Journal of Herpetology, Vol. 49, No. 1, 46–52, 2015
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Extended Vocal Repertoire in *Hypsiboas punctatus* (Anura: Hylidae)

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Abstract.—**Male *Hypsiboas punctatus* emit seven different types of calls: three consist of repeated trains of notes, and four are single-note calls with frequency modulation. Behavioral observations allowed assigning the calls to specific functions: (1) and (2) advertisement calls (short and long duration), (3) territorial signaling, (4) courtship interactions, (5)–(7) aggressive interactions (aggressive, fighting, and release calls). All calls consist of a single note and possess harmonic structure. The harmonic structure from the advertisement call suggests a missing fundamental frequency. Advertisement calls exhibit inter- and intraindividual variation in the dominant frequency. Our results indicate that previous comparisons among vocalizations of *H. punctatus* were based on different types of calls.**

Most of our knowledge of communication in anurans comes from the study of acoustic signals (Gerhardt and Huber, 2002; Wells and Schwartz, 2006). Anuran calls are classified based on the context in which they are emitted. In his seminal work, Bogert (1960) recognized five major call types, the mating call, the territorial call, the distress call, the warning call, and the release call. This classification was later modified by Wells (1977, 1988, 2007), who also provided some tools to interpret the function of the different types of calls in the context of social behavior. This framework has improved our understanding of the diversity of call types that may be part of an extended vocal repertoire in some species of anurans.

In the large hylid subfamily Hylinae, some examples of extensive vocal repertoire come from studies in species of *Dendropsophus* (e.g., Wells, 1988), *Scinax* (e.g., Toledo and Haddad, 2005), *Pseudacris* (e.g., Schwartz, 1989), and *Hyla* (e.g., Fellers, 1979). Within the tribe Cophomantini extensive vocal repertoires have been described in species of *Aplastodiscus* (Hartmann et al., 2004; Haddad et al., 2005; Zina and Haddad, 2006), and in two species groups of *Hypsiboas*—the *Hypsiboas albopunctatus* Group (Guimarães and Bastos, 2003) and the *Hypsiboas faber* Group (Kluge, 1981; Martins and Haddad, 1988; Giasson and Haddad, 2006; Loebmann et al., 2008). Different vocalizations have been described in the *Hypsiboas pulchellus* Group, but without being assigned to any specific function (e.g., Menin et al., 2004; Garcia and Haddad, 2008). Despite these examples, information from the other three genera of Cophomantini (i.e., *Bokermannohyla*, *Hyloscirtus*, and *Myersiohyla*), and from the six other species groups of *Hypsiboas* (*Hypsiboas benitezi*, *Hypsiboas pellucens*, *H. pulchellus*, *Hypsiboas punctatus*, *Hypsiboas raniceps*, and *Hypsiboas semilineatus* groups) regarding their diversity of call repertoires in particular, and their reproductive biology in general, remains scarce.

Hypsiboas punctatus is a common species that occurs in South America throughout the Amazon basin, southwards to the Chaco region of Paraguay, and along the banks of the Río Paraguay-Parana, Argentina (La Marca et al., 2010). This species has a prolonged reproductive pattern and congregates during the breeding season in the middle of large water bodies (Duellman, 1978; Márquez et al., 1993; Prado et al., 2005). Knowledge of the reproductive biology of *H. punctatus* is limited to some references to its advertisement call (Barrio, 1965; Duellman, 1978; Hoogmoed, 1979; Lescure and Marty, 2001) and call comparison with the morphologically similar species *Hypsiboas atlanticus* (Napoli and Cruz, 2005). The presence of two types of sexually dimorphic skin glands (SDSGs) in mental and lateral body regions suggests some sort of chemical communication during courtship and/or male interactions (Hoogmoed, 1979; Brunetti et al., 2012). In this article we describe the vocal repertoire in males of *H. punctatus*, as well as the context in which the different call types are emitted.

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DOI: 10.1670/13-206

Materials and Methods

Study Areas and Periods.—Field work was conducted in two different populations of *H. punctatus* along the basin of the Parana River in Argentina. Population 1 was located along the coast of a small river near Laguna Setúbal, in the locality of Alto Verde, near Santa Fe City, Santa Fe Province. Population 2 was located in a small lagoon connected to a floodplain, in Toropí, 8 km south of Bella Vista, Corrientes Province. At both localities, *H. punctatus* was associated strongly with *Eichornia crassipes* (Water Hyacinth), *Pistia stratiotes* (Water Lettuce), *Salvinia biloba* (Giant Salvinia), and *Azolla filiculoides* (Water Fern). Air and water temperatures were 26–32°C and 29–31°C, respectively, during midday, and 18–31°C and 20–29°C at night. We undertook one survey in February 2011, and two surveys during February 2012 at locality 1, and one survey in February 2013 at locality 2, with 3–5 days of observations per survey. Observations and recordings were made from a small canoe with minimal light intensity. We began at dusk and finished when anuran activity had decreased or ceased (approximately 2030 h to 0400 h).

