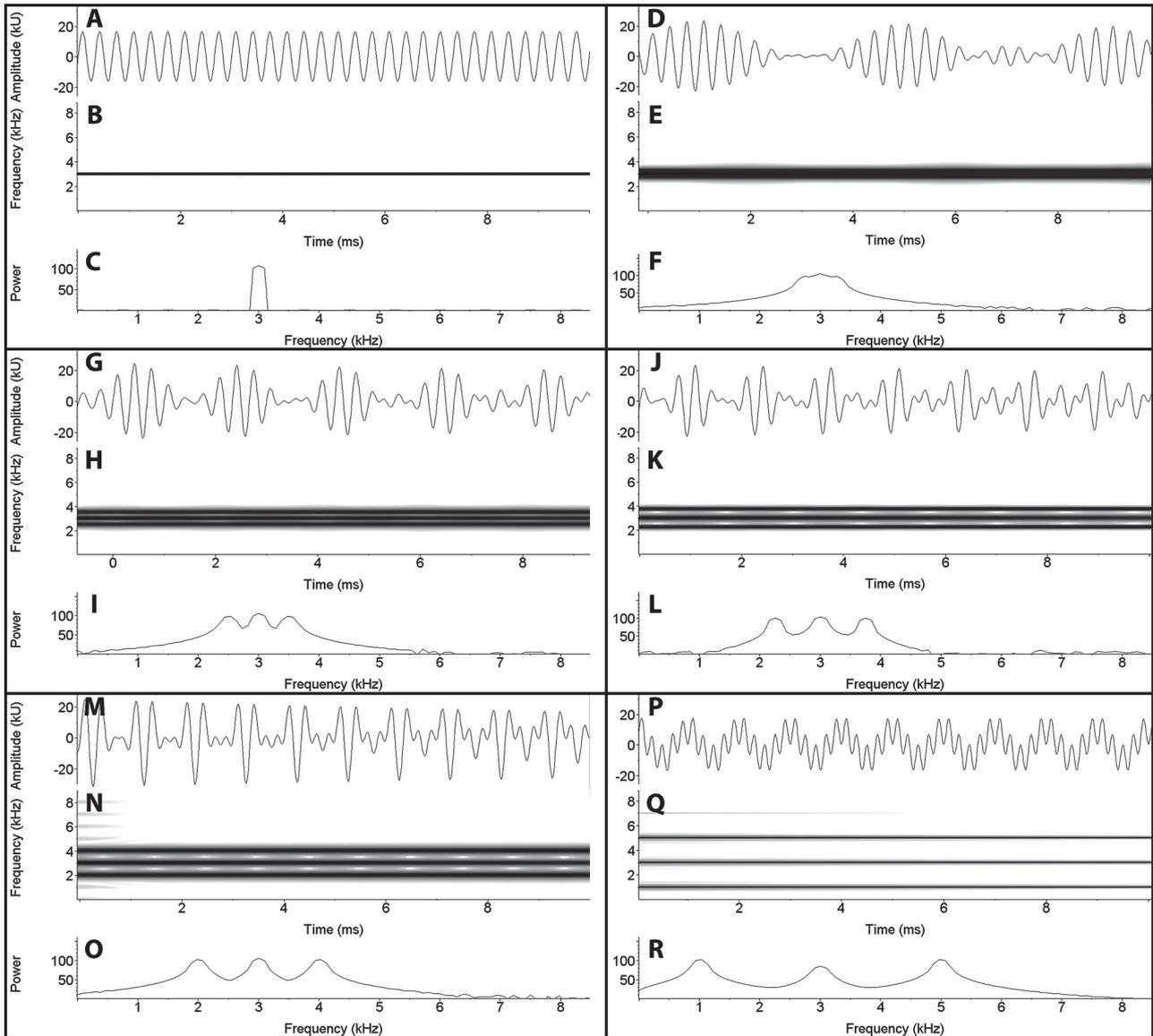


Figure 1. (A–C) Carrier frequency at 3,000 Hz modulated periodically in amplitude; (D–F) at 250 Hz; (G–I) 500 Hz; (J–L) 750 Hz; (M–O) 1,000 Hz; and (P–R) 2,000 Hz. (A, D, G, J, M, P) oscillograms; (B, E, H, K, N, Q) spectrograms; and (C, F, I, L, O, R) power spectra. Note that sideband distances are equal to the amplitude modulation rates, i.e., pulse rates. Spectrograms and power spectra with window function Hann, amplitude logarithmic, bandwidth 124 Hz, overlap 99%.

Table 2. Acoustic measurements of the calls described of the species of the *Scinax catharinae* species group. Call parameters according to the literature (Table 1): CD – call duration; DF – dominant frequency; FR – frequency range; NN – number of notes per call; ND – note duration; NR – note rate; NI – note interval. Parameters without minima and maxima are given as single values, otherwise as mean \pm standard deviation (when available). Identification numbers (column 'ID') associate the parameter values with the names of acoustic structures used in the literature (Table 1). In the acoustic pattern column ('AP'), 'S' refers to a short-call pattern and L to a long-call pattern (see text). The call duration value of the 'advertisement call' of *S. catharinae* (one asterisk) is approximate, adopted from the original description: "somewhat more than two seconds" (HEYER 1980). No number of notes was given for *S. ranki*'s 'sequence 3' (two asterisks) by ANDRADE & CARDOSO (1991), but it was described as a 'sequence of notes'.

Species	AP	IN	CD (s)	DF (kHz)	FR (kHz)	NN	ND (s)	NR (N/s)	NI (s)
<i>S. agilis</i>	–	1	–	7.45–7.92	–	1	0.36–0.40	–	–
		2	–	5.60–7.88	–	13–29	0.0106–0.0320	–	0.0624–0.1335
<i>S. albicans</i>	S	3	0.7	3.300–4.100	–	–	0.03	–	–
<i>S. angrensis</i>	S	4	0.17–0.7	2.15–3.70	1.11–5.75	1–7	0.025 \pm 0.012	0.072	0.023–0.076
<i>S. argyreornatus</i>	L	5	0.8	5.0–6.5	3.6–9.0	5	0.02–0.04	–	–
		6	10–25	5.0–6.5	3.6–8.0	130–280	0.02–0.09	–	0.04–0.08
<i>S. aromothyella</i>	L	7	1.04–20.76	4.769–5.414	1.477–8.777	2–74	0.04–0.22	1.02–4.36	0.05–0.48
		8	–	4.842–5.534	1.513–9.109	0–3	0.30–0.61	0–0.37	–
<i>S. berthae</i>	L	9	–	3.600–5.000	–	–	0.18	–	0.20
		10	–	–	–	–	1	–	–
		11	3.2–52.04	4477–5285	2.235–7.727	4–620	0.03–0.14	1.18–9.35	0.06–0.60
		12	–	4410–5361	2.275–7.289	0–52	0.13–0.59	0–0.86	–
<i>S. canastrensis</i>	S	13	–	–	1.4–5.6	6–7	–	–	< 0.1
		14	–	3.0	1.8–6.1	–	0.4	–	–
<i>S. catharinae</i>	S	15	~2*	2.200–3.100	–	–	0.04	–	–
<i>S. centralis</i>	S	16	0.37 \pm 0.06	3.2–4.6	2.8–6.2	–	–	–	–
		17	–	3.2–4.6	2.8–5.8	–	–	–	–
		18	3.90–9.09	3.49–4.89	–	1–10	20–35.5	–	–
		19	1.10–5.97	3.78–4.47	–	1	1.10–5.97	–	–
		20	0.30–0.46	3.78–4.57	–	1	0.30–0.46	–	–
		21	1.401–1.988	4.3–4.4	–	6–7	0.46–7.50	–	–
<i>S. heyeri</i>	S	22	0.4–0.5	–	2.5–3.5	6–8	0.05–0.1	–	–
		23	0.14–0.16	–	2–4.5	1	0.14–0.16	–	–
		24	0.341–0.560	2.842–3.876	–	6–9	0.002–0.013	16.1–20.2	0.055–0.061
		25	0.136–0.213	3.876–3.962	–	4–6	0.026–0.038	28.2–29.4	0.000–0.013
		26	0.551	3.876	–	10	0.009–0.040	18.1	0.000–0.076
<i>S. hiemalis</i>	S	27	–	2.0–3.8	–	1	–	–	–
		28	–	2.2–4.3	2.0–7.0	1	–	–	–
		29	0.688 \pm 0.088	–	–	–	–	–	–
<i>S. humilis</i>	–	30	0.109–0.345	3.094–3.937	–	3–5	0.002–0.006	11.6–38.2	0.003–0.055
<i>S. littoralis</i>	S	31	0.21–0.79	1.89–3.53	1.47–5.57	3–4	0.050 \pm 0.013	0.082	0.024–0.066
<i>S. longilineus</i>	S	32	0.613–1.418	2.067–2.756	–	8–19	0.016–0.067	11.8–14.4	0.024–0.141
		33	0.494–0.713	2.067–2.153	–	3	0.007–0.304	4.2–6.1	0.040–0.435
<i>S. luizotavioi</i>	S	34	0.12–0.49	2.76–4.13	2.07–5.08	2–6	0.005–0.018	–	0.078–0.435
		35	0.08–0.54	3.06–4.05	2.24–4.48	2–4	0.003–0.008	–	0.063–0.075
<i>S. machadoi</i>	–	36	–	3.500	–	6–7	0.05	–	–
<i>S. ranki</i>	S	37	–	–	2.2–5.5	4–5	–	–	0.12–0.3
		38	–	–	2.7–4.7	1	0.12	–	–
		39	–	–	2.5–6.6	2–3	0.05	–	0.4
		40	–	–	3.3–4.8	1	0.06	–	–
		41	–	–	2.5–4.8	3–5	0.05	–	0.390
		42	–	–	2.7–4.2	sequence**	–	–	–
<i>S. rizibilis</i>	L	43	–	2.000–4.500	–	3–10	–	–	–
		44	–	2.000–4.500	–	1	–	–	–
		45	0.74–2.95	2.8–4.0	2.0–5.5	7–23	1.0–4.7	–	–
		46	2.166 \pm 0.218	–	–	–	–	–	–
		47	0.032 \pm 0.001	–	–	–	–	–	–
		48	0.350 \pm 0.032	–	–	–	–	–	–
<i>S. strigilatus</i>	–	49	0.011–0.017	2.625–3.379	–	1	0.011–0.017	–	–
<i>S. skaios</i>	S	50	4.42–7.9	2.205–2.243	–	42–73	0.013–0.056	–	0.036–0.168
		51	0.017–0.049	2.310–2.348	–	1	0.017–0.049	–	–
<i>S. trapicheiroi</i>	S	52	0.006–2.218	2.713–3.316	–	1–8	0.006–0.337	3.6–8.2	0.002–0.645

