Advertisement calls of Bolivian species of *Scinax* (Amphibia, Anura, Hylidae)

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Abstract

The advertisement calls of eight Bolivian species of *Scinax* are described including information on the calling behaviour of each species. A characteristic audiospectrogram and oscillogram are presented for each species, as well as numerical information about the spectral and temporal features of the calls. Two phenograms based on the characteristics of the mating calls are constructed, the first one using a traditional multivariate technique (UPGMA) and the second one using audiospectrogram correlation, a new technique that allows holistic comparisons of single vocalizations.

Resumen

Se describen las llamadas de apareamiento de ocho especies de *Scinax* de Bolivia, aportando información sobre su comportamiento fonador. Un audiospectrograma y un oscilograma son presentados para cada especie junto con información numérica sobre las características temporales y espectrales de las vocalizaciones. Se presentan dos fenogramas basados en las características de las llamadas, uno de ellos usando metodología multivariante tradicional (UPGMA), y el segundo usando una novedosa metodología basada en la correlación de los archivos de imagen de los audioespectrogramas.

Introduction

The Neotropics contain by far the most diverse anuran fauna in the world, and a great number of species is being described each year. Central and South America are the subject of a number of exploratory studies that provide an ever more complex view of the richness in anuran diversity (see Donnelly &

Myers, 1991; Duellman & Salas, 1991). Among the South American countries, Bolivia contains some of the least known areas, and its anuran fauna has been the subject of several recent discoveries (De la Riva, 1990a, 1990b, 1992a, 1992b, 1993; Reynolds & Foster, 1992).

In this study we contribute to the knowledge of Bolivian herpetofauna by presenting the characteristics of the advertisement calls of eight species in the hylid genus *Scinax*, previously known as *Ololygon* (see Duellman & Wiens, 1992). The advertisement calls of two of these species are described for the first time.

The genus *Scinax* was known for many years as *Ololygon* Fitzinger, 1843. *Ololygon* was resurrected from the synonymy of *Hyla* by Fouquette & Delahoussage (1977), based on sperm characters. Although the validity of this feature was questioned by some authors, some characteristic morphological features are shared by all the species in this genus. Recently the correct nomenclature for the genus was considered to be *Scinax* (see Duellman & Wiens, 1992). Among other morphological features, this genus differs from *Hyla* mainly by lacking a membrane between toes I and II or having only a vestigial fringe along the inner margin of the second toe. Additionally, they have truncate disks, which are wider than long, on the hands (Duellman & Wiens, 1992).

The genus *Scinax* is one of the most abundant and conspicuous groups of frogs in the Neotropics. Frost (1985) reports 54 species in the genus (as *Ololygon*) and several more have been described

since then. De la Riva (1990) lists eight species present in Bolivia, although two additional species have been described since then (De la Riva, 1990b, 1993). The genus has been divided into several phenetic groups. The eight species considered in the present study belong to at least three (possibly four) different species groups. The first group is the *S. rubra* group that includes *S. rubra*, as well as probably *S. chiquitana*, *S. fuscovaria*, and *S. nasica*. The second group is the *S. rostrata* group, that would include *S. garbei* and *S. nebulosa*. The third group is the *S. staufferi* group which includes *S. parkeri* and possibly *S. nasica*. The fourth potential group is the *S. x-signata* group to which *S. nasica* has been assigned according to some authors. Of these four groups only the *S. rostrata* group appears to have solid phylogenetic consistency (see Duellman & Wiens, 1992, for further details on the taxonomy of the group). These four groups include all eight species considered in the present study except for *S. castroviejoi*, which has not been assigned to any group (De la Riva, 1993).

Since the inception of sound analysis techniques, anuran mating calls have been considered to be important taxonomic determinants due to their role as pre-zygotic species isolating mechanisms (Blair, 1955, 1958, 1959; Jameson, 1955; Johnson, 1959). The richness of the anuran tropical fauna allows for comparative studies of the vocalisations, either from ecological (Hödl, 1977; Drewry & Rand, 1983; Zimmerman, 1983) or from taxonomic standpoints (Barrio, 1965, 1966).

In general terms, it is accepted that the mating calls of anurans do not show homologies above the genus level, but some similarities among calls that may have phylogenetic significance at generic and infrageneric level may be expected. The validity of vocalisations in phylogenetic studies is, however, limited and depends on the group of anurans considered. According to Schiøtz (1973:313) "the voice follows the taxonomy to a certain extent, which is quite natural as the voice is a product of the morphology of the species." However, convergences are often found between species of different families and acoustic partitioning in allopatric anuran communities seems to have similar characteristics (Duellman & Pyles, 1983).

In the present paper, the calls of eight species of *Scinax* from Bolivia are compared with previously published descriptions from other areas of South America, to point to possible inconsistencies in taxonomy, or future areas of taxonomic research. Finally, two different methodologies are used to generate phenetic trees of affinities among vocalisations which allow to discuss some relationships of the species within *Scinax*. The first method is a multivariate technique, and the second method is an innovative technique based on the correlation of audiospectrograms. The relationships resulting from the study of the advertisement calls are compared with the currently accepted species groups.