Data Collection and Analysis.—Calls from individuals in population 1 and population 2 were recorded with a Sony WM-D6C tape recorder equipped with an external microphone (Sony ECM-909A), and with a Marantz PMD-430 tape recorder with the use of an Audiotechnika At-835B microphone, respectively. In all cases, microphones were positioned 40–70 cm from the calling male. Calls were recorded on chrome cassette tapes at 4.75 cm/s. Calls were digitized and analyzed with the use of the software Raven Pro 1.3 (22 kHz of frequency sampling, 16-bit precision). Audiospectrograms and spectral slices of selected notes were constructed with the use of fast Fourier transform and a frame length of 512 points for advertisement calls, and 256 points for other call types, with 80% overlap, Hann's sampling window, and an effective bandwidth of 124 Hz for advertisement calls and 62 Hz for other call types. The following temporal parameters were measured from the wave-

TABLE 1. Summary of acoustic parameters for vocalizations of adult males of *Hypsiboas punctatus*. Values are expressed as mean ± SD, followed by the range in parentheses. Abbreviations are as follows: f_0 = fundamental frequency; f_1 = second harmonic; f_2 = third harmonic; LAC = long advertisement call; SAC = short advertisement call.

	SAC	LAC	Territorial call	Courtship call	Aggressive call	Fighting call	Release call
n (frogs)	12	8	12	10	4	4	3
n (calls)	14	8	16	14	6	4	3
Temperature (°C)	23.0–31.0	23.0–31.0	20.0–31.0	18.5–26.5	23.0–27.0	23.5–24.8	23.5–24.8
Call type	Multinote	Multinote	Multinote	Single note	Single note	Single note	Single note
Note type	Pulsed	Pulsed	Unpulsed	Unpulsed	Pulsed	Pulsed	Unpulsed
Call rate (call/min)	11.4 ± 6.6	2.58 ± 0.3	3.0 ± 1.8	15.6 ± 8.4	19.2 ± 9.6	39.0 ± 15.0	33.6 ± 0.33
Call duration (ms)	306.0 ± 82.8	1,264 ± 453	258.1 ± 63.6	50.6 ± 8.6	48.9 ± 3.2	66.3 ± 2.3	41.7 ± 3.8
	(170–520)	(863–2,180)	(184–450)	(49–67)	(42–55)	(58–70)	(38.0–48–0)
Notes/call	5.0 ± 1.3	22.0 ± 7.3	3.6 ± 0.4	1	1	1	1
	(3–8)	(12–33)	(3–5)	1	1	1	1
Note duration (ms)[a]	20.6 ± 2.5	20.2 ± 3.3	23.1 ± 2.6	50.6 ± 8.6	48.9 ± 3.2	66.3 ± 2.3	41.7 ± 3.8
	(18–25)	(18–26)	(20–31)	(49–67)	(42–55)	(58–70)	(38.0–48–0)
Internote interval[b]	73.5 ± 7.2 ms	57.7 ± 5.0 ms	87.8 ± 10.1 ms	3.8 ± 2.4 s	2.6 ± 0.4 s	1.6 ± 0.6 s	2.3 ± 1.3 s
	(66–83)	(51–64)	(81–112)	(1.1–8.7)	(1.9–4.4)	(1.1–2.5)	(0.7–4.9)
Note duty cycle	0.31 ± 0.03	0.35 ± 0.05	0.27 ± 0.03	0.02 ± 0.02	0.019 ± 0.005	0.04 ± 0.01	0.02 ± 0.01
	(0.26–0.34)	(0.32–0.40)	(0.20–0.29)	(0.007–0.050)	(0.015–0.026)	(0.03–0.06)	(0.01–0.03)
Note rate (notes/s)[c]	13.8 ± 1.3	17.0 ± 1.4	11.5 ± 1.2	[c]	[c]	[c]	[c]
	(12.3–15.8)	(15.2–19.1)	(9.8–13.1)				
Observed harmonics	4–10	5–11	3–5	2–6	3–6	3–6	3–4
Observed frequency band (Hz)	630–4,100	800–4,100	840–4,500	840–5,400	840–4,300	870–3,700	920–5,000
Lower observed frequency (Hz)	934 ± 80 (f_2)	892 ± 54 (f_2)	f_0	f_0	f_0	f_0	f_0
	(814–1,052)	(818–990)					
Fundamental frequency (f_0, Hz)	326 ± 47	305 ± 18	1,323 ± 90	1,540 ± 166	1,414 ± 104	1,164 ± 29	1,307 ± 69
	(267–392)	(264–334)	(1,201–1,524)	(1,380–1,850)	(930–1,860)	(1,130–1,187)	(1,240–1,380)
Dominant frequency (Hz)	Variable	Variable	f_0	f_0	f_0	f_0 or f_1	f_0 or f_1