were obtained from MNVOC or sound guides published by HADDAD et al. (2005), KWET & MÁRQUEZ (2000), and TOLEDO et al. (2007) (Appendix).

Results

Click-like, long, and short squawk-like notes

We found three note types in the calls of the species described here (*Scinax heyeri*, *S. humilis*, *S. longilineus*, and *S. trapicheiroi*), which are referred as click-like, long squawk-like, and short squawk-like notes (see Fig. 2, WELLS & SCHWARTZ 2006, BASTOS et al. 2011).

Each species presented at least two note types; most of them (three species) presented all three note types. The differences between the sounds of these notes are mainly due to their different durations and sideband distances (i.e., pulse rate, see GERHARDT 1998).

The click-like note had the shortest duration ($x = 0.006 \text{ s} \pm 0.003$; $Mo = 0.006$; $n = 91$) and the largest distance between sidebands ($x = 811.3 \text{ Hz} \pm 99.6$; $Mo = 770.7$; $n = 148$) followed by the short squawk-like note that had an intermediate duration ($x = 0.018 \text{ s} \pm 0.011$; $Mo = 0.006$; $n = 715$) and sideband distance ($x = 576 \text{ Hz} \pm 191.7$; $Mo = 540.3$; $n = 526$), and the long squawk-like note that had the longest duration ($x = 0.100 \text{ s} \pm 0.056$; $Mo = 0.061$; $n = 119$) and a shorter sideband distance ($x = 442 \text{ Hz} \pm 112.4$; $Mo = 494.3$; $n = 107$). Click-like notes are promptly distinguished from squawk-like notes by their attack being much shorter than their decay (amplitude peak near the beginning of the note; Fig. 2), while the attack was longer than the decay in the squawk-like notes (amplitude peak at the end of the note; Fig. 2). Occasionally, squawk-like notes may be emitted in sequences without silent intervals, resulting in a juxtaposed position (see call type B of *S. heyeri* below).

The sideband distances of the click-like notes described here were slightly larger than those of the squawk-like notes (see Fig. 2). This spectral difference is a direct consequence of the difference between the repetition rates of the pulses of the two note types (Fig. 3). The click-like notes have higher pulse rates ($x = 835 \text{ pulses/s} \pm 113.7$; $Mo = 449.7$; $n = 148$) than squawk-like notes ($x = 429 \text{ pulses/s} \pm 99.6$; $Mo = 438.9$; $n = 225$) and also have a larger sideband distance (Fig. 2). The distance between the sidebands is equal to the repetition rate of the acoustic structure responsible for the sideband formation, i.e., the pulses (see WATKINS 1967, BRADBURY & VEHCAMP 1998, GERHARDT 1998, GERHARDT & HUBER 2002).

Scinax heyeri

All specimens were observed vocalizing at night, perched on bushes at the edge of a shallow stream (ca 10 cm deep), about one metre above the ground. There were six males that were calling often. They were spaced at about five metres from each other. All vocalizations had low intensities as is typically described for the *Scinax catharinae* group

(see CARDOSO & HADDAD 1982). The calls of one male were recorded. Click-like and short squawk-like notes were observed, organized in three different call types referred to here as call A, call B, and call C. The multipulsed structure of the notes resulted in sidebands (Figs 4B+C). The pulse rate and sideband distances ranged from 592.8 to 1136.5 pulses/s ($x = 837.6 \pm 109.6$; $Mo = 949.7$; $n = 128$) and 599.4 to 1,016.9 Hz ($x = 801.2 \pm 96.5$; $Mo = 770.7$; $n = 128$) in click-like notes and 414.0 to 746.4 pulses/s ($x = 530.3 \pm 98.9$; $n = 13$) and 340.6 to 749.3 Hz ($x = 514.7 \pm 117.3$; $Mo = 484.4$; $n = 13$) in squawk-like notes, respectively (Figs 4C+F).

Call Type A (Figs 4A–C): Twenty calls from one specimen were analysed. The call was composed of a sequence of 6 to 9 click-like notes ($x = 7.0 \pm 0.9$; $Mo = 7.0$; $n = 20$) repeated quasi-periodically (Figs 4A+B). Single notes were emitted between complete calls on two occasions. The notes were composed of a series of pulses (sensu LITTLEJOHN 2001). A note with a long beginning and relatively very low amplitude was more distinctly visible in the highest-amplitude notes. The amplitude of the call increased slightly throughout the first three or four notes and thenceforth faster until the last note. The last half of the call was the part with highest amplitude, commonly the last note (Fig. 4A). Call duration ranged from 0.341 s to 0.560 s ($x = 0.414 \pm 0.062$; $Mo = 0.347$; $n = 20$), and note duration from 0.002 to 0.013 s ($x = 0.007 \pm 0.002$; $Mo = 0.006$; $n = 143$). Note durations increased slightly and gradually throughout the call; the duration of the first note ranged from 0.002 to 0.008 s ($x = 0.005 \pm 0.001$; $Mo = 0.005$; $n = 20$) and that of the last note from 0.008 to 0.013 s ($x = 0.011 \pm 0.001$; $Mo = 0.010$; $n = 20$). Note intervals ranged from 0.055 to 0.073 s ($x = 0.061 \pm 0.002$; $Mo = 0.060$; $n = 121$). And note periods from 0.059 to 0.083 s ($x = 0.067 \pm 0.003$; $Mo = 0.067$; $n = 121$); they increased slightly and gradually throughout the call; the first period ranged from 0.059 to 0.069 s ($x = 0.063 \pm 0.002$; $Mo = 0.063$; $n = 20$) and the last period from 0.067 to 0.083 s ($x = 0.071 \pm 0.003$; $Mo = 0.071$; $n = 20$). Note rate ranged from 16.1 to 20.2 notes per second ($x = 17.1 \pm 0.8$; $Mo = 17.3$; $n = 20$), varying throughout the call in a manner inverse to the pulse periods. Dominant frequency ranged from 2,842.4 to 3,876 Hz ($x = 3,061.6 \pm 231.3$; $Mo = 3,014.6$; $n = 22$) (Fig. 4C). The call had a slight ascending frequency modulation as had the notes, which was more evident in the last notes (Fig. 4B).

Call Type B (Figs 4D–F): Two calls from one specimen were analysed. The calls were composed of a sequence of four or six short squawk-like notes ($x = 5.0 \pm 1.4$; $n = 2$) repeated quasi-periodically and juxtaposed (Figs 4D+E). The notes were composed of a series of pulses (sensu LITTLEJOHN 2001). The first note had an attack that was shorter than its decay; the last note had an attack that was longer than its decay; and in the middle notes, the attack was as long as the decay (Fig. 4D). The difference between the amplitudes of the notes was smaller than that in call type A. The first and last notes presented greater amplitudes than the middle ones (Fig. 4D). Call durations were 0.136 and 0.213 s ($x = 0.174 \pm 0.054$; $n = 2$). Note duration ranged from 0.026 to 0.038 s ($x = 0.033 \pm 0.005$; $Mo = 0.026$;

n = 10). Note durations increased slightly and gradually throughout the call; durations of the first notes were 0.026 and 0.028 s ($x = 0.027 \pm 0.001$; n = 2) and those of the last notes were 0.030 and 0.037 s ($x = 0.033 \pm 0.005$; n = 2). Note intervals ranged from 0.000 to 0.013 s ($x = 0.003 \pm 0.004$; Mo = 0.001; n = 8), and note periods from 0.026 to 0.047 s ($x = 0.035 \pm 0.007$; Mo = 0.040; n = 8); they increased slightly and gradually throughout the call; the first periods were 0.026 and 0.029 s ($x = 0.027 \pm 0.002$; n =

2) and last periods 0.039 and 0.047 s ($x = 0.043 \pm 0.006$; n = 2). Note rates were 29.4 and 28.2 notes per second ($x = 28.8 \pm 0.9$; n = 2), varying throughout the call in a manner inverse to the pulse periods. The values of dominant frequency were 3,876 and 3,962.1 Hz ($x = 3,919.0 \pm 60.8$; n = 2) (Fig. 4F). The notes had slight ascending-descending frequency modulations.

