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Description of the advertisement calls of some South American Hylidae (Amphibia, Anura): taxonomic and methodological consequences

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Abstract. Calling behavior and advertisement call structure of five hylid species from South America are described. Characteristic audiospectrograms and oscillograms are presented, as well as numerical information on spectral and temporal features of the calls of each species. Variation in different call parameters is compared with previously published descriptions of the advertisement calls of these species. Taxonomic and methodological issues of the use of bioacoustical data are discussed. The recognition of *Hyla walfordi* and *Scinax parkeri* as valid taxa is recommended.

Key words. Anura, Hylidae, *Hyla albopunctata, H. carnifex, H. granosa, H. walfordi, Scinax quinquefasciata, S. parkeri*, Bolivia, Ecuador, advertisement calls.

Introduction

Anuran vocalizations play a crucial role as mechanisms for species recognition and are essential components of the characterisation of species accounts. In tropical anurans relationships among taxa are particularly complex, and comparisons of advertisement calls represent an alternative way of determining differences and affinities based on a quantifiable parameter (e. g. Hödl 1977; Schlüter 1979, 1980, 1981; Duellman & Pyles 1983; Zimmerman 1983; Zimmerman & Hödl 1983; Zimmerman & Bogart 1984).

In this paper we contribute to the knowledge of some South American species of hylid frogs by studying the acoustic characteristics of their advertisement calls. This report is a complement to previously published reports of other species of hylids from the Amazonian region (Márquez et al. 1993, De la Riva et al. 1994; 1995) from recordings obtained in Bolivia and Ecuador. The objectives of this paper are to (1) describe the advertisement calls of five species, (2) compare our findings to previous descriptions, (3) discuss taxonomic issues for some of the species studied, and (4) comment about the methodological problems associated with the study of bioacoustics in anurans.

Materials and methods

Recordings were obtained in Ecuador and Bolivia. Recording equipment included either a Sony WM D6C or a Sanyo M1120 tape recorder and a Sennheiser Me 80 directional microphone. An audiospectrogram and oscillogram were obtained for a 2.5 s recording segment of each species. A longer recording (20—60 s) of a single male was analyzed to obtain numerical information on the spectral and temporal characteristics of the calls. The characteristic call was selected based on quality of the recording and on the subjective criteria of a learned human listener who perceived the call as a "normal" advertisement call of the species (i. e., the call was not emitted in specific situations which could indicate that they would be reciprocation, release, or distress calls and so on).

Digitalization and editing were completed with a Macintosh-based digital signal analysis system 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. Information on frequency domain was obtained through fast Fourier transform (FFT) (width 1024 points). Advertisement call terminology follows Heyer et al. (1990).

A total of 10 different call characteristics were considered. The variables considered were: number of notes per call, note duration, fundamental frequency, dominant frequency, other frequency with substantial energy, number of pulses per note, pulse rate (pulses/s), pulse ratio (pulse duration/pulse period), note repetition rate (notes per min within the call), and call repetition rate (calls per min). Unless otherwise specified, individual sizes (snout-vent length, SVL) were measured from collected individuals which were deposited in the Museo de Historia Natural "Noel Kempff Mercado", Santa Cruz de la Sierra, Bolivia. No specimens were collected in Ecuador.

Results

An audiospectrogram and an oscillogram is presented for a 2.5 sec. section of the call of each species (Figs. 1 to 5). A summary of the numerical information from the sound analyses is shown in Table 1.

Hyla albopunctata Spix, 1824 is a medium-sized species [SVL males = 60 mm (Cei 1980] of the *H. albopunctata* group. It occurs in the cerrado domain of Central Brazil, northeastern Argentina, and eastern Paraguay. Our recordings were obtained from a single male calling from a marshy area at camp Huanchaca I, Noel Kempff Mercado National Park, Santa Cruz Department, Bolivia (13° 54' S / 60° 47' W). This is the first record of the species for Bolivia. The only calls recorded were composed of a sequence of three loud, single pulsed notes repeated at regular short inter-