[a] In single-note calls: note duration = call duration.
[b] In single-note calls equivalent to intercall interval.
[c] In single-note calls correspond to call rate (call/min = note/min).

form: duration of note, number of notes per call, and internote interval. Frequency spectra, dominant frequencies, and fundamental frequencies (with the exception of fundamental frequency from advertisement calls—see next paragraph), were obtained from audiospectrograms and spectral slices. We also calculated call rate (calls/min), note rate (notes/s), and note duty cycle (ratio of note duration and internote interval).

The frequency components of advertisement calls appeared to be formed by multiple harmonics that were not integer multiples of the lowest frequency displayed in the audiospectrogram. Moreover, when successive harmonics were subtracted a similar frequency of 280–340 Hz was found repeatedly in different calls. Based on previous evidence (Bee and Gerhardt, 2001), we considered that the observed harmonics were integer multiples of a missing fundamental frequency (f_0). To estimate f_0 we used the following procedure: a pulse was selected from the middle of each note and three to five frequencies (depending on the note resolution) were calculated from subtracting two consecutive and clearly distinguishable harmonics. These frequencies were averaged, and the obtained value was considered as the fundamental frequency of each note.

The classification of different call types follows Wells (2007), except for territorial and fighting calls, which follow Kluge (1981) and Martins et al. (1998), respectively. In this article, the term *note* refers to the unit of sound (Duellman and Trueb, 1986; Heyer et al., 1990; McLister et al., 1995), consisting of one or more pulses, produced during a single airflow cycle. The number of notes per call can be determined by observing the vocal sacs of calling frogs (McLister et al., 1995); based on our observations, the vocal sac in *H. punctatus* undergoes a single inflation during fighting, release, aggressive, and courtship calls, but it increases and decreases in volume many times per call in conjunction with each pulse during both advertisement and territorial calls. Call variables measured follow the terminology of Heyer et al. (1990) and the mechanistic coding used by Robillard et al. (2006).

Because differences in call parameters within each population exceeded those between both populations, we plotted all data in a single analysis. Calling sites were categorized according to their proximity to the water surface, i.e., at the level of water surface or above water surface. Air temperature was measured with an alcohol thermometer to the nearest 0.5°C. However, as samples sizes of each call type did not allow for temperature correction, we only indicate temperature ranges for each call type. Voucher specimens were deposited in the herpetological collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN).

RESULTS

Considering the context in which they were produced and their acoustic parameters (Table 1), we distinguished seven types of vocalizations emitted by males of *H. punctatus*: short advertisement calls (SACs), long advertisement calls (LACs), territorial calls (TCs), courtship calls (CCs), aggressive calls (AgCs), fighting calls (FCs), and release calls (RCs). Temporal variables and parameters are summarized in Table 1.

Advertisement Call (Fig. 1A,C).—Short advertisement calls (SACs) and LACs consist in a repeated train of pulsed notes (multinote calls); each note is composed by 2–5 closely packed and poorly resolved pulses (Fig. 1A,C, insets). SACs and LACs may be distinguished by their call duration (SAC: 170–520 ms; LAC: 863–2180 ms), and number of notes per call (SAC: 3–8; LAC: 12–33). They also differ in other temporal features, among which are internote interval (SAC: 66–83 ms; LAC: 51–64 ms) and