Call Type C (Figs 4G–H): One call composed of short squawk-like and click-like notes was analysed. This call

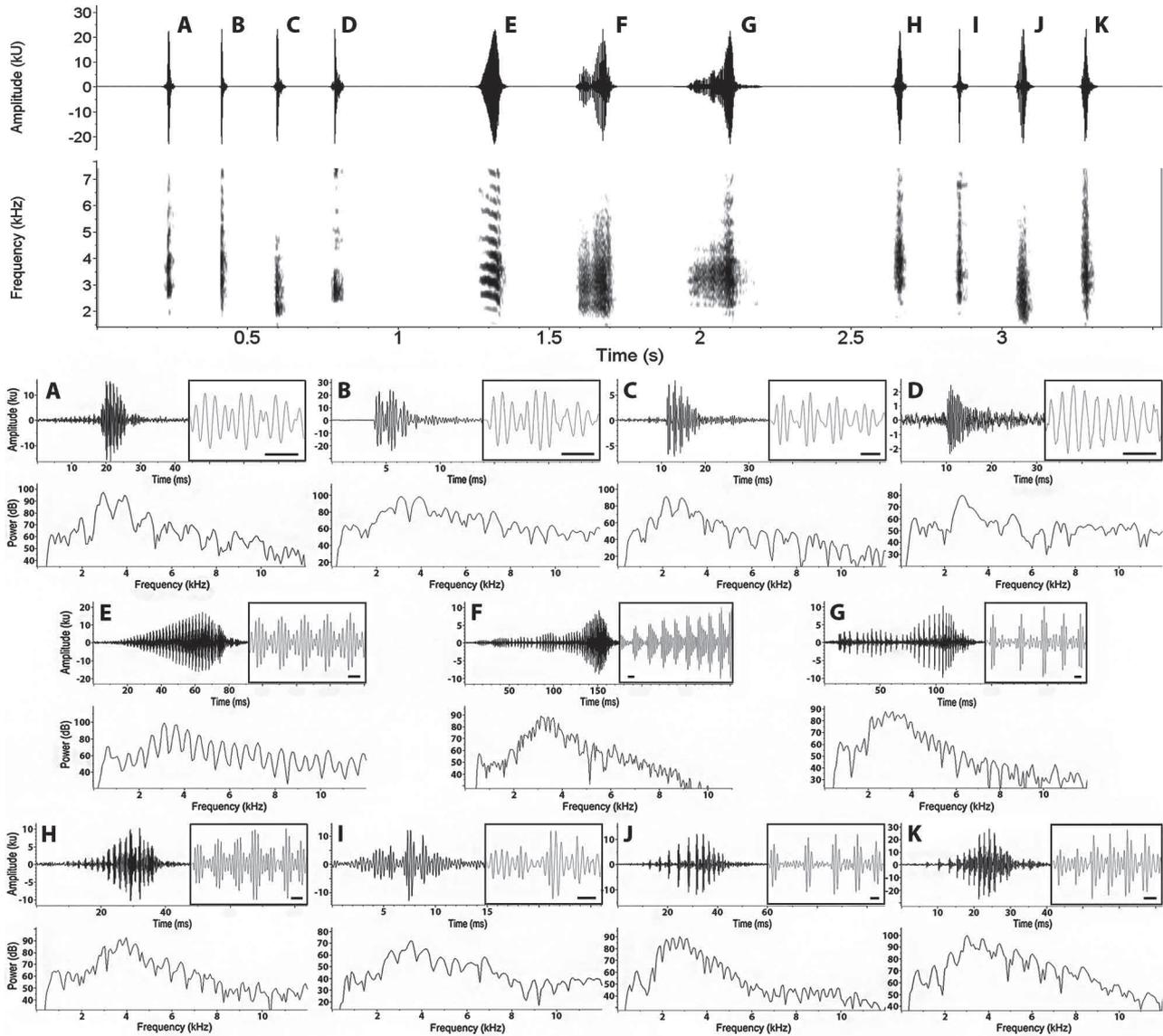


Figure 2. Click- and squawk-like notes of *Scinax heyeri*, *S. humilis*, *S. longilineus*, and *S. trapicheiroi*. (A–D) Click-like notes of *S. heyeri* (A), *S. humilis* (B), *S. longilineus* (C), and *S. trapicheiroi* (D). (E–G) Long squawk-like notes of *S. humilis* (E), *S. longilineus* (F), and *S. trapicheiroi* (G). (H–K) Short squawk-like notes of *S. heyeri* (H), *S. humilis* (I), *S. longilineus* (J), and *S. trapicheiroi* (K). Top: oscillograms and spectrograms of all notes at the same time scale. Bottom: oscillograms (above) and power spectra (below) of the same notes in detail. Oscillograms on the right (inside the squares) are the notes in zoom-in view. Scale bar = 1 ms. Note the periodic amplitude modulation of the notes and the shorter distances between the sidebands of the squawk-like notes and those of click-like ones. All recordings were low-cut filtered at 500 Hz. Power spectra with window function Hann, amplitude logarithmic, bandwidth 124 Hz, overlap 99%.

was composed of a sequence of 10 notes with the first five notes being short squawk-like ones (first part) and the last five click-like ones (second part) (Figs 4G+H). Within each part, the notes were repeated quasi-periodically (juxtaposed in the first part). In both parts, the amplitudes of the notes increased gradually, except for the first note of each part, which presented a relatively high amplitude (almost reaching the amplitude of the last note of the second part) (Fig. 4G). Call duration was 0.551 s. In each part, the note periods increased slightly and gradually: in the first part, note periods ranged from 0.031 to 0.037 s ($x = 0.034 \pm 0.002$; $n = 4$) and note intervals from 0.000 to 0.007 s ($x = 0.002 \pm 0.003$; $Mo = 0.001$; $n = 4$); in the second part, note periods ranged from 0.069 to 0.074 s ($x = 0.072 \pm 0.003$; $Mo = 0.074$; $n = 4$) and note intervals from 0.059 to 0.063 s ($x = 0.061 \pm 0.002$; $n = 4$). The interval between the parts was 0.076 s. Note rates were 28.4 and 16.1 notes per second for the first and second parts, respectively. Dominant frequency was 3,876 Hz.

Scinax humilis

Males were observed vocalizing at night on a fallen log over a shallow swamp (ca 10 cm deep), about one and a half metres above the water surface. They were spaced at about six metres from each other. A female was observed at about one metre from a male. The call had the low intensity as is typically described for the *Scinax catharinae* group (see CARDOSO & HADDAD 1982). Calls of three males were recorded. Click-like and long and short squawk-like notes were observed, organized in a single call type classified here as call type A. The multipulsed structure of the notes resulted in sidebands (Figs 5B, C, D, + F). The pulse rate and sideband distances ranged from 640.6 to 886.5 pulses/s ($x = 732.7 \pm 83.4$; $n = 12$) and 687.4 to 1,071.9 Hz ($x = 874.3 \pm 108.5$; $n = 12$) in click-like notes and 395.2 to 566.1 pulses/s ($x = 482.5 \pm 27.9$; $n = 27$) and 280.1 to 535.9 Hz ($x = 458.2 \pm 62.5$; $Mo = 494.3$; $n = 27$) in squawk-like notes, respectively (Figs 5C+D).

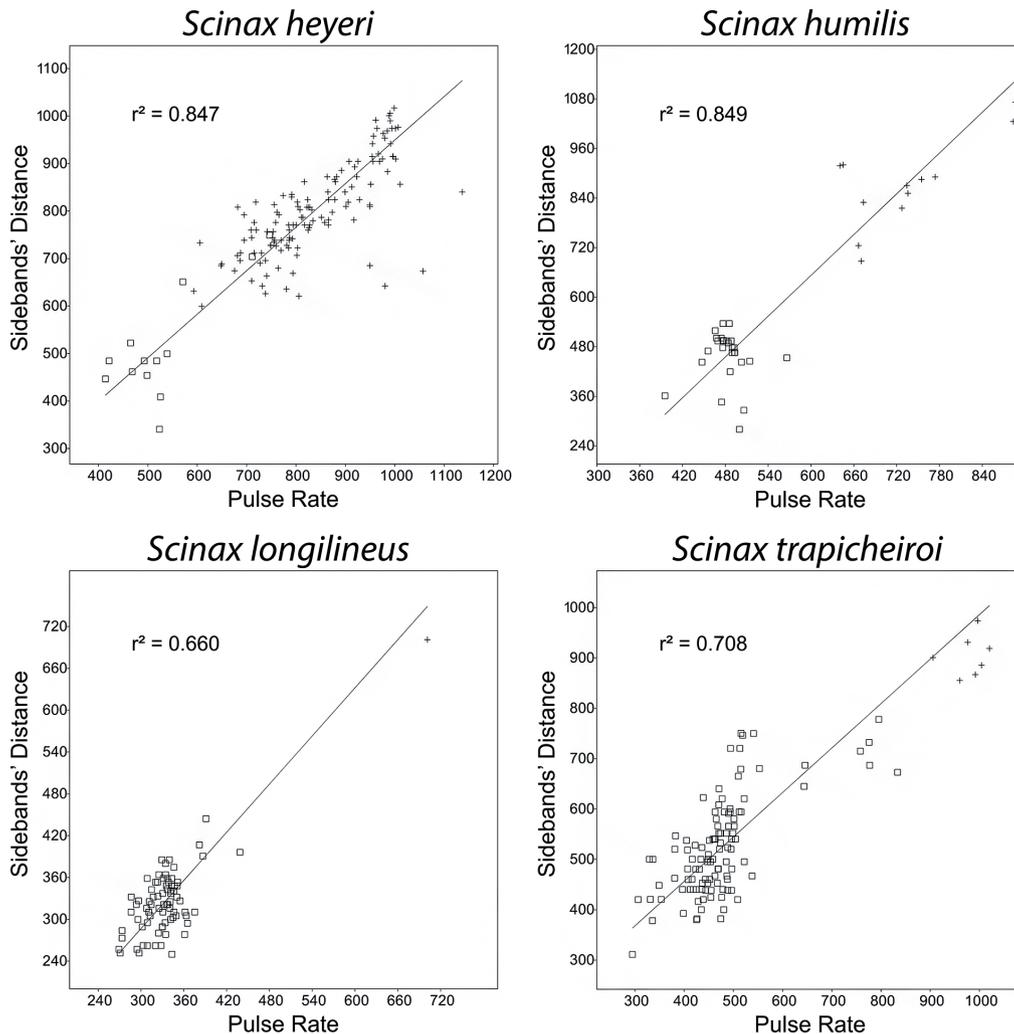


Figure 3. Regression analysis between sideband distances and pulse rates of the click (cross) and squawk-like (square) notes of the all calls described for four species of the *Scinax catharinae* group.