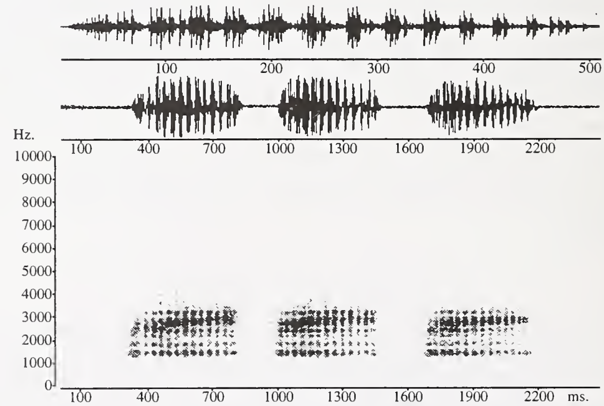

FIG. 1

Figs: 1—5: Audiospectrograms and oscillograms of a characteristic advertisement call. Fig. 1 *Hyla albopunctata*, Fig. 2 *Hyla carnifex*, Fig. 3 *Hyla granosa*, Fig. 4 *Hyla walfordi*, Fig. 5 *Scinax quinquefasciata*.

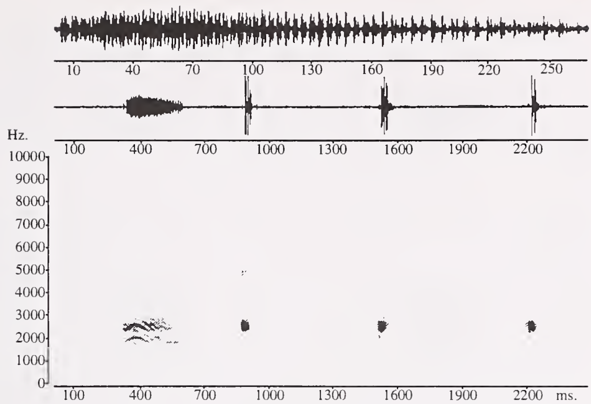

FIG. 2

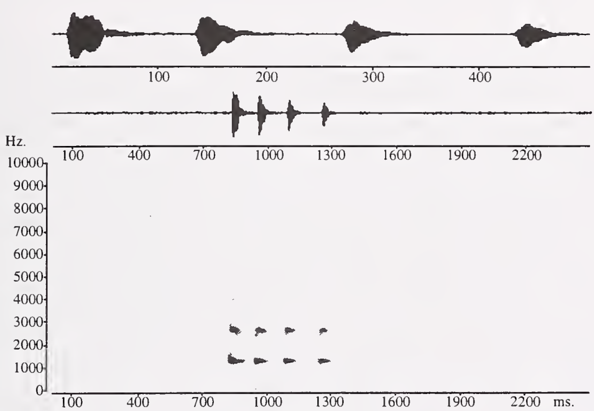

FIG. 3

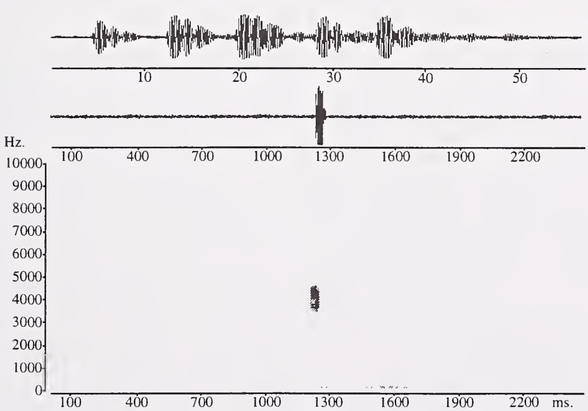

FIG. 4

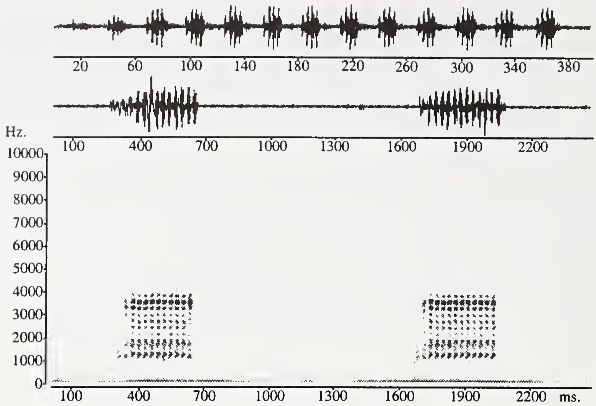

FIG. 5

vals (Fig. 1). The structure of the individual pulses was strongly amplitude-modulated, showing sub-pulses. The calls showed substantial energy in the 1300—3300 Hz range, with an average dominant frequency of 2692.3 Hz. The dominant frequency increased gradually towards the end of the call (average increase, 289.4 Hz, range 201.9—424.0 Hz).