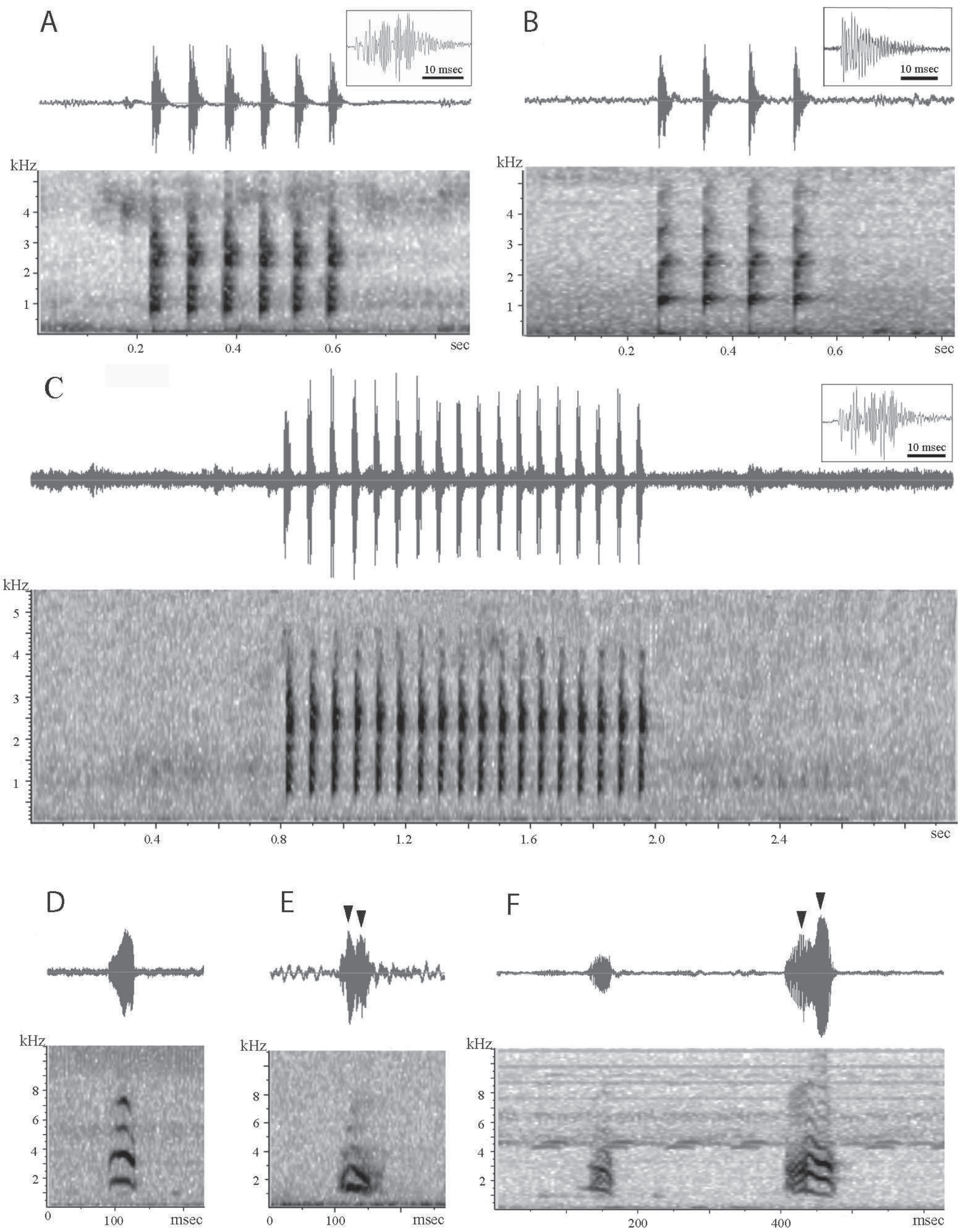

FIG. 1. Vocal repertoire of *Hypsiboas punctatus*. Waveforms are shown on top of each call type, sound spectrogram on the bottom. (A) Short advertisement call (SAC); (B) territorial call (TC); (C) long advertisement call (LAC); (D) courtship call, (E) aggressive call, (F) release call and fighting call, at left and on the right, respectively. Insets (A)–(C): expanded waveform of one note, showing poorly resolved pulses in SAC and LAC (A) and (C), and an absence of pulses in TC (B). Arrowheads indicate different pulses within aggressive (E) and fighting calls [(F), right side].

note repetition rate (SAC: 12.3–15.8 notes/s; LAC 15.2–19.1 notes/s). The notes in SACs and LACs consist in a series of up to 10 and 11 harmonics (f_2–f_{12}), respectively, that are integer multiples of a missing fundamental frequency (f_0). The calculated f_0 was similar in both call types (SAC: 267–392 Hz; LAC: 264–334). The dominant frequency was variable within each call type (see below under *Advertisement call variability*), but was frequently represented by a bimodal spectrum with one energy peak located within the harmonics f_2–f_4, and a second between f_7 and f_8.