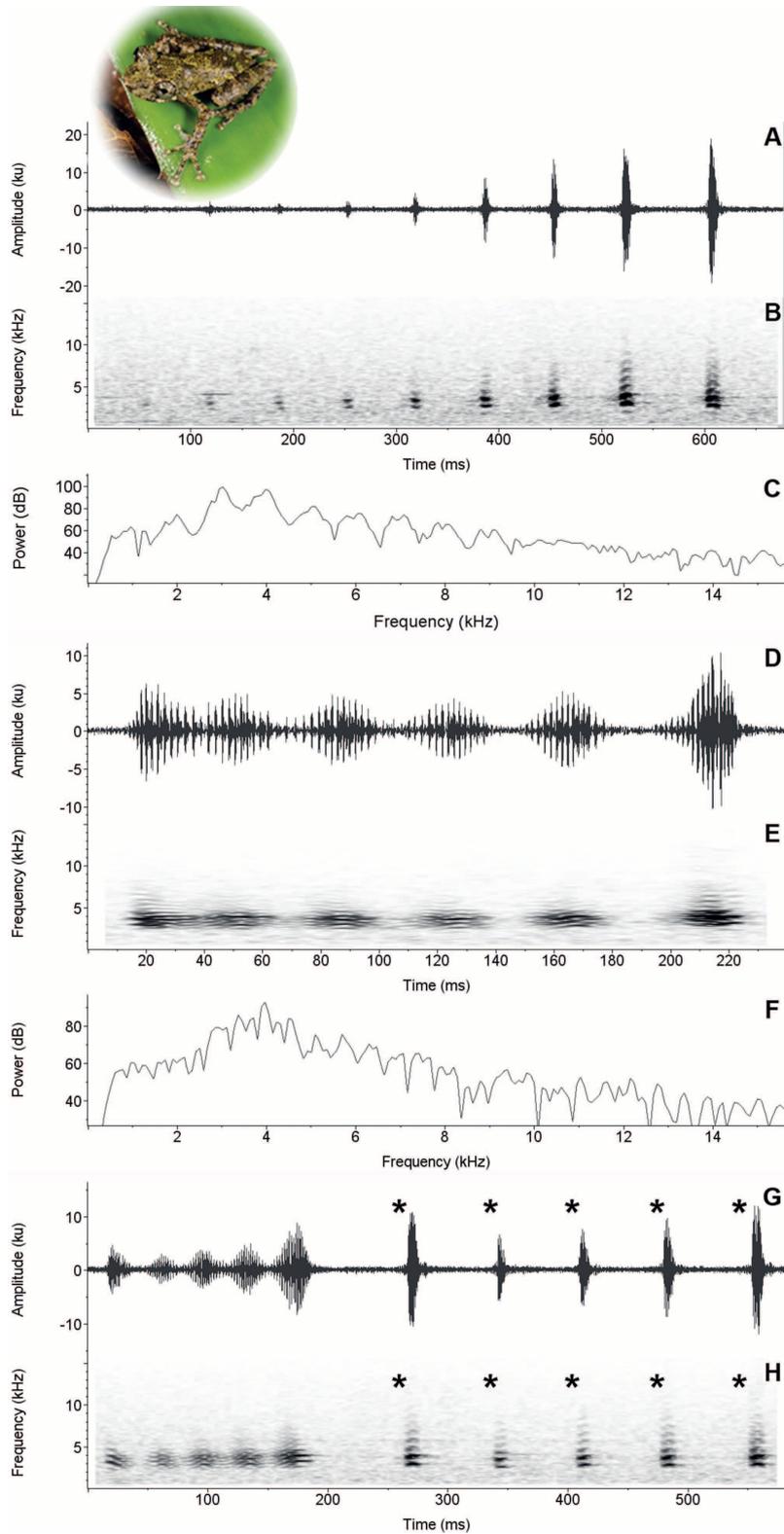


Figure 4. *Scinax heyeri*. (A) oscillogram; (B) spectrogram; and (C) power spectrum of one call A with nine short squawk-like notes. (D) oscillogram; (E) spectrogram; and (F) power spectrum of one call B with six long squawk-like notes; note the juxtaposed position of the first notes in call B; (G) oscillogram and (H) spectrogram of one call C with five long squawk-like notes and five short squawk-like notes (marked with asterisks). Spectrograms and power spectra with window function Hann, amplitude logarithmic, bandwidth 124 Hz, overlap 99%.

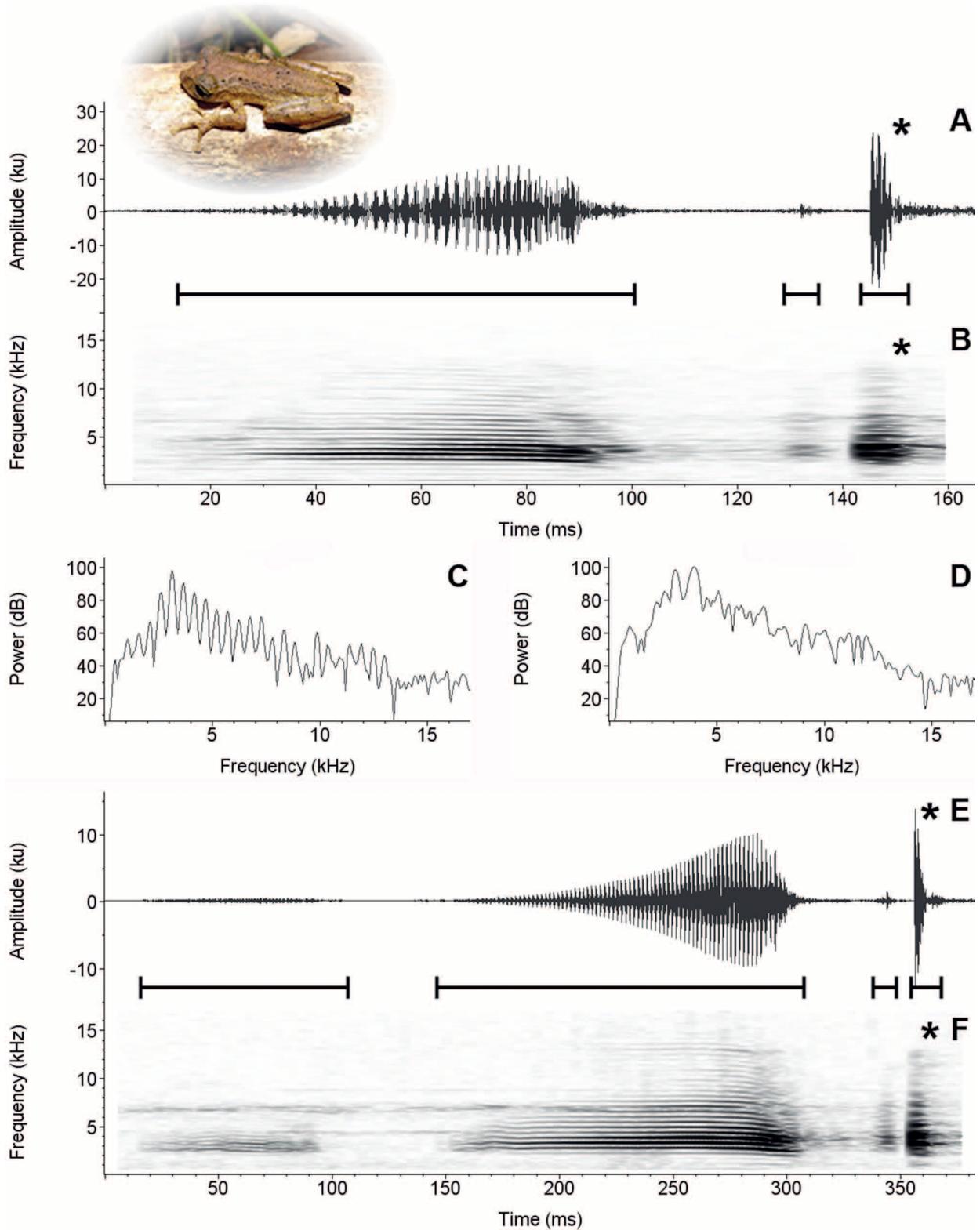


Figure 5. *Scinax humilis*. (A) oscillogram and (B) spectrogram of one call type A with three notes. Power spectra of (C) a squawk-like note (first one) and (D) a click-like note (last one); see the shorter sideband distances of the squawk-like notes (C) than those of the click-like notes (D). (E) oscillogram and (F) spectrogram of one call type A with four notes. Brackets indicate the notes. Click-like notes are marked with asterisks. Note that the last note is always a click-like note. Recordings were low-cut filtered at 500 Hz. Spectrograms and power spectra with window function Hann, amplitude logarithmic, bandwidth 124 Hz, overlap 99%.