Material and methods

Recordings were obtained in Bolivia by the first author from 1987 to 1990. Unless otherwise specified, calls were recorded in Puerto Almacén, northwestern part of Santa Cruz Department (15°46′S 62°15′W), an Amazonian locality in wet subtropical forest (Tosi et al., 1975). Recording equipment included either a Sony WM D6C or a Sanyo M1120 tape recorder and a Sennheiser Me 80 directional microphone. A representative audiospectrogram and oscillogram were presented for a 2.5 seconds recording segment for each species. A longer recording (20–60 seconds) was analysed to generate numerical information on the spectral and temporal characteristics of the sounds. For each species, we selected for analysis the calls of a single representative individual which emitted vocalisations which appeared to be "normal" to the human ear. The criteria for the choices were also based on the certainty of the identification of the recorded individual and in the quality of the recording.

Recordings were processed with a Macintosh-based digital signal analysis system. Digitalisation and editing were completed at a sampling frequency of 44.1 kHz and 16 bit resolution with Sound Tools hardware and software. Signalyze software was used to obtain numerical information and to generate audiospectrograms and oscillograms. Frequency information was obtained through fast Fourier transform (FFT, width 1024 points). The terminology used for the description of the advertisement calls follows Heyer et al. (1990).

A total of 12 different call characteristics were compared in a phenetic analysis. The variables considered were: note duration, pulse rate (pulses per second), dominant frequency, fundamental frequency, other frequency with substantial energy, minimum number of notes per call, maximum number of notes per call, number of pulses per note, call repetition rate (calls per minute), note repetition rate (notes per minute within the call), number of different types of notes, and ratio pulse duration/interpulse interval. Variables were linearly transformed in the original matrix in order to standardise the scales of the different variables. The standardised matrix was used to calcu-

late the "average taxonomic distance" between each species pair (after Sneath & Sokal, 1973). The resulting unrooted phenetic tree was generated through the application of an unweighted pair-group-method arithmetic average (UPGMA) on the previously calculated matrix (NTSYS statistical package, Rohlf, 1992). The methodology and the parameters used were similar to those used for the comparison of advertisement calls of 18 species of *Hyla* from Bolivia by Márquez et al. (1993).

In addition to the UPGMA analysis, a second method for quantitatively comparing animal vocalisations was used, based on the comparison of the audiospectrograms of single notes of the advertisement call. This method, described in Clark et al. (1987) allows for a comparison of a full representation of a sound's structure in time and frequency rather than of individual acoustical features. The software used for the correlation process was available in "Canary" (Cornell Lab. of Ornithology, Ithaca, New York). To the best of our knowledge, it is the first time that this method is applied to the quantitative comparison of the vocalisations of different taxa. When the advertisement call was composed of more than one note, the primary note was used for comparisons (we defined the primary note as the note which was never omitted from the call or the loudest note).

Unless otherwise specified, collected individuals were deposited in the Centro de Estudios Tropicales, Sevilla, Spain, and/or in the Museo de Historia Natural "Noel Kempff Mercado", Santa Cruz de la Sierra, Bolivia.

Results and discussion

Description of the advertisement calls

The audiospectrograms and oscillograms of a 2.5 second section of the calls of the different species are shown in Figs. 1 and 2. A summary of the numerical information from the sound analyses is shown in Table I. The phenetic trees produced by the UPGMA analyses and by audiospectrogram correlation are shown in Figs. 3 and 4.

Scinax castroviejoi (De la Riva, 1993)
This recently described large species of *Scinax* (maximum snout-vent length (SVL): males 41.9 mm, single female known 48.7 mm) occurs in temperate valleys of the eastern slopes of the Andes from Bolivia to northern Argentina. Calls were recorded in a small lagoon near Bermejo (Dept. of Santa Cruz, Bolivia, 18°97′S 63°38′W). Males migrated to the shore at dusk, and called perched on small bushes or rushes. *Scinax castroviejoi* is probably a prolonged breeder because it did not rain during the two days when the pond was visited and males were active and calling.

The mating call always consisted of two similar notes emitted together in rapid succession (Fig. 1a). Both were short (26 and 28 milliseconds), with a high number of pulses, low fundamental frequency (891 Hz), and a relatively high dominant frequency (2400 and 2850 Hz). For the quantitative comparisons with other calls the second note in the sequence was considered as the primary note because of its greater intensity. De la Riva (1993) described the calls of this species from the same locality and from the same recordings.

Scinax chiquitana (De la Riva, 1990a)
This medium-sized species (maximum SVL: males 32.0 mm, females 35.3 mm) probably belongs to the *S. rubra* group (De la Riva, 1990b) and occurs in the rain forests of northern Bolivia and southern Peru (Duellman & Salas, 1991). At Puerto Almacén it was an explosive breeder, forming large aggregations of males during the rainy season. However, mating calls were only heard sporadically.