The short advertisement call was the most frequent type of vocalization. It was heard soon after sunset (2000 h) until 0400–0500 h. It was emitted by males standing on *P. stratiotes* or leaves of *E. crassipes* at the water surface level with a fully extended vocal sac. Two, less commonly three, nearby males were heard alternating SACs without overlap. During these duets and trios one of the males, or sometimes two, modified the call pattern, giving LACs that were interspersed with SACs. Unlike SACs, the LACs of one male were frequently overlapped with calls of the other interacting male. Occasionally, males vocalizing alone emitted LACs.

Territorial Call (Fig. 1B).—The territorial call consists of a series of 3–4 notes, which makes this call more stereotyped than both types of advertisement calls. Unlike advertisement calls, notes in TCs were not pulsed (Fig. 1B, inset). Call duration was similar to SAC (170–520 ms and 184–450 ms, respectively). Comparatively, it had the highest internote interval (81–112 ms) and the lowest note repetition rate (9.8–13.1 notes/s). Although each note may consist of up to five harmonics, three harmonics was the most common. In contrast to advertisement calls, the fundamental frequency (f_0) was present (at 1,201–1,524 Hz) and corresponded to the dominant frequency.

Territorial calls were emitted by males perched on *E. crassipes* at different heights (20–180 cm above the water). We heard this type of vocalization in four different situations. In the first situation, the TC was recorded from males that were initially producing advertisement calls at the water surface level and began to climb. These individuals started to emit TCs while they were moving slowly by jumping and climbing in a circular path at variable distances (30–100 cm) around their initial calling site. They eventually returned to their calling site and resumed advertisement calls. This behavior lasted 30–50 min ($n = 4$ individuals), and a single male performed it twice during the same night. In the second situation, the male abandoned his site and began to move around, directing his TC to other calling males. Eventually, we recorded TCs when the male jumped on silent nearby males ($n = 5$). In the third situation, the male emitted TC sporadically during amplexus ($n = 2$). In the last situation, individuals that were removed by the observer while emitting advertisement calls began emitting TCs when they were returned to the same site. Twenty to thirty minutes later they shifted to short advertisement calls ($n = 4$).

Courtship Call (Fig. 1D).—This call consists of a single unpulsed note of short duration (49–67 ms). The frequency was positively modulated from the beginning to the first third of the call, then followed an unmodulated period, and the last third was negatively modulated. The fundamental frequency was also the dominant frequency (1,380–1,850 Hz). Males gave CCs in two different situations. In the first, the male was emitting advertisement calls and shifted to courtship call after noticing a female ($n = 6$). Moreover, when a female was at the water level, the male approached a female up to a shorter distance, gave 2–3 CCs, and finally guided her to his calling site ($n = 4$). In the second, when the female left the male's calling site without the occurrence of amplexus, the male followed her for a certain distance (10–20 cm) emitting CCs.

Aggressive Call (Fig. 1E).—This call consists of a single note of 2–3 compressed pulses. The note duration of the aggressive call overlaps that of courtship call, but was comparatively shorter in the former (42–55 ms and 49–67, respectively). The fundamental frequency was also the dominant frequency (930–1,860 Hz). The frequency modulation of this call was more evident in the second harmonic. The first (and when present, the second) pulse was positively modulated in frequency, whereas the last pulse was negatively modulated. A male emitted aggressive calls (AgCs) when a nearby male approached at distances closer than 50 cm from his calling site ($n = 6$). In turn, the intruder answered with short advertisement calls. Resident male and intruder were heard to be interacting by advertisement calls interspersed with AgCs during 5–20 min. After that time they began fighting ($n = 4$). Alternatively they resumed advertisement calls at much closer distance (30 cm; $n = 2$).

Fighting and Release Calls (Fig. 1F,G).—These calls consist of a single note, which was composed of 2–3 pulses in FCs, but was unpulsed in RCs. Fighting calls have the longest duration among the single-note calls (58–70 ms), and RCs have the shortest (38–48 ms). Both calls are emitted at a similar calling rate with an average rate of 39.0 call/min and 33.6 call/min (for FCs and for RCs, respectively). They are also distinguished by their fundamental frequencies (FCs: 1,130–1,187 Hz; RCs: 1,240–1,380 Hz). In both, the dominant frequency coincides with the fundamental frequency in some notes, or with the second harmonic in others. Release calls were negatively modulated in frequency, whereas in FCs the first pulse is positively modulated, and the second and third pulses were mostly negatively modulated. Fighting calls and RCs were emitted by males when fighting. Both males emitted fighting calls at the beginning of the contest, whereas at the end, with an obvious winner, the opponent began to emit release calls.