Call Type A (Figs 5A–F): Forty-eight calls from three specimens were analysed. The call was composed of three to five notes in total ($x = 3.6 \pm 0.7$; $Mo = 3$; $n = 46$). In all calls, only the last note was click-like (Figs 5A, B, E, + F). Single short click-like notes with few pulses were emitted between complete calls only in two instances. Notes were composed of a series of pulses (sensu LITTLEJOHN 2001). Call duration ranged from 0.109 s to 0.345 s ($x = 0.156 \pm 0.047$; $Mo = 0.131$; $n = 46$). Calls were organized in two parts (note groups) separated by a longer interval. The first part had only squawk-like notes ranging from one to three notes ($x = 1.6 \pm 0.7$; $Mo = 1$; $n = 46$). In this part, the duration of the first note ranged from 0.001 to 0.076 s ($x = 0.014 \pm 0.030$; $Mo = 0.002$; $n = 6$); that of the second from 0.001 to 0.003 ($x = 0.002 \pm 0.000$; $Mo = 0.002$; $n = 20$); and the third note (the nearest to the second group) was always present and the longest one, with its duration ranging from 0.053 to 0.194 s ($x = 0.092 \pm 0.036$; $Mo = 0.067$; $n = 46$). The second part had a short squawk-like and a click-like note (always two notes; $n = 46$) in this order (Figs 5E+F); their durations ranged, respectively, from 0.001 to 0.011 s ($x = 0.007 \pm 0.002$; $Mo = 0.006$; $n = 46$) and from 0.002 to 0.007 s ($x = 0.004 \pm 0.001$; $Mo = 0.003$; $n = 46$). The first notes of each part exhibited lower amplitudes than the last ones. The last note of the call (click-like) had the highest amplitude, slightly higher than the last note of the first part (squawk-like). Note periods ranged from 0.004 to 0.130 s ($x = 0.015 \pm 0.015$; $Mo = 0.006$; $n = 72$), note intervals from 0.003 to 0.055 s ($x = 0.009 \pm 0.007$; $Mo = 0.005$; $n = 73$), note rate from 11.6 to 38.2 notes per second ($x = 24.2 \pm 7.2$; $Mo = 21.1$; $n = 46$), and dominant frequency from 3,093.8 to 3,937.5 Hz ($x = 3,377.0 \pm 206.0$; $Mo = 3,468.8$; $n = 48$) (Fig. 5C). The longest squawk-like note had an ascending-descending frequency modulation sequence. Other notes presented no frequency modulation or only a slightly ascending modulation.

Scinax longilineus

Males were observed vocalizing at night, perched on bushes at the edge of a stream and over a stem (in a hole) about one metre above the water surface. Some calling males were spaced at about one and a half metre from each other. Calls of two males were recorded. Click-like and long and short squawk-like notes were observed, organized in two call types referred to here as call types A and B. The multipulsed structure of the notes resulted in sidebands (Figs 6B, C, E, F, + G). The values of pulse rate and sideband distance were 701.5 pulses/s and 701.1 Hz in click-like notes and ranged from 269.1 to 438.9 pulses/s ($x = 330.5 \pm 28.7$; $n = 76$) and 249.8 to 444.2 Hz ($x = 322.3 \pm 40.1$; $Mo = 321.1$; $n = 76$) in squawk-like notes, respectively (Figs 6C, F, + D).

Call Type A (Figs 6A–C): Nine calls from two specimens were analysed. The call was composed of a sequence of 8 to 19 short squawk-like notes ($x = 15.1 \pm 3.4$; $Mo = 15.0$;

$n = 8$) repeated quasi-periodically (Figs 6A+B). One single note was emitted between complete calls. Notes were composed of a series of pulses (sensu LITTLEJOHN 2001). The amplitudes of the notes increased gradually throughout the call. The amplitude peaked in the last notes, commonly in the last or penultimate one (Fig. 6A). Call duration ranged from 0.613 s to 1.417 s ($x = 1.153 \pm 0.255$; $n = 8$), and note duration from 0.016 to 0.062 s ($x = 0.037 \pm 0.006$; $Mo = 0.041$; $n = 111$). Note durations increased slightly and gradually from the middle of the call to the end. Note periods ranged from 0.059 to 0.177 s ($x = 0.079 \pm 0.018$; $Mo = 0.072$; $n = 103$). The first and final note periods frequently were the longest ones (the first note period was the longest in five calls); the first note period ranged from 0.072 to 0.177 s ($x = 0.118 \pm 0.038$; $n = 7$) and the last from 0.077 to 0.148 s ($x = 0.118 \pm 0.038$; $n = 7$). Note intervals ranged from 0.025 to 0.141 s ($x = 0.007 \pm 0.017$; $Mo = 0.036$; $n = 103$), and note rate from 11.7 to 14.4 notes per second ($x = 13.1 \pm 0.9$; $n = 8$), varying throughout the call in a manner inverse to the pulse periods. Dominant frequency ranged from 2,067.2 to 2,756.2 Hz ($x = 2,344.6 \pm 268.2$; $Mo = 2,067.2$; $n = 9$) (Fig. 6C). The notes often presented several sequences of ascending and descending frequency modulation.

Call Type B (Figs 6D–G): Two calls from two specimens were analysed. They were each composed of three notes ($x = 3.0 \pm 0.0$; $Mo = 3.0$; $n = 2$). In one call, all notes were long squawk-like notes; the other call was composed of two long squawk-like notes and one click-like note (second note) (Figs 6D+E). The notes were composed of a series of pulses (sensu LITTLEJOHN 2001). Some long notes resembled a series of juxtaposed notes. The amplitudes of the calls were irregular. In one call, the first note reached the highest amplitude (peak) (Fig. 6D) and in the other call, it was in the last note that did so. Call duration ranged from 0.494 s to 0.713 s ($x = 0.603 \pm 0.155$; $n = 2$). The third note was longer than the first two (Figs 6D+E). Duration of the squawk-like notes ranged from 0.037 to 0.304 s ($x = 0.110 \pm 0.114$; $n = 5$), while that of the click-like note was 0.008 s. Note periods were highly variable, ranging from 0.077 to 0.479 s ($x = 0.195 \pm 0.190$; $n = 4$). Note intervals ranged from 0.040 to 0.435 s ($x = 0.162 \pm 0.184$; $n = 4$). In both calls, the second (last) note period was shorter than the first: the first note period ranged from 0.113 to 0.479 s ($x = 0.296 \pm 0.259$; $n = 2$) and the second from 0.077 to 0.109 s ($x = 0.093 \pm 0.023$; $n = 2$). Note rate ranged from 4.2 to 6.1 notes per second ($x = 5.1 \pm 1.3$; $n = 2$). Spectral features of the squawk-like notes resembled the note type of call type A, whereas call type B had a slight higher variation in the pulse rate inside the notes, resulting in a slightly higher variation in the number of sidebands and their interval values. Dominant frequency ranged from 2,067.2 to 2,153.3 Hz ($x = 2,110.2 \pm 60.8$; $n = 2$) (Figs 6F+G). The squawk-like notes often had several sequences of ascending and descending frequency modulation. The click-like note had an ascending-descending frequency modulation sequence.