Males usually called while perched on aquatic plants or bushes emerging from temporal ponds or in their near vicinity. The advertisement call was composed of a single type of note of intermediate duration (243 ms), pulsed, and repeated at regular intervals (Fig. 1b). The mean dominant frequency was of 2172 Hz. No previous records of the vocalisations of this species were available.

Scinax fuscovaria (Lutz, 1925)
This large species (maximum SVL: males 50.2 mm, females 53.2 mm) probably belongs in the *S. rubra* group (Fouquette & Delahoussaye, 1977; Frost, 1985). It occurs in open and forest habitats throughout the Chaco, Cerrado, and the subtropical forests of Brazil, Argentina, Paraguay, and Bolivia. At Puerto Almacén *S. fuscovaria* was an explosive breeder forming large choruses in temporal ponds following heavy rains.

Males called from bushes or small trees, usually perching directly on trunks or thick branches. The call was short and consisted of one note with low frequency (860 Hz) and a low pulse rate (50 pulses per second) (Fig. 1c). The call was emitted in fast succession at regular intervals. De la Riva (1993) provided basic parameters of the calls of *S. fus-*
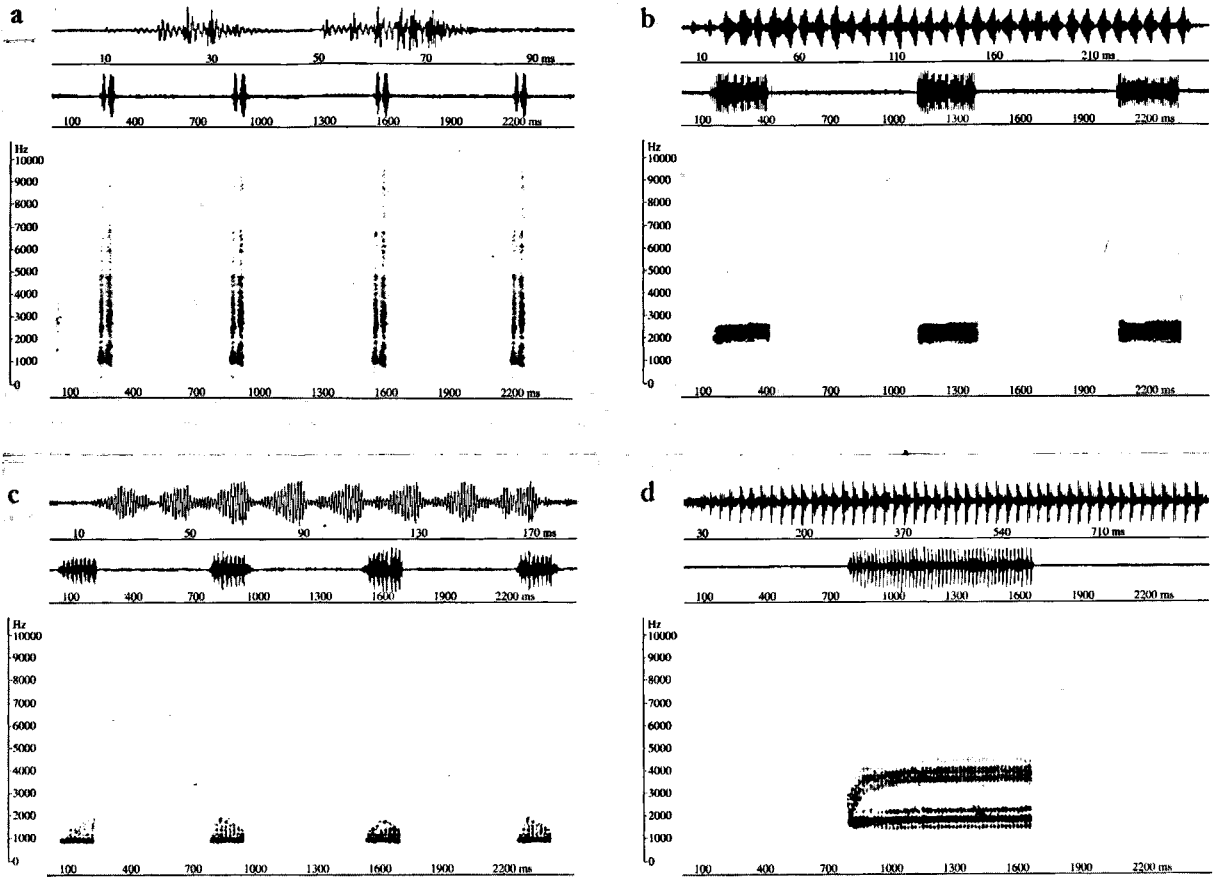
Fig. 1. From bottom to top: audiospectrogram and oscillogram of a 2.5 second recording of a characteristic mating call. Top: expanded oscillogram showing the temporal details of the notes; a, *Scinax castroviejoi*; b, *Scinax chiquitana*, c, *Scinax fuscovaria*; d, *Scinax garbei*.

covaria from Puerto Almacén which are coincident with our description.