Advertisement Call Variability (Fig. 2).—Besides the bimodal spectrum described (Fig. 1A), males of *H. punctatus* emit advertisement calls that have a variable spectrum, with the energy peaks at different frequencies and variation in the number of observed harmonics. Some males were often heard emitting advertisement calls with energy peaks within 2,000 and 2,700 Hz (f_7 and f_8; Fig. 2A), whereas others concentrated the energy within 814 and 1,400 Hz (f_2 and f_3; Fig. 2B). Although less common, in some advertisement calls the energy peaks were extended from the first emphasized harmonics (f_2–f_4) to the f_5 harmonic (Fig. 2C), whereas in some calls they encompass most of the emphasized harmonics f_2–f_9 (Fig. 2D). Most males were heard to alternate among at least two of these variants.

Discussion

We have described seven types of vocalizations from *H. punctatus*. They are emitted in different social contexts and are distinguished clearly by their acoustic parameters. Although call variation in *H. punctatus* has been mentioned in literature, references to this phenomenon are isolated and did not consider the rich call repertoire described in the present study (Barrio, 1965; Hödl, 1977; Duellman, 1978; Hoogmoed, 1979; Duellman and Pyles, 1983; Cardoso and Vielliard, 1990; Márquez et al., 1993; Lescure and Marty, 2001; Marquez et al., 2002). Call diversity has behavioral and taxonomic implications.

Call Diversity and Social Context.—Males of *H. punctatus* emit two types of advertisement calls: SACs and LACs. The term *advertisement call* is currently preferred over *mating call* because this call often serves more than one function (Gerhardt, 1992). The two most accepted functions are female attraction and the spacing of individual males (Wells, 2007). Many authors have suggested that female anurans might choose mates on the basis of call features, especially the dominant frequency of male calls (reviewed by Gerhardt and Huber, 2002). However, this may not be the case for all species (e.g., Schwartz and Gerhardt, 1998) or may be dependent on the sound pressure level of different frequencies (Gerhardt, 1981). Males of *H. punctatus* exhibit great variability in the ranges of the dominant frequency. Whether or not this conveys information upon which females might discriminate or choose a specific male needs to be determined by preference tests. Another possibility to explain this complex variation is that the dominant frequency might be carrying different cues that males may use during interactions with other males. These cues could serve as a mechanism of individual recognition in order to discriminate between neighbors or strangers (i.e., habituation), and to be aware of the potential threat to their territory (Bee and Gerhardt, 2001).

Courtship calls are emitted either from a static location or while trying to guide the female to the male's calling site. Although it is not clear what information this call communicates to the female, it is only emitted in close-range interactions. This type of call has not been reported previously in *H. punctatus*, but it has been documented in related species: *H. faber* (Martins and Haddad, 1988), *Hypsiboas rosenbergi* (Kluge, 1981), and four species of the genus *Aplastodiscus* (Haddad and Sawaya, 2000;