Hyla carnifex Duellman, 1969 is a relatively small species [mean SVL males = 26.1, Duellman (1969)] in the *H. columbiana* group that occurs in the Pacific Andean slopes of Colombia and Ecuador. Our recordings were obtained in Las Palmeras, Pichincha Province, Ecuador (00°17' S / 78° 45' W) where males called at night on the vegetation near a river bank, concurrently with males of *Centrolene ballux*. The advertisement call consisted of two note types: a long note (265 ms duration) followed by a sequence of three short notes (34 ms duration). The long note is frequency-modulated and tonal in its first half, becoming more pulsed towards the end. The short notes are more pulsed (3 pulses per note), showing some power in the second harmonic (Fig. 2). The dominant frequency of both note types is concentrated around 2400 Hz.

Hyla granosa Boulenger, 1882, is a medium-sized species (males, 54 mm SVL) of widespread occurrence in the Upper Amazon Basin and Guianas and belongs to the *Hyla punctata* group. It has been observed (in Ecuador, Peru and Bolivia), calling from large leaves (as those of the "elephant ear" plants, *Heliconia*, etc) near or above ponds. In two of the three localities where the species was observed, it was calling in association with *Hyla lanciformis*. The recording shown in Fig. 3 was obtained near the River Napo, Ecuador (00° 25' S / 77° 47' W). The call consisted of a series of two to seven short notes of decreasing intensity. The notes were tonal and well-tuned, with a mean dominant frequency of 1327 Hz and substantial power in the second harmonic (2650 Hz). The mean duration of the notes was 46 ms.

Hyla walfordi Bokermann, 1962 is a small species (SVL males = 23 mm) of the *H. microcephala* group. Recordings were obtained in a flooded, open area at Flor de Oro, on the Bolivian bank of the Guaporé river (13° 33' S / 6° 00' W). This is the first record of the species for the country, although its occurrence in Bolivia was already suspected (Langone & Basso 1987; De la Riva 1990). The only other species heard calling concomitantly was *Scinax parkeri*. The call is an extremely brief note (average duration, 38 ms) with most of its energy in the 3400—4400 Hz range. An average of five pulses (range 4—7) were discernible in the structure of the note (Fig. 4).

Scinax quinquefasciata (Fowler, 1913) is a relatively small species [35 mm SVL in both sexes (Duellman 1971)] of the *S. rubra* group. It occurs in the Pacific lowlands of Colombia and Ecuador. Recordings were obtained in Same, Esmeraldas Province, Ecuador (00° 50' N / 79° 55' W) where males called from a grassy area near a small stream in the mangrove. *Trachycephalus jordani* and *Bufo marinus* were the only other anuran species that were found there. The call is composed of a single note, 472.5 ms average duration, with a variable number of pulses (average 16 pulses/note) and a complex spectral structure (range 1400—4000 Hz) with a dominant frequency of 3446.2 Hz (Fig. 5). The call was repeated at a relatively fast rate (average 29.2 calls/minute).

Discussion

Cardoso (1981) analyzed calls of *H. albopunctata* from Campinas, Brazil. He distinguished a nuptial call and a territorial call (both considered, in a broad sense, as "advertisement calls"). He found that the nuptial call has a higher number of pulses and is slightly higher pitched than the territorial call, and that both calls consist of two notes, sometimes followed by a third, different note. Aside from a high number of pulses (118) in the first note of the nuptial call (that we considered equivalent to our subpulses) and a longer note duration (600 ms) in the specimens from Campinas, our results are in general agreement with Cardoso (1981). Haddad et al. (1988) described the calls of *H. albopunctata* from Serra da Canastra, Minas Gerais, Brazil. They described a call typically consisting of a series of two pulsed notes separated by an interval of 200 ms, the first one having a duration of 500 ms and the second one being longer (900 ms). Occasionally they perceived a third note which was shorter but louder. They determined through playback tests that the third note found to be particularly effective in eliciting calling by other males. Our recordings do not coincide with their description since only one type of note was heard in Bolivia. Heyer et al. (1990) described the call of *H. albopunctata* from Boracéia (Brazil). Their description does not coincide with ours to the extent that they described two different note types. Their type I note was not heard in the Bolivian specimens. However, our description vaguely resembles their type II note in duration, frequency range, and structure (strong side bands) but differs in that they do not find frequency modulation and we find that the upper emphasized harmonic shows an upwards frequency sweep (2800—3100 Hz). Differences in all these results appear to be due to the different social context in which frogs were at the time of recording.