Scinax garbei (Miranda-Ribeiro, 1926)
This is a medium-sized species (maximum SVL: males 39.8 mm, females 42.1 mm) of the *S. rostrata* group (Duellman, 1972). It is widespread in the upper Amazon Basin from Colombia to Bolivia. Apparently, there are marked differences in size between populations (Heyer, 1977). At Puerto Almacén *S. garbei* was a prolonged breeder during the rainy season.

Males called perched head-down on trunks or leaves near the shore of temporal or semi-permanent ponds. The call consisted of one long note (950 ms), highly pulsed, with a dominant frequency of

3715 Hz and a fundamental frequency of 1695 Hz (Fig. 1d). The calls were separated by long intervals of variable duration, averaging 1300 ms.

Duellman (1970a, 1972, 1978) described the mating call of *Scinax garbei* from Santa Cecilia, Ecuador (in 1970a and 1972, Duellman considered the species to be in the genus *Garbeana*; in 1978, Duellman referred to it as *Hyla*). He described the call as being a single, moderately long pulsed note, repeated at a rate of 14 notes per minute. The note repetition rate of our recordings is nearly twice that figure, whereas the duration of the note reported for the Ecuadorian frogs (range 160–260 ms) is markedly shorter than the duration found by us (range 295–1469 ms). The pulse rates do not show much agreement either; calls from Ecuador had
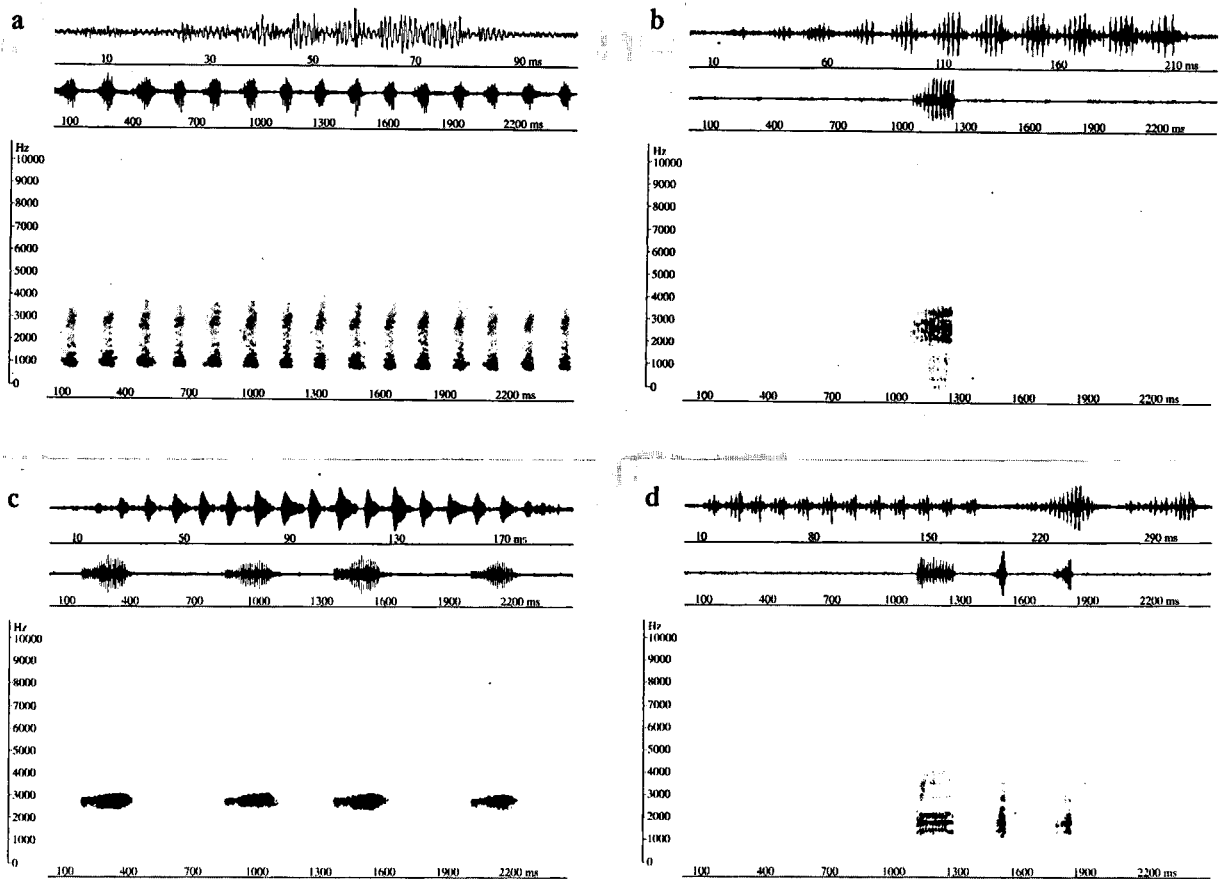
Fig. 2. From bottom to top: audiospectrogram and oscillogram of a 2.5 second recording of a characteristic mating call. Top: expanded oscillogram showing the temporal details of the notes; a, *Scinax nasica*; b, *Scinax nebulosa*, c, *Scinax parkeri*; d, *Scinax rubra*.