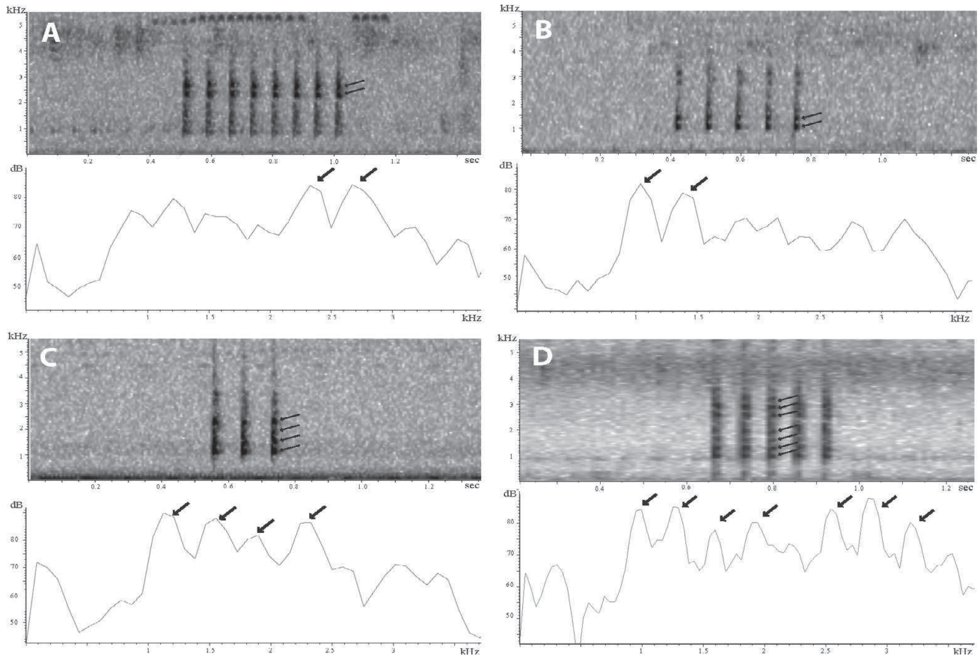

FIG. 2. Call variation in short advertisement calls of *Hypsiboas punctatus*. Sound spectrograms are shown on top of each call, power spectrum on the bottom. Arrows indicate harmonics (*f*) of higher intensity, which correspond to (A) f_7–f_8, (B) f_2–f_3, (C) f_2–f_5, and (D) similar intensities in the harmonics f_2–f_5 and f_7–f_9. Note that most nonemphasized harmonics are hardly distinguishable.

Hartmann et al., 2004; Haddad et al., 2005; Zina and Haddad, 2007), as well as in other species of anurans (reviewed by Wells, 2007). Structurally, the CC of *H. punctatus* resembles that from species of *Aplastodiscus*, because both consist of a frequency-modulated tonelike note, whereas in *H. rosenbergi* and *H. faber* it consists in a multinote call (Kluge, 1981; Martins and Haddad, 1988).

Distinctive CCs occur in species in which the male leads the female to concealed oviposition sites (e.g., Haddad et al., 2005), or less commonly, in species in which the males call from a fixed location (Kluge, 1981). Camurugi and Juncá (2013) described a CC in other species of the *H. punctatus* Group, *H. atlanticus*, which is structurally related to the advertisement call of *H. punctatus*. These authors hypothesized the function of this call from the observation of a single event in which a female was approaching to a male emitting advertisement calls, but without providing information regarding the presence of nearby males. Based on our results and considering that the term *advertisement call* may also be applied to similar situations (Wells, 2007), it is likely that these authors were referring to LAC. However, further observations are needed to support this inference.

Males of *H. punctatus* appear to be territorial. Territorial calls (TCs) are AgCs emitted by males in long-range interactions (Wells, 2007). Although in *H. punctatus* TCs may occasionally increase aggressiveness of neighbor males at some level, our observations suggest that they would be used primarily in a spacing function, and in this sense to signify the territory to other males. Similar ritualized spacing functions were observed in advertisement calls of *Hyla versicolor* (= mating call in Fellers, 1979), and territorial calls in *Hypsiboas rosenbergi* (Kluge, 1981).

Aggressive calls, FCs, and RCs were emitted by two rival males when both are present at the calling site of one of them. These calls can be better understood in the context of graded aggressive interactions (Wells and Schwartz, 1984; Martins et al., 1998). The results presented in those studies and in this paper allow consideration of the LAC of *H. punctatus* within this type of interaction, while AgCs and fighting calls FCs can be generalized as aggressive calls emitted in close-range encounters (Wells, 2007). Aggressive calls and FCs from *H. punctatus* are related to specific situations, in which AgCs precede physical contact, whereas FCs are emitted exclusively by wrestling males.

The use of more than one kind of call during aggressive interactions by *H. punctatus* has been observed in several other hylids (e.g., Schwartz, 1989; Toledo and Haddad, 2005; Zank et al., 2008). Within Cophomantini, gradation in aggressive interaction has been reported in *Hypsiboas albomarginatus*, *H. faber*, and *H. rosenbergi* of the *H. faber* Group (Kluge, 1981; Martins et al. 1998; Giasson and Haddad, 2006). *Hypsiboas punctatus* and these species have well developed prepollical spines (Faivovich et al., 2005), which are used against opponents during combat, sometimes causing severe injuries (Kluge, 1981; Martins et al., 1998; Brunetti et al., in press). Combat is costly in terms of time, energy, and risk of injury (Robertson, 1986), and LACs and AgCs may be important cues for males to avoid fights. Although combat has been reported in the literature for some species of Cophomantini since the 1940s, RCs had not been interpreted previously as a distinct call (e.g., Kluge, 1981; Martins and Haddad, 1988; Martins et al., 1998). However, this call may be one of the "growl encounter calls" emitted by males of *H. rosenbergi* during fights (Kluge, 1981).