Duellman & Trueb (1983) provided an accurate description of the call of *H. carnifex* from a locality close to ours. Although they found a larger number of calls per minute than us, the rest of the data are coincident.

Table 1: Summary of numerical parameters of the vocalizations.

	Individuals analyzed	Notes analyzed	Notes per call	Note duration (msec)	Fundamental frequency (Hz)	Dominant frequency (Hz)	Other frequency (Hz)	Pulses/ note	Pulses/ second	Pulse duration/ pulse period	Notes/ minute	Calls/ minute
H. albopunctata	1	3	–	461.4 (29.3) 428.3–484.1	1332.7 (20.2) 1312.5–1352.9	2692.3 (11.7) 2685.6–2705.8	–	12.3 (0.6) 12–13	26.8 (1.7) 24.8–28	0.6 (0.1) 0.4–0.9	94.3 (9.7) 87.4–101.3	–
H. carnifex Long	1	2	1	263.5 (11.8) 255.2–271.9	2433.2 (14.3) 2423.1–2443.3	2433.2 (14.3) 2423.1–2443.3	1918.3 (28.6) 1898.1–1938.5	56.5 (0.7) 56–57	214.5 (6.9) 209.6–219.4	–	–	4.2
Short	1	6	3	34.3 (6.3) 29–44.1	2490.4 (39.7) 2423.1–2544.2	2490.4 (39.7) 2423.1–2544.2	4876.4 (83.5) 4765.4–4987.5	3 (0) 3–3	89.7 (14.8) 68–103.4	0.7 (0.1) 0.6–0.9	91.1 (4.9) 85.8–95.7	–
H. granosa	6	23	2.9 (1) 2–5	40 (10.7) 21.2–72.1	1426.9 (26.4) 1352.9–1453.8	1426.9 (26.4) 1352.9–1453.8	2861.2 (57.1) (2705.8–2927.9)	–	–	1	415.9 (67.5) (281.6–679.5)	21.8 (10.7) 8.7–47.8
H. walfordi	5	15	1	38.8 (6.6) 25.4–46.6	4282.2 (184.3) 4038.5–4583.7	4282.2 (184.3) 4038.5–4583.7	3811.3 (257.6) 3574–4401.9	5 (0.7) 4–6	130.5 (13) 107.3–157.5	0.7 (0.1) 0.3–0.9	8.4 (3.2) 4.3–12.1	8.4 (3.2) 4.3–12.1
S. quinquefasciata	1	12	1	335.5 (112.4) 168.3–577.5	1156.1 (12.6) 1130.8–1171.2	3446.2 (24.9) 3392.3–3473.1	6108.2 (14.3) 6098.1–6118.3	11.8 (3.9) 6–20	35.2 (0.5) 34.4–35.9	0.6 (0.1) 0.5–0.7	29.2 (9.8) 17.4–46.3	29.2 (9.8) 17.4–46.3

Duellman (1978) and Duellman & Pyles (1983) described the call of *H. granosa* from Santa Cecilia, Ecuador, a locality close to ours. The three sets of data are consistent. Our audiospectrogram of the characteristic advertisement call of *H. granosa* (Fig. 3) also closely resembles the description from Surinam published by Hoogmoed (1979). The audiospectrogram in Schlüter (1979) shows great similarity to ours as well, although we do not find the upwards frequency modulation shown in the second harmonic found in Peruvian frogs. Both our audiospectrogram and the numerical data obtained for the sound samples are comparable to the calls described by Zimmerman & Bogart (1984) for frogs recorded in Tapajós (Brazil). Cardoso & Vielliard (1990) also described the call of Brazilian specimens of *H. granosa*. Their data coincide with ours except for the characteristic three or four notes per call that we found. Their specimens emitted one or two notes per call.