pulse rates ranging from 195 to 240 pulses/second, but Bolivian recordings showed pulse rates ranging from 53 to 57 pulses/second. The only parameter that shows slightly less dramatic differences between the calls described, is the dominant frequency: 3250 Hz according to Duellman (1978) and ranging from 3453 Hz to 3958 Hz in the present study. In spite of the differences in pulse rate and duration, the audiospectrograms provided (Fig. 1 in Duellman, 1970 and Fig. 3 in Duellman, 1972) show some structural similarities with our Fig. 1d, emphasising two wide, flat, frequency bands, the upper one raising in frequency at the beginning of the call.

Duellman & Pyles (1983) provided numerical data on the calls of *S. garbei* (then *Ololygon*) from Santa Cecilia (Ecuador). Curiously enough, several of the variables are not even within the ranges of the previously published data for recordings obtained in the same site (Duellman, 1978). The discrepancies include the following parameters: note repetition rate ranging from 54.5 to 72.3 notes/minute in 1983 and reported to be 14 notes/minute in 1978; call duration, ranging from 370 to 650 ms in 1983 and from 160–260 ms in 1978; pulse rate, ranging from 80 to 100 pulses/second in 1983 and from 195 to 240 pulses/second in 1978; dominant frequency, ranging from 1564 to 1926 Hz in 1983 and estimated to be 3250 Hz in 1978. In any event, our data on the mating calls from Bolivian *S. garbei* do not coincide with most of the numerical parameters reported for the mating calls of Ecuadorian frogs of this species, either as reported by Duellman (1970a, 1972, 1978) or as described later by Duellman & Pyles (1983).

Further research on this widespread and highly variable species could provide information about the actual taxonomic status of different populations.

Scinax nasica (Cope, 1862)

This is a medium-sized species (maximum SVL: 37.0 mm) of uncertain phylogenetic relationships which has been considered a member of the *S. rubra*, *x-signata*, and *staufferi* groups (Duellman & Wiens, 1992; De la Riva, 1993). It occurs throughout the same range as *S. fuscovaria*. Its mating system is explosive and breeding occurs in temporary ponds.

Recordings were obtained at Santa Cruz de la Sierra (14°48′S 63°10′W) where males called after heavy rains from short grasses, in the middle of a pond, or on the ground near the shore. The mating call consisted of one pulsed note, of short duration, with low dominant and fundamental frequencies (970 Hz) and it was emitted in long call groups in rapid succession (337 calls per minute) at regular intervals (Fig. 2a). De la Riva (1993) described the vocalisations of this species recorded at the same time and locality. His description is based on the same recordings as ours.

Scinax nebulosa (Spix, 1824)

This is a relatively small species (maximum SVL: males 29.5 mm, females 36.0 mm) of the *S. rostrata* group (Duellman, 1972). It inhabits open areas in the lower Amazon Basin from the Guiana region to Mato Grosso (Brazil) and Bolivia.

Recordings were obtained at Puerto Almacén where the species had a prolonged breeding system, lasting during the whole rainy season and probably beyond it. Males called perched on riverine plants on river banks or near semi-permanent ponds. Calls were emitted by males spaced at long distance from each other. The advertisement call consisted of one note (240 ms) emitted sporadically, with a low number of pulses and high dominant frequency (2870 Hz) (Fig. 2b).

Duellman (1972) described the calls of *Hyla egleri* (a junior synonym according to Hoogmoed & Gruber, 1983). He described a call composed of 4–7 notes, repeated at a rate of 39.5 notes/minute.

The note had a mean duration of 160 ms, a pulse rate of 58 pulses/second and emphasised harmonics at 720 and 1050 Hz. Whereas the pulse rate reported is similar to the values found by us (mean 55.6), the durations (our mean 240 ms), and particularly the emphasised frequencies (2374–2867 Hz in the Bolivian recordings), are far from the values reported by Duellman (1972). However, the audiospectrogram provided (Duellman, 1972: 195, fig. 1) shows a call over 200 ms in duration and with emphasised frequencies from 2500 Hz to 5000 Hz, showing a general structure very similar to our Fig. 2b.

Hödl (1977) described the calls of *H. egleri* from the area of Manaus (central Amazon, Brazil). He described a call composed of two types of notes: a primary note and a much shorter secondary note. We did not detect the existence of secondary notes in our recordings from Bolivia. Furthermore, neither the temporal nor the spectral values reported by Hödl (1977) agree with our recordings of Bolivian frogs.