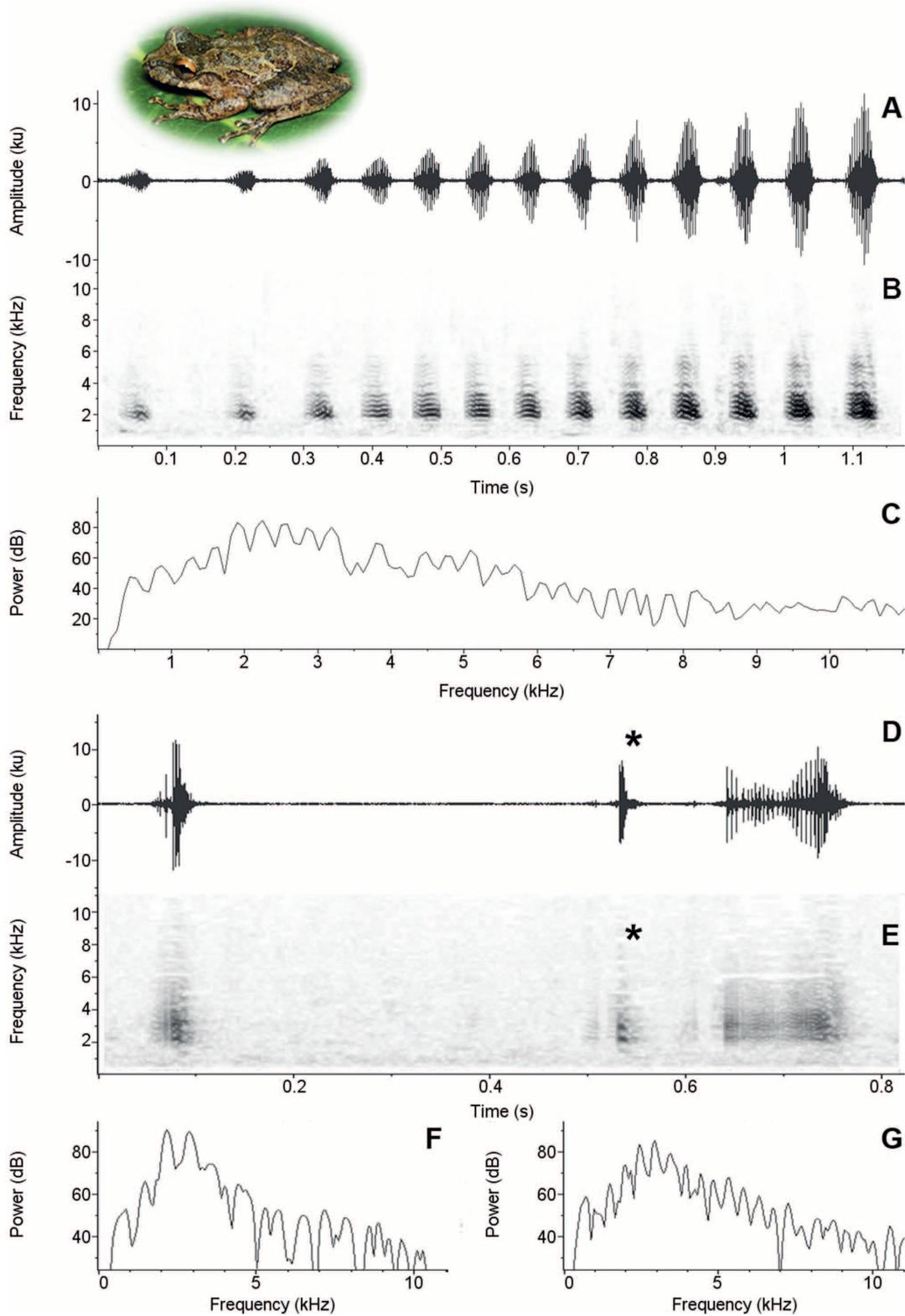


Figure 6. *Scinax longilineus*. (A) oscillogram; (B) spectrogram; and (C) power spectrum of one call type A with thirteen notes. (D) oscillogram; (E) spectrogram of one call type B with three notes. (F) Power spectrum of the click-like note marked with asterisks (D+E). (G) Power spectrum of the third squawk-like note (D+E). Note the difference between sideband distances in the click-like note (F) and the squawk-like note (G). All recordings were low-cut filtered at 500 Hz. Spectrograms and power spectra with window function Hann, amplitude logarithmic, bandwidth 124 Hz, overlap 99%.

Scinax trapicheiroi

Males were observed vocalizing at night on two occasions. On the first one, the males were perched on bushes in the vicinity of an artificial water reservoir. In the second, the males were perched about 50 cm above the water surface at the edge of a stream, clustered in small groups of up to 10 individuals (males and females). The groups were located far (more than 10 m) from each other along the stream. Within their groups, males and females were spaced at varying distances from each other, ranging from 10 to 150 cm. The calls of nine males were recorded. Click-like and long and short squawk-like notes were observed, organized in two call types referred to here as call types A and B. Males often emitted single calls of type A. Calls of type B were emitted when neighbouring males called in immediate response or at the same time. The multipulsed structure of the notes resulted in sidebands (Figs 7B, D, E, + F). The pulse rate and sideband distances ranged from 905.6 to 1,020.2 pulses/s ($x = 979.2 \pm 37.7$; $n = 7$) and 855.3 to 974.0 Hz ($x = 904.6 \pm 40.7$; $n = 7$) in click-like notes and 295.1 to 833.6 pulses/s ($x = 472.6 \pm 89.6$; $Mo = 485.5$; $n = 109$) and 311.3 to 778.1 Hz ($x = 524.4 \pm 98.1$; $Mo = 438.7$; $n = 109$) in squawk-like notes, respectively (Figs 5E+F).

Call Type A (Figs 7A, B, + F): Twenty-one calls from four specimens were analysed. Calls of type A were composed of a sequence of 8 to 61 short squawk-like notes ($x = 19.9 \pm 16.0$; $Mo = 14$; $n = 21$) that were repeated quasi-periodically (Figs 7A+B) and ended ($n = 4$) or began ($n = 1$) with a long squawk-like note. Notes were composed of a series of pulses (sensu LITTLEJOHN 2001). The amplitudes of the notes increased gradually throughout the call. The amplitude peaked in the last notes, commonly in the last or penultimate note (Fig. 7A). Call duration ranged from 0.436 s to 3.637 s ($x = 1.171 \pm 0.950$; $n = 21$), duration of short squawk-like notes from 0.004 to 0.043 s ($x = 0.018 \pm 0.006$; $Mo = 0.020$; $n = 394$), and duration of long squawk-like notes from 0.109 to 0.157 s ($x = 0.126 \pm 0.019$; $n = 5$). The durations of the short squawk-like notes increased slightly and gradually throughout the call. Note periods ranged from 0.029 to 0.235 s ($x = 0.059 \pm 0.022$; $Mo = 0.053$; $n = 398$). The first and final note periods frequently were the longest ones: the first note period ranged from 0.040 to 0.208 s ($x = 0.097 \pm 0.051$; $n = 20$) and the last from 0.049 to 0.209 s ($x = 0.085 \pm 0.041$; $n = 21$). Note intervals ranged from 0.022 to 0.199 s ($x = 0.041 \pm 0.022$; $Mo = 0.031$; $n = 398$), note rate from 12.3 to 21.0 notes per second ($x = 17.4 \pm 2.4$; $n = 21$), varying throughout the call in a manner inverse to the pulse periods, and dominant frequency from 2,625.0 to 3,750.0 Hz ($x = 3,160.7 \pm 275.1$; $Mo = 3,187.5$; $n = 21$) (Fig. 7F). The notes often presented several sequences of ascending and descending frequency modulation.

Call Type B (Figs 7C–F): Forty-nine calls from five specimens were analysed. The call was composed of a sequence of 1 to 8 click-like and/or squawk-like notes ($x = 2.0 \pm 2.0$; $Mo = 1$; $n = 49$) that were repeated at irregular intervals (Figs 7C+D). There was no defined note sequence with a variable number of total notes and of squawk- or

click-like notes. Both note types were composed of series of pulses (sensu LITTLEJOHN 2001). Some long squawk-like notes resembled a series of juxtaposed notes. In the calls with more than one note, the call amplitude varied considerably throughout the notes with neither increasing nor decreasing patterns. The position of the amplitude peak in the call with two or more notes was not the same. However, the calls with two notes often had similar amplitudes in both notes. Call duration ranged from 0.003 to 2.218 s ($x = 0.247 \pm 0.458$; $Mo = 0.008$; $n = 49$); that of click-like notes from 0.006 to 0.014 s ($x = 0.009 \pm 0.003$; $Mo = 0.006$; $n = 14$); that of short squawk-like notes from 0.004 to 0.043 s ($x = 0.018 \pm 0.006$; $Mo = 0.020$; $n = 411$); and that of long squawk-like notes from 0.044 to 0.337 s ($x = 0.126 \pm 0.055$; $Mo = 0.049$; $n = 53$). Note periods ranged from 0.014 to 0.706 s ($x = 0.207 \pm 0.152$; $n = 48$), note intervals from 0.002 to 0.645 s ($x = 0.115 \pm 0.130$; $Mo = 0.163$; $n = 48$), and note rate from 3.6 to 11.2 notes per second ($x = 5.8 \pm 2.2$; $n = 14$). The dominant frequency ranged in both from 2,713.2 to 3,316.1 Hz ($x = 2,913.3 \pm 189.5$; $Mo = 2,799.3$; $n = 17$) (Figs 7D–F). Click-like and squawk-like notes presented no modulation and a slight ascending or descending frequency modulation, respectively.

Review of the acoustic traits of the
Scinax catharinae species group

The calls of the *Scinax catharinae* species group are typically composed of pulsed notes. The high repetition rates of the pulse sequences result in sidebands showing in the spectrograms and power spectra (Fig. 2).

The calls of seventeen species were classified in two mutually exclusive classes (acoustic patterns) according to their similarity: (1) long call or (2) short call (Fig. 8).

The short call was the most widespread acoustic pattern in the *S. catharinae* group, with thirteen species, *S. albicans*, *S. angrensis*, *S. canastrensis*, *S. catharinae*, *S. centralis*, *S. heyeri*, *S. hiemalis*, *S. littoralis*, *S. longilineus*, *S. luizotavi-oi*, *S. ranki*, *S. skaios*, and *S. trapicheiroi*, being known to use it (Table 1, Fig. 8). The type A calls of these species were composed of a sequence of notes and present a rapidly ascending amplitude modulation, i.e., there was a considerable note-by-note increase in amplitude; the amplitude peak of the call was in the end of the call, in the last notes (Fig. 8). Some incomplete type-A calls presented the amplitude peak slightly displaced before the end and closer to the middle of the call (e.g., in *S. littoralis*).