The comparison of the calls of *H. walfordi* and *H. nana* Boulenger, 1889 can provide some insight in the taxonomic validity of the former species. The taxonomic status of *H. walfordi* has been controversial. This species was placed in the synonymy of *H. nana* by Lutz (1973), which was followed by Duellman (1977) and Frost (1985), but not by Heyer (1976; 1977). Langone & Basso (1987) resurrected *H. walfordi* based on comparisons of preserved specimens and supposed differences in the mating call [Cardoso, in Langone & Basso 1987)]. However, Duellman (1993) did not include the species in his additions and corrections to Frost's (1985) list. Living specimens of this species can be differenciated from those of *H. nana* by the shape of the snout and some features of the color pattern (Langone & Basso 1987; De la Riva pers. obs.). Furthermore, if we compare the calls of *H. walfordi* with those of *H. nana* obtained with similar analysis and recording equipment (Márquez et al. 1993: 437, 438), substantial differences can be found in call structure, since *H. walfordi* has a markedly pulsed call structure which is much less evident in *H. nana*. The call of this species is much more tuned and therefore sounds much more tonal than the calls of *H. walfordi*. Based on these observations, we support the recognition of *H. walfordi* as a valid species. Langone & Basso (1987) suggested that the taxonomic status of the small yellow frogs commonly ascribed to *H. nana* in the central and northern Amazon basin should be reconsidered. Hödl (1977) provided analyses of the call of a so-called *Hyla* cf. *nana* frog from Manaus, which supposedly could be actually *H. walfordi*. Comparisons of his data with ours do not support this hypothesis. The number of calls/minute (159) in *H.* cf. *nana* is by far higher than in *H. walfordi* ($\bar{x}$ = 8.4). The mean dominant frequency is also a little higher (4835 Hz vs. 4282) and the note duration is much shorter (12 ms vs. 38.3). In fact, the call of *H.* cf. *nana* seems to be more similar to that of *H. nana*, although *H. nana* shows a lower dominant frequency (4526 Hz), a longer note duration (38.3 ms) and a lower number of calls/minute (103) (Márquez et al. 1993). Thus, from these data, no definite conclusion seems evident regarding the taxonomic status of *H.* cf. *nana*. It seems plausible that *H.* cf. *nana* is really *H. minima* Ahl, 1933, or an undescribed species in the *H. microcephala* group (see Zimmermann & Rodrigues 1990). Finally, Langone & Basso (1987) stated that the characteristics of the calls of *H. minuscula* Rivero, 1971 from Venezuela provided by Rivero (1971) are not consistent with those of the same species from Belém, Brasil, recorded by Duellman & Pyles (1983), and Langone & Basso (1987) recommended a reassessment of the taxonomic status of the Brazilian population. Langone (pers. comm.) suggested that it could be *H. walfordi*. However, direct comparisons of Venezuelan specimens of *H. minuscula* in the collection of the Museum of Natural History, The University of Kansas (KU 167131-43) with those from Belém (KU 127646-745) indicate that they are conspecific. Thus, the occurrence of *H. walfordi* in Belém is not supported by the available data.

Duellman (1971) described the calls of specimens of *S. quinquefasciata* recorded in Santo Domingo de los Colorados, Ecuador, a locality about 150 km southeast (air line) from ours. Although the frequency range and the general structure of the call coincides with our recordings, other characteristics such as the pulse rate [65 pulses / second in Duellman (1971)] remain rather different to our data (35 pulses / second). In addition, the note duration that is represented in the audiospectrogram depicted by Duellman (1971: 216) is about 300 ms in duration, a value that is within the ranges that we find (168—1978 ms) but the range and average duration reported in the text by Duellman (140—150 ms, average 145 ms) is lower than any of the values found by us.