Duellman & Pyles (1983) provided numerical data on calls of *S. nebulosa* (then *Ololygon egleri*) from Belém de Pará (Brazil). The descriptive data for the call of *S. nebulosa* do not agree with the previously published description by the senior author (Duellman, 1972). According to that description *S. nebulosa* has only one note per call, with an average note repetition rate of 62.3 notes/minute, an average duration of 130 ms, an average pulse rate of 60 pulses/second, and dominant frequencies ranging from 3840 to 4147 Hz. While the values for pulse rate are close to those found by us, the other values do not show similarities with our results.

In summary, the descriptions of the calls of *S. nebulosa* appear to be rather conflictive. However, the uniformity of the morphological characteristics of this species throughout its range (De la Riva, unpublished data) leads us to believe that the differences in call descriptions reported may be the result of differences in methods of analysis rather than actual taxonomic differences between populations.

Scinax parkeri (Gaige, 1929)

This extremely small species (maximum SVL: 23.3

Table I. Summary of numerical parameters of the vocalisations. For each of the parameters, the mean values are followed by the standard deviations between parentheses. Ranges are shown next. When more than one type is considered, the note followed by an asterisk is used for the construction of the phenetic trees.

	Number of calls	Note duration (ms)	Fundamental frequency (Hz)	Dominant frequency (Hz)	Notes /call	Pulses /note	Pulses /second	Notes /minute	Calls /minute	Pulse duration /inter-pulse interval
Scinax castroviejoi 1st note	38	27.8 (1.6) (24.6–32.3)	905.6 (53.1) (868.3–1070.2)	2406 (43.1) (2301.9–2584.6)	1	6 (0) (6–6)	216.1 (11.8) (185.8–243.9)	1504.2 (79.6) (1348.3–1685.4)	80.6 (26.6) (6.9–115.6)	0.842 (0.047) (0.766–0.913)
Scinax castroviejoi 2nd note*	39	26.1 (2.6) (21.7–32.5)	891.1 (17.4) (848.1–928.8)	2848.7 (47.1) (2766.3–2988.5)	1	6.1 (0.4) (5–7)	234.3 (25.1) (157.7–276.5)	1504.2 (79.6) (1348.3–1685.4)	80.6 (26.6) (6.9–115.6)	
Scinax chiquitana	12	243 (48.6) (185.3–338.8)	2172.4 (59.9) (2100–2261.5)	2172.4 (59.9) (2100–2261.5)	1	30 (6) (23–42)	122.1 (3.7) (114.2–128.4)	64.4 (12.8) (48.2–84.2)	64.4 (12.8) (48.2–84.2)	0.596 (0.075) (0.524–0.805)
Scinax fuscovaria	25	162.2 (13) (137.7–187.3)	864.1 (24.5) (827.9–928.8)	864.1 (24.5) (827.9–928.8)	1	8.12 (0.6) (7–9)	50.12 (1.8) (46.6–56.5)	100.2 (15.7) (62.9–121.9)	100.2 (15.7) (62.9–121.9)	0.678 (0.074) (0.5–0.767)
Scinax garbei	19	947 (275) (295–1469)	1695.1 (93.9) (1514.4–1776.9)	3715.4 (136.9) (3452.9–3957.7)	1	53.1 (15.6) (16–83)	56 (1) (53.8–57.8)	29.3 (8.9) (11.2–49.4)	29.3 (8.9) (11.2–49.4)	0.663 (0.084) (0.543–0.848)
Scinax nasica	61	57.5 (10.3) (42.5–98.7)	972.9 (56.2) (848.1–1110.6)	972.9 (56.2) (848.1–1110.6)	1	5.1 (0.9) (4–6)	91.1 (15) (74.7–113.4)	337.1 (56.3) (223.8–457.8)	337.1 (56.3) (223.8–457.8)	0.828 (0.063) (0.724–0.912)
Scinax nebulosa	5	240.6 (43.6) (201.1–305)	2374.6 (124.9) (2221.2–2564.4)	2867.3 (167.7) (2685.6–3129.8)	1	13.4 (2.6) (11–17)	55.6 (1.3) (54.2–57.5)	22.5 (22.8) (2.4–47.5)	22.5 (22.8) (2.4–47.5)	0.641 (0.045) (0.567–0.707)
Scinax parkeri	7	185.7 (17.6) (167.1–218.4)	2307.7 (88.6) (2201–2402.9)	2777.9 (50.6) (2705.8–2826.9)	1	18.6 (1.4) (17–21)	100.2 (2.9) (96.2–104.9)	151.1 (54.6) (83–206.7)	151.1 (54.6) (83–206.7)	0.612 (0.137) (0.45–0.81)
Scinax rubra 1st note*	11	162.9 (16.2) (142.7–197.5)	2096 (34.1) (2019.2–2140.4)	2096 (34.1) (2019.2–2140.4)	0–2	11.4 (1.3) (10–14)	69.7 (1.983) (67.4–74.4)	136.7 (28.8) (103.6–156)	33.6 (15.5) (16.6–46.8)	0.708 (0.065) (0.644–0.843)
Scinax rubra 2nd note	5	29.5 (3.7) (24–34.3)	1865.76 (111.1) (1776.9–2059.6)	1865.76 (111.1) (1776.9–2059.6)	1	10 (0.7) (9–11)	342.1 (33.7) (291.5–375)	185.4 (29.2) (164.7–206)	33.6 (15.5) (16.6–46.8)	