Of the species with short calls, *Scinax canastrensis*, *S. catharinae*, *S. centralis*, *S. humilis*, *S. littoralis*, *S. longilineus*, *S. trapicheiroi*, and *S. skaios* emit the three note types described in the present study. Only click- and short squawk-like notes were observed in *Scinax heyeri*. Type-A calls were composed of short squawk-like notes, while those of type B were composed of click-like and long squawk-like notes.

The vocalizations of four species exhibited the long-call pattern: *S. argyreornatus*, *S. aromothyella*, *S. berthae*, and *S. rizibilis* (Table 1, Fig. 8). These species emit long series

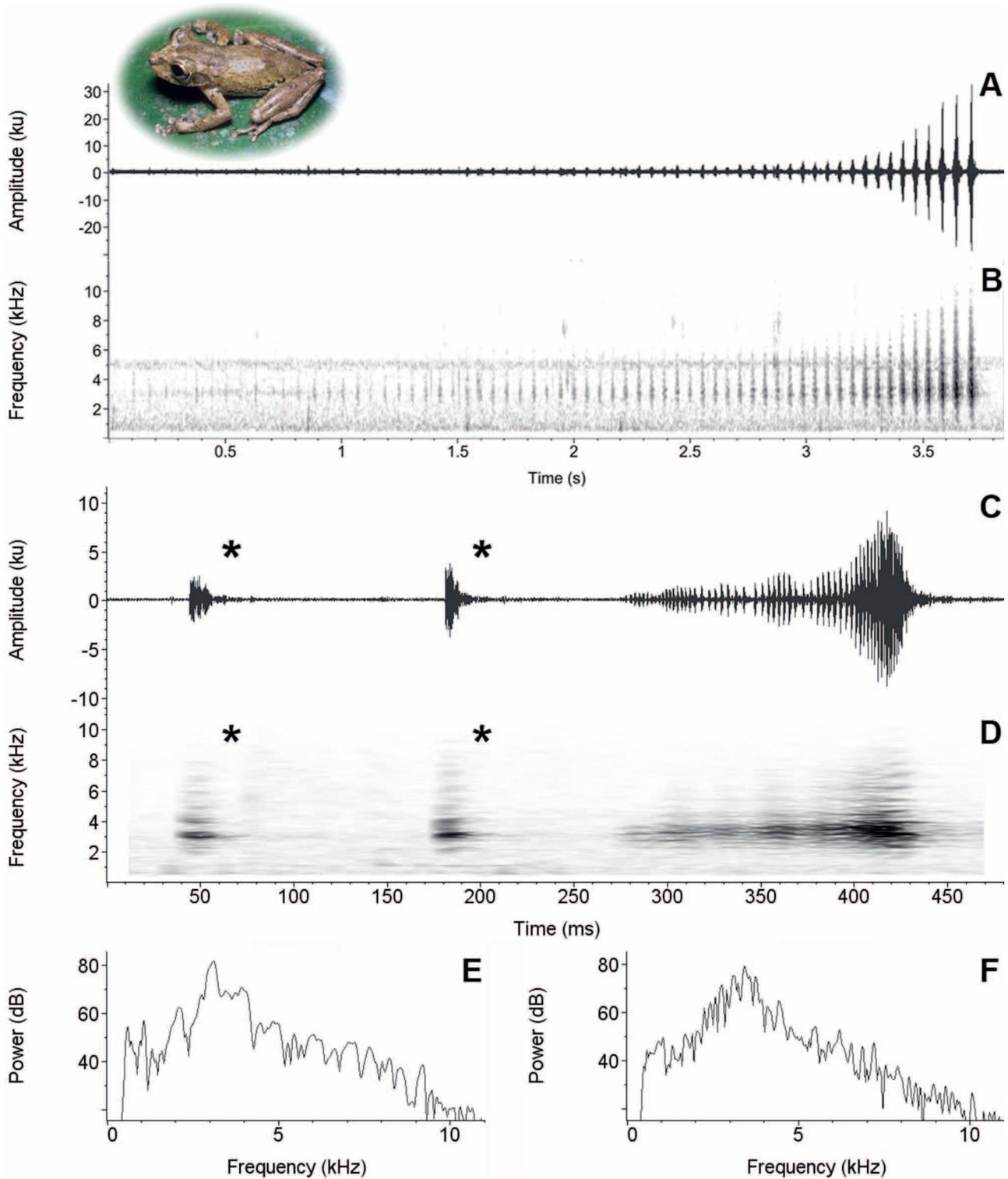


Figure 7. *Scinax trapicheiroi*. (A) oscillogram and (B) spectrogram of one call type A with 61 short squawk-like notes. (C) oscillogram and (D) spectrogram of one call type B with two click-like notes (marked with asterisks) and one long squawk-like note. Power spectra of (E) a click-like note and (F) a long squawk-like note. Note the longer sideband distances of the click-like notes (E) compared to those of the squawk-like notes (F). All recordings were low-cut filtered at 500 Hz. Spectrograms and power spectra with window function Hann, amplitude logarithmic, bandwidth 124 Hz, overlap 99%.

of short squawk-like notes as their most frequent calls, referred to here as type A. This call showed a gradually ascending amplitude and long durations (see Fig. 8). All these species used both short and long squawk-like notes. With the short squawk-like notes resembling those described here for the four species with a short-call pattern (i.e., *S. heyeri*, *S. humilis*, *S. longilineus*, and *S. trapicheiroi*) but with higher dominant frequencies (reaching 6.5 kHz in *S. aromothyella*). They emit a single long squawk-like note as call type B with a lower pulse rate (except *S. argyreornatus* which does not have a clearly lower pulse rate in its long notes). Due to their high dominant frequencies and the length of their calls with many notes, type-A calls of these species sound like sequences of human laughter (e.g., *S. rizibilis*; see BOKERMANN 1964).

The call of *S. humilis* did not match any of the two patterns above. Like other species of the *S. catharinae* group, this species emits all three note types, however its note organization and short call duration were quite different from those of the other species of the group. The call of *S. humilis* was the only one that always exhibited a sequence of notes with two note types (click- and squawk-like notes), the last one was a click-like note, and the others were squawk-like (Fig. 5).

Scinax agilis produced a call that was completely different from those of other species of the *S. catharinae* group. Traits such as much longer notes and lower pulse rates resemble the acoustic pattern commonly observed in the *Scinax ruber* clade (see PUGLIESE et al. 2004, NUNES et al. 2007, BEVIER et al. 2008).

Species that emit calls with different patterns can be promptly differentiated, i.e., through qualitative features.

When it comes to species using the same acoustic pattern, quantitative data will aid in differentiating them (see Table 2).

Discussion

The pulsed compositions of the notes (see Fig. 2) is shared by other species in the genus *Scinax*, including species of the *S. ruber* and *S. perpusillus* groups (see POMBAL et al. 1995, POMBAL & BASTOS 2003). However, the species of the *S. catharinae* group emit calls that will be more variable in amplitude, spectral and temporal traits when compared to those of the *S. ruber* group (BEVIER et al. 2008, PEREYRA et al. 2012).

The acoustic diversity of notes observed here, i.e., three different note types, is recurrent in literature about the acoustic repertoire of the *S. catharinae* group and may be directly related to functional diversity (cf. BASTOS et al. 2011). In addition to the species examined here, *S. ranki* apparently also uses a click-like note ('secondary note' and 'quick emission'), a short squawk-like note (in 'common call' and 'sequence 3'), and long squawk-like notes ('notes a' and 'b', ANDRADE & CARDOSO 1987, ANDRADE & CARDOSO 1991, see Table 1). We were not able to identify the two note types of *Scinax hiemalis* described by HADDAD & POMBAL (1987).

CARDOSO & HADDAD (1982) noted that the type-B calls (composed of long squawk-like notes) of *S. canastrensis* were emitted when two calling males were near each other. This observation led the authors to associate this call type with an aggressive function. BARRIO (1962) observed that

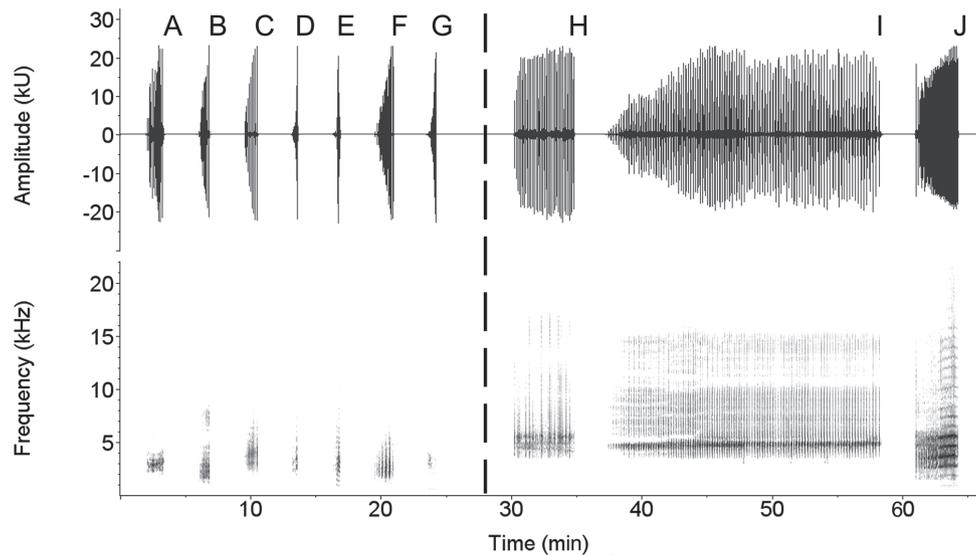


Figure 8. Acoustic patterns in the *Scinax catharinae* species group. On the left of the dashed line, calls with a short-call pattern and, on the right, with a long-call pattern. Oscillograms and spectrograms of call type A of (A) *S. canastrensis*; (B) *S. catharinae*; (C) *S. centralis*; (D) *S. heyeri*; (E) *S. littoralis*; (F) *S. longilineus*; (G) *S. trapicheiroi*; (H) *S. argyreornatus*; (I) *S. berthae*; and (J) *S. rizibilis*. Spectrograms with window function Hann, amplitude logarithmic, bandwidth 124 Hz, overlap 99%.

the type-B calls (long squawk-like note) of *S. berthae* were emitted in antagonistic encounters. In fact, the calls referred to here as type B, usually composed of long squawk-like notes, of representatives of the *S. catharinae* group were reported as less common and seem to have an aggressive function (see BASTOS et al. 2011, PEREYRA et al. 2012). The calls type B of *S. heyeri* and *S. longilineus* were apparently emitted in antagonistic contexts such as after louder common calls from neighbours. In *S. humilis*, which presented only one call type with a different note composition, the note type may still have different functions. Calling males of this species emitted calls with more long squawk-like notes (Figs 5E+F) in response to calls from neighbours, indicating an antagonistic function of this note. Probably the same note relationship should exist in other compound calls such as the type-C calls of *S. heyeri*.