In a previous paper (De la Riva et al. 1994) we described the call of *Scinax parkeri* (Gaige, 1929) from Bolivia, and we stated that no recordings of the species had been published. Actually, we overlooked Duellman & Pyles's (1983) numerical data from recordings obtained in Belém, although they did not show sonogramas or oscillograms. Our results are not consistent with those of Duellman & Pyles. Calls from Bolivian specimens have a higher mean number of notes/minute (151.1 vs. 27.6), are much shorter (185.7 ms vs. 640), have less pulses/s (100.2 vs. 177), and show a lower dominant frequency (2777 Hz vs. 4558). These data seem to belong to different species. *Scinax parkeri* has been considered by some authors (Lutz 1973; Frost 1985; De la Riva 1990) as a synonym of *S. fuscomarginata* (A. Lutz, 1925), a species occurring in southeastern Brazil. However, Duellman & Wiens (1992) considered *S. parkeri* as a valid species, without explanation. There are two other species of the perplexing *S. staufferi* group described from this part of the Amazon basin, *S. goinorum* (Bokermann, 1962) and *S. madeirae* (Bokermann, 1964) [the later placed also in the synonymy of *S. fuscomarginata* by Lutz (1973)]. All these species look quite similar in appearance. The call of *S. fuscomarginata* was described by Cardoso (1981) from specimens recorded in Campinas. He found a single kind of note when individuals were calling alone, and two notes when they were calling in pairs. All the parameters allowing comparisons from Cardoso (1981) and De la Riva et al. (1994) show strong differences between the calls of *S. fuscomarginata* and *S. parkeri*. Because our recordings of *S. parkeri* were obtained at Buenavista (type locality of the species) while Cardoso's were obtained from the state of São Paulo (type locality of *S. fuscomarginata*), we conclude that *S. parkeri* is a valid species. On the other hand, data by Cardoso (1981) are quite similar to those by Duellman & Pyles (1983). A reassessment of the taxonomic status of all the described Amazonian species in the *S. staufferi* group is needed.

As we have seen, the vocalizations of some of the species studied were already described from different localities by other authors. Comparisons with those previous reports sometimes showed concordant results. In other cases, potential inconsistencies were revealed which would suggest lines for further research. The problem is frustrating in some of these cases, because inconsistencies may be due to a vast array of causes. First, slight intraspecific regional variations in the advertisement calls may exist. Among other reasons, these variations may be a response to slightly different acoustic niche availability in different communities. The different composition of anuran communities from site to site may drive a particular species to expand or squeeze its acoustic niche, depending on particular acoustic constraints. For example, recordings of *Leptodactylus mystaceus* from Peru differ markedly from recordings of the same species obtained in Bolivia. This may be due to the presence in Bolivia of a second species with a similar call, *L. elenae*, or to the fact that two species may actually be involved under the name *L. mystaceus* (Márquez et al. 1995). While this paper was in press, Heyer et al. (1996, Amphibia-Reptilia 17: 7—31) described *Leptodactylus didymus* from SE Peru, confirming this hypothesis. Particular conditions at the time of the recording (i.e., temperature), as well as some characteristics of the frogs themselves (i.e., size or social context) may also affect the results. In this sense, there are different kinds of calls among those commonly considered as "advertisement calls". A male can modify some features of the call if there is another male close to it, even though they are not involved in a duet. In such a case, it is very common that the "normal" structure of the call undergoes some sort of change. For the researcher not familiar with the vocalizations of a particular species, it may be difficult to interpret and distinguish what kind of call is being recorded. Finally, there may be differences in the way in which recordings are obtained, analyzed, and presented, and there are many different kinds of recorders, microphones, vibralizers, hardware, software, and so forth. Thus, it is necessary to be as careful as possible before making taxonomic guesswork derived from these comparisons. Furthermore, we know little about the intraspecific variation of the mating calls in Neotropical anurans. We suggest that unless strong differences are found, no taxonomic implications should be supposed in the absence of another kind of evidence. If material and procedures, as well as the pertinent biological information, are not thoroughly explained, confusion and erroneous conclusions will result. If we wish to establish useful comparisons between data of recordings by different researchers, a standardization of the methods, variables considered, and terminology employed is needed.

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Zusammenfassung

Das Rufverhalten und die Struktur der Werberufe von 5 südamerikanischen Hyliden-Arten werden anhand von Oszillogrammen und Lautspektrogrammen sowie Messungen ihrer Strukturparameter darin beschrieben. Die Varianz der einzelnen Parameter wird mit bereits dazu publizierten Befunden verglichen. Taxonomische und methodische Aspekte der Verwendung bioakustischer Daten werden diskutiert. *Hyla walfordi* und *Scinax parkeri* sollten als eigenständige Arten anerkannt werden.

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