mm) presumably is a member of the dubious *S. staufferi* group (Duellman & Wiens, 1992). It was formerly considered by Lutz (1973) a junior synonym of *S. fuscomarginata* (Lutz, 1925) a position followed by several authors (Frost, 1985; De la Riva, 1990a) although Duellman & Wiens (1992) considered *S. parkeri* as a valid species. It occurs at least in northern Bolivia and adjacent Brazil. It is characteristic of open habitats, and is probably a prolonged breeder during the whole rainy season.

Recordings were obtained at the type locality, Buenavista (17°27'S 63°40'W), where males called perched on low grasses in a large flooded area. The call consisted of one short pulsed note (186 ms) with high dominant and fundamental frequencies (approximately 2300 and 2800 Hz) (Fig. 2c). Calling activity was sporadic. To the best of our knowledge, no previous descriptions of the calls of *Scinax parkeri* have been published.

Scinax rubra (Laurenti, 1768)

This medium-sized species (maximum SVL: males 36.1 mm, females 43.6 mm) is widespread in the Neotropics from southern Panama throughout northern South America east of the Andes to central Bolivia, and southeastern Brazil. It is likely that a complex of species is currently being included under this name (Frost, 1985). The habitat of *S. rubra* includes both forests and open, disturbed areas.

Recordings were obtained at Puerto Almacén, where *S. rubra* is an explosive species breeding in temporal ponds. Males emitted their calls while perching on both leaves and branches of bushes and small trees. Males formed large choruses that often persisted until dawn. The call was emitted sporadically and consisted of two pulsed notes (Fig. 2d). The longer note (primary note) is often emitted in isolation and is longer in duration and higher in frequency than the second (163 ms and 2100 Hz, versus 29 ms and 1865 Hz in the second note). The second note can be repeated with a high number of pulses (342 pulses per second).

Rivero (1969) described the call of *S. rubra* (then *Hyla rubra*) from Estado Bolívar, Venezuela as a 200 ms long pulsed call with dominant frequency of about 1250 Hz. He compared this call with that of

Hyla x-signata (Spix, 1824) and found them to be different. Both the audiospectrogram and the numerical data reported for *S. rubra* in Venezuela differ markedly from our recordings of Bolivian *S. rubra*. However, the structure of the call of *H. x-signata* from Estado Miranda, Venezuela (fig. 1 in Rivero, 1969) resembles our Fig. 2d, but it shows a slightly lower fundamental frequency. It would not be unlikely that Rivero considered *S. x-signata* what actually was *S. rubra* (and vice versa) since the taxonomy of both species is very complex.

Duellman (1970b) described the mating call of *S. rubra* (then *Hyla rubra*) from Santa Cecilia (Ecuador) as being a single short note (mean duration 130 ms) with dominant frequency centered at 1581 Hz and an average pulse rate of 63 pulses/second. Campbell (1971) later described the mating call of *Scinax rubra* (then *Hyla*) from Panama as one pulsed note (pulse frequency 66–72 pulses/second) with a dominant frequency of 1600 Hz and a duration of 140–150 ms. Whereas the duration and pulse rate are somewhat comparable to the characteristics of the longer note described by us (duration range 142–197 ms, pulse rate range 67–74 pulses/second), his description does not agree with our recordings because it does not report the existence of a secondary note. However, the fact that the dominant frequency of the call was located at 1600 Hz is not reflected at all in the audiospectrogram of the call (fig. 2 of Campbell, 1971). At any rate, the spectral characteristics of the call of the Panamanian frogs as depicted in this figure do resemble those found in our analyses. Campbell (1971) indicated that the call characteristics of his recordings were similar to those reported for this species in Ecuador by Duellman (1970b).

Duellman (1978) provided a description of the mating call of *Scinax rubra* (then *Hyla*) from Santa Cecilia (Ecuador) which coincided with that of the Panamanian calls of this species described by Campbell (1971). On the other hand, Schlüter (1979) described the call of *Scinax rubra* (then *Hyla*) from Peru as being composed of two different types of calls, a long (200 ms) pulsed note and a shorter note (50 ms approximately). Similarly, our recordings from Bolivia show two note types as well, though with shorter durations (long 142–167
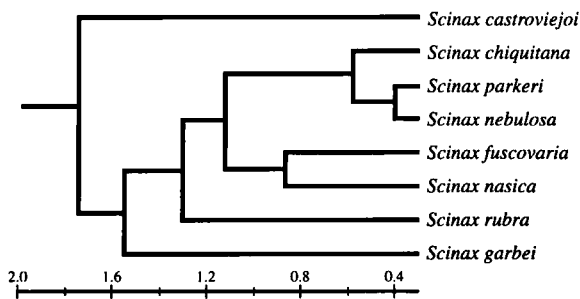
Scinax castroviejoi
Scinax chiquitana
Scinax parkeri
Scinax nebulosa
Scinax fuscovaria
Scinax nasica
Scinax rubra
Scinax garbei