Call Diversity and Some Taxonomic Implications.—Vocalizations of *H. punctatus* have been described from specimens from different localities covering most of the species' geographic range (Barrio, 1965; Hödl, 1977; Duellman, 1978; Pyburn, 1978; Hoogmoed, 1979; Duellman and Pyles, 1983; Cardoso and Viellard, 1990; Márquez et al., 1993; Lescure and Marty, 2001; Márquez et al., 2002). Napoli and Cruz (2005) described the advertisement call from the similar species *H. atlanticus*, and discussed comparatively most of the physical parameters available in the literature regarding the vocalization of both species. These authors highlighted two important aspects: differences in the range of the dominant frequency, and a great variability in the number of notes/call. Camurugi and Juncá (2013) have differentiated advertisement call and CC of *H. atlanticus* based mostly in the number of notes/call. Considering our findings, there are a few confounding points. The advertisement calls of *H. punctatus* described by Barrio (1965) and Marquez et al. (2002) correspond in frequency ranges and note duration to TCs. The vocalizations described for *H. punctatus* by other authors would correspond to our SAC, whereas some of these authors have also referred to LACs when describing "long calls" or "calls with a large number of notes per call" (Hödl, 1977; Duellman, 1978; Hoogmoed, 1979; Duellman and Pyles, 1983). The CC described by Camurugi and Juncá (2013) in *H. atlanticus* could be a LAC.

The results presented here demonstrate that the dominant frequency of advertisement call of *H. punctatus* varies even within the same individual. This may explain the variation found by Napoli and Cruz (2005) while they were reviewing calls from different populations of this species. Moreover, considering that dominant frequency is often used taxonomically (e.g., Cocroft and Ryan, 1995), this parameter should be interpreted carefully at least in some species.

The frequency components of the advertisement call of *H. punctatus* are harmonics of a missing fundamental. Although such a phenomenon has not been mentioned before in this species, a closer observation of audiospectrograms from previous reports (Hödl, 1977; Hoogmoed, 1979; Márquez et al., 1993) and from Camurugi and Juncá (2013) in the similar species *H. atlanticus,* reveal the presence of multiple harmonics that do not seem to be integer multiples of the lowest frequency displayed. Although in these cases the audiospectrograms have poor resolution, the missing fundamental phenomenon becomes evident in the power spectrum of *H. atlanticus* published by Napoli and Cruz (2005). This spectrum has two frequency peaks with a similar intensity to those considered by the authors as the only two harmonics. Among anurans we have found only two other explicit mentions of missing fundamental frequency (e.g., Bee and Gerhardt, 2001; Gerhardt, 2001) but it is probable that in some cases it went unnoticed. This may be inferred, for example, from the audiospectrograms of four species of *Hyla* presented in Wells (2007).

Finally, Márquez et al. (1993) mentioned that in *H. punctatus* a single call "was sometimes followed by a long sequence of notes," whereas Cardoso and Vielliard (1990) have explained differences in the number of notes within a call ("pulses within a phrase" in their terminology) as depending on the existence of an exciting or perturbing stimulus. Regarding other species of Cophomantini, the audiospectrograms of *Hypsiboas ornatissimus,* a member of the *H. benitezi* Group (Faivovich et al., 2013), presented by Hoogmoed (1979) has two distinct calls; one of 17 notes and another of apparently 6 notes, which he referred as long call and "normal" short call, respectively. In turn, Cardoso (1983) described long notes of 15–18 pulses and short notes of 5–6 pulses in the vocalization of *Bokermannhoyla ibitiguara*. Although a reanalysis is needed in most cases, from current results it may be inferred that those studies were referring to SACs and LACs described in our study. Moreover, the number of notes within a call is highly variable and may be more informative in the analysis of social behavior rather than for taxonomic purposes.

Final Considerations.—We associated seven types of vocalizations to particular biological contexts, representing an extended call repertoire for a species of *Hypsiboas*. Extended repertoires have been described in a few of the 171 species of the tribe Cophomantini. Considering that the acoustic repertoire of *H. punctatus* has passed unnoticed in previous studies, it would be interesting to explore the diversity of call types occurring in other species of this tribe, coupled with behavioral and ecological studies to understand the social context in which they are emitted.

Acknowledgments.—The authors thank B. Blotto, C. Tomatis, and C. Luna for their company in the field. Mr. Reyes and Mr. Piri provided valuable help and the canoes during fieldwork. A. Amador gave useful advice for interpretation of the spectra. V. G. D. Orrico kindly read the manuscript and provided insightful comments, as did an anonymous reviewer and the associate editor. Financial support for this project was provided by ANPCyT PICT 2007-2202, 2011-1895, 2013-404, FAPESP 2012/10000-5, and 2013/50741-7, UBACyT 2012-2015 20020110200213, PIP 2011 0889, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).

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Accepted: 15 May 2014.