The call type, which we call 'call type A' here is currently widely referred to as "advertisement call" in the literature (Table 1) and supposed to have, at least, a function in courtship. The calls of the type A described here for *S. heyeri*, *S. humilis*, *S. longilineus*, and *S. trapicheiroi* were the most frequently recorded calls and apparently emitted without being triggered by other calling males. Therefore, type-A calls of these species might have a function in courtship, likewise corresponding to what is usually called "advertisement call".

BASTOS et al. (2011) identified four vocalization types in *S. centralis*: advertisement call, two types of aggressive calls, and a displacement call. We examined the analysed calls by BASTOS et al. (2011) and found their advertisement, aggressive (both), and displacement calls to be composed of short squawk-like, long squawk-like, and click-like notes, respectively. Some of the functions of these notes may be widespread in the *S. catharinae* group (see *S. heyeri* above for an exception). However, as was pointed out by POMBAL & BASTOS (1996) (see also ANDRADE & CARDOSO 1987, HADDAD & POMBAL 1987, POMBAL et al. 1995), the high acoustic complexity in this species group has rendered deciphering the functions of calls difficult, and experiments with other species should be employed to clarify this question.

We were unable to assess the acoustic patterns of *S. machadoi* and *S. strigilatus* based on their original descriptions, but according to BOKERMANN & SAZIMA (1973), the call of *S. machadoi* resembles those of *S. brienii*, *S. obtriangulatus* and *S. trapicheiroi*. The advertisement call of *S. strigilatus* was described as being composed of a single note. This note closely resembles the short squawk-like notes of the short-call pattern (cf. MENDES et al. 2013). The call of this species may be composed of a single squawk-like note; however it is possible that only incomplete calls (e.g., calls emitted by partially excited males) were recorded by MENDES et al (2013).

Morphologically, *S. humilis* closely resembles *S. angrensis* and *S. littoralis*, however the call of *S. humilis*, composed of few notes of both types, is structurally quite different from those of *S. angrensis* and *S. littoralis*, which have a typical short-call pattern with rapidly ascending amplitude modulation (cf. Fig. 5 of the current study and Fig. 2 of

GAREY et al. 2012). GAREY et al. (2012) found values of 0.072 and 0.082 notes per second in *S. angrensis* and *S. littoralis*, respectively. These are quite different from those found by us for *S. heyeri*, *S. humilis*, *S. longilineus*, and *S. trapicheiroi*. Analysis of the same call type in *S. littoralis* (see Appendix) described by GAREY et al. (composed of squawk-like notes) found the note rate varying from 12.4 to 17.6 ($x = 13.9 \pm 1.4$; $n = 14$). These values are more compatible with the note rates for the species described here.

A phylogenetic study of *Scinax* (FAIVOVICH 2002) positioned *S. agilis* as a sister taxon to the *S. catharinae* group and pointed out that *S. agilis* exhibited morphological synapomorphies of the *S. catharinae* group. However, as seen in the call, other traits like the presence of a pectoral fold, which is observed in almost all species of the *S. ruber* group, have also been identified in *S. agilis* (FAIVOVICH 2002, LOURENÇO et al. 2014). This provides an interesting mosaic of character states from both major clades of *Scinax* and reinforces the necessity of a widely based phylogenetic study involving more characters and terminal taxa of the genus *Scinax*.

Acoustic data have been demonstrated to be useful for unravelling the taxonomy within many anuran groups (e.g., HADDAD & POMBAL 1998, LINGNAU et al. 2008, HEPP et al. 2012, 2015). The acoustic differences found here between the species of the *Scinax catharinae* species group reinforce this data source as a useful tool for resolving taxonomic issues that persist in this group. Moreover, proposals of acoustic character evolution have been derived from methods of ancestral state reconstruction (e.g., RON 2008), and acoustic characters have recently aided in the construction of phylogenetic hypotheses (e.g., GOICOECHEA et al. 2010, ROBILLARD et al. 2010). Further phylogenetic applications of the acoustic features (codified in phylogenetic characters) of the *S. catharinae* group may clarify the evolutionary history of the acoustic similarities observed, such as common calls composed of long series of short notes with more a regular amplitude (as in the long-call pattern); common calls composed of series of notes with rapidly ascending amplitude modulation (as in the short-call pattern); occasional calls composed of long notes resembling laughter; and occasional calls composed of squawk- or click-like notes.

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Note added in proof

A recently published study by DUELLMAN et al. (2016) proposed a phylogenetic hypothesis for the hylid frogs. The authors resurected the generic name *Ololygon* FITZINGER, 1843 to encompass *Scinax catharinae* and *S. perpusillus* species groups (see introduction). Therefore, the so-called “*Scinax catharinae* species group” in the present study is currently recognized as “*Ololygon catharinae* species group”.

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Appendix

Recordings examined

Scinax argyreornatus: Brazil, state of Santa Catarina, municipality of Florianópolis, Ilha de Santa Catarina – track A38 cuts 1 and 2 (KWET & MÁRQUEZ 2000), municipality of Ubatuba – track 31 (HADDAD et al. 2005).

Scinax berthae: Brazil, state of Rio Grande do Sul, municipality of Torres – track A40 cut 1 (KWET & MÁRQUEZ 2000); Brazil, state of Santa Catarina, municipality of Lagunas – A40 cut 2 (KWET & MÁRQUEZ 2000).

Scinax canastrensis: Brazil, state of Minas Gerais, municipality of São Roque de Minas – track 33 (TOLEDO et al. 2007).

Scinax catharinae: Brazil, state of Rio Grande do Sul, municipality of São Francisco de Paula – track A41 cut 1 (KWET & MÁRQUEZ 2000); Brazil, state of Santa Catarina, municipality of Florianópolis, Ilha de Santa Catarina – track A41 cut 2 (KWET & MÁRQUEZ 2000); Brazil, state of Santa Catarina, municipality of Rancho Queimado: MNVOC 041; voucher specimen MNRJ 72426.

Scinax centralis: Brazil, state of Goiás, municipality of Silvânia – track 34 in ‘Guia Interativo dos Anfíbios Anuros do Cerrado, Campo Rupestre & Pantanal’; Brazil, state of Goiás, municipality of Silvânia – 13 recordings from six specimens, including advertisement, long and short aggressive, and displacement calls (see BASTOS et al. 2011) from sound collections of ROGÉRIO BASTOS & ALESSANDO MORAIS.

Scinax heyeri: Brazil, state of Espírito Santo, municipality of Santa Teresa, ReBio Santa Lúcia: MNVOC 045-04; voucher specimen MNRJ 84072.

Scinax humilis: Brazil, state of Rio de Janeiro, municipality of Maricá, Ponta Negra: MNVOC 044-01 to 04; voucher specimens MNRJ 80704 (MNVOC 044-01 and 02), 80705 (MNVOC 044-03) and 80706 (MNVOC 044-04).

Scinax littoralis: Brazil, state of São Paulo, municipality of Iguape: MNVOC 047-01; voucher specimens MNRJ 87577–87586.

Scinax longilineus: Brazil, state of Minas Gerais, municipality of Ouro Preto, Estação Ecológica do Tripui, córrego Volta Grande: MNVOC 040-05 to 06; voucher specimens MNRJ 75746 (MNVOC 040-05) and 75747 (MNVOC 040-06).

Scinax rizibilis: Brazil, state of Rio Grande do Sul, municipality of Terra de Areia – track A42 in ‘Sound guide of the calls of frogs and toads from southern Brazil and Uruguay’; Brazil, state of São Paulo, municipality of Ribeirão Branco – track 41 (HADDAD et al. 2005).

Scinax skaios: Brazil, state of Goiás, municipality of Santa Rita do Novo Destino: MNVOC 049-01 to 02; voucher specimen MC-NAM 6221 (paratype).

Scinax trapicheiroi: Brazil, state of Rio de Janeiro, municipality of Rio de Janeiro, Feema, Vista Chinesa, Tijuca Forest: MNVOC 016-02. Brazil, state of Rio de Janeiro, municipality of Mendes, Centro Marista São José das Paineiras: ZUFRJ-20140810-0.