2.0   1.6   1.2   0.8   0.4

Fig. 3. Phenetic tree resulting from the UPGMA analyses of 12 numerical parameters of the calls of eight species of *Scinax* from Bolivia. The scale represents standard distances.
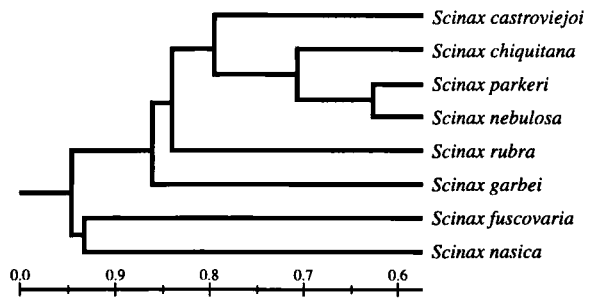

Scinax castroviejoi
Scinax chiquitana
Scinax parkeri
Scinax nebulosa
Scinax rubra
Scinax garbei
Scinax fuscovaria
Scinax nasica

0.0   0.9   0.8   0.7   0.6

Fig. 4. Phenetic tree resulting from the audiospectrographic correlations of the primary notes of the calls of eight species of *Scinax* from Bolivia. The scale represents correlations.

ms, short 24—34 ms). The dominant frequencies of our recordings appear to be slightly lower for both notes than those shown by Schlüter (1979), however, the pulse rate of the longer note shown for the Peruvian frogs (estimated to be 60 pulses/second) is similar to that found by us (range 67—74 pulses/second). The discrepancy in mating calls between the descriptions of the calls from Panama and Ecuador on the one hand, and from Peru and Bolivia on the other hand, suggests that the individuals recorded in these locations may belong to two different types or may have developed distinctly different dialects. A careful re-evaluation of the taxonomic status of *S. rubra* in these locations may be fruitful.

Quantitative comparisons of the advertisement calls

The UPGMA phenetic tree (Fig. 3) has a co-phenetic correlation coefficient of 0.897, which indicates a solid level of consistency. On the other hand, the consistency between the tree and the currently accepted phylogenetic relationships within the genus *Scinax* (see Duellman & Wiens, 1992) is not high, although the relationships among the species are not clear to taxonomists. The few established affinities are not well reflected by the phenogram. *S. nebulosa* and *S. garbei* are closely related (both belong to the *rostrata* group) but their calls are not grouped in the tree. On the other hand, *S. parkeri* is clearly different from the rest of the species, because of its small size, although it currently is included with *S. nasica* in the *S. staufferi* group,

whose monophyly is not demonstrated (Duellman & Wiens, 1992). The advertisement call of *S. parkeri* is similar to that of *S. nebulosa*, according to both Figs. 3 and 4.

The audiospectrographic correlation phenogram (Fig. 4) is rather consistent with the UPGMA phenetic tree, but does not show concordance with the tentative phylogeny of the genus. Again, *S. castroviejoi* is markedly separated, but not to the same degree as in Fig. 3. This species is grouped with *S. chiquitana*, and *S. nebulosa* and *S. parkeri* (the pair most closely clustered). These four species probably belong to four different species groups. Although in both Fig. 3 and Fig. 4, *S. rubra* and *S. garbei*, and *S. fuscovaria* and *S. nasica*, are clustered together, the relative positions of the pairs are not the same.

The two phenograms cluster the species in a similar way. The affinity between the trees resulting from the two methodologies is even more striking if we consider that the audiospectrographic correlation method does neither include any variables related to the rate of emission of the utterances nor to the number of different notes in a call (five out of twelve parameters included in the UPGMA). However, as we can see, there is no correlation between phylogeny and characteristics of the calls. The phenograms do not clearly reflect ecological relationships either. Most of the species considered are mainly open habitat dwellers. *Scinax chiquitana* lives in the forest, and *S. garbei* and *S. rubra* are euryoecious species found both in the open and in forest formations. These last two species are distantly associated in the phenograms, and the difference in habitat of *S. chiquitana* is not reflected in either of the phenograms.

In summary, although according to some authors closely related species may show similarities in their calls (Schiøtz, 1973), the study of the genus *Scinax* does not conform to this trend and supports the results of Duellman (1970b) who did not find great coherence between the classification of the species of *Hyla* and the similarities among mating calls (but see Márquez et al., 1993). This lack of consistency may be a result of the fact that the intrageneric relationships of this group are far from being clearly established. On the other hand, the agreement between the two methods of analysis suggests that the holistic approach provided by the audiospectrographic correlation is a powerful technique for comparison of sounds. This new technique may eventually become a more objective and agile alternative to the labor-intensive technique of extraction of numerical variables for multivariate analysis.

Acknowledgments

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