Journal of Natural History, 2007; 41(17–20): 1227–1235

Vocalizations of the Brazilian torrent frog *Hylodes heyeri* (Anura: Hylodidae): Repertoire and influence of air temperature on advertisement call variation

RODRIGO LINGNAU[1] & ROGÉRIO P. BASTOS[2]

[1]*Programa de Pós-Graduação em Zoologia, Faculdade de Biociências, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil, and* [2]*Departamento de Biologia Geral, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Goiânia, Brazil*

(*Accepted 12 April 2007*)

Abstract
In this study we analysed the acoustic activity of *Hylodes heyeri* in areas of Atlantic Forest, in southern Brazil. Observations were made in November 2001 and from January to April 2002, at Estação II Instituto Agronômico do Paraná, municipality of Morretes, State of Paraná. Males displayed three different vocalizations: advertisement calls, territorial calls, and courtship calls. Temporal and spectral parameters of advertisement and territorial calls were analysed, along with call intensity. The duration of the advertisement call showed a negative correlation with air temperature, with males decreasing the duration of advertisement calls at higher temperatures. Male body size was not correlated with any of the acoustic parameters. Details on habitat use, distances to nearest vocalizing neighbour, and daily calling activity are also included.

Keywords: *Advertisement call, Anura,* Hylodes heyeri*, Hylodidae, territorial call, vocalization*

Introduction

Communication studies in anurans began about one century ago, and today they incorporate a vast range of areas, including animal behaviour, developmental biology, endocrinology, evolution, ecology, and neurobiology (Ryan 2001). The calls of some species are highly variable, due to factors such as temperature (Giacoma et al. 1997; Navas and Bevier 2001), size and weight of males (Robertson 1986; Giacoma et al. 1997), and social interactions among individuals in the reproductive aggregation (Wells 1988).

The South American tropical forests have rich anuran communities. At some sites it is common to find more than 40 species, sometimes many of them calling synchronously (e.g. Heyer et al. 1990; Bertoluci and Rodrigues 2002). Many of these species have not yet had their vocal repertoires described, but there is recent progress in this area (Garcia et al. 2003; Kwet and Baldo 2003). Descriptions of temporal and spectral properties of vocalizations

Correspondence: Rodrigo Lingnau, Centro Integrado de Análise e Monitoramento Ambiental, Universidade Estadual de Mato Grosso do Sul, Rodovia Dourados Itahum Km 12, Cidade Universitária, 79804-970, Dourados, MS, Brazil. Email: rodrigolingnau@yahoo.com.br

ISSN 0022-2933 print/ISSN 1464-5262 online
DOI: 10.1080/00222930701395626

are increasing, but few studies on South American species include measurements of the intensities of these vocalizations (Penna and Solís 1998; Guimarães and Bastos 2003).

Frogs of the genus *Hylodes* are diurnal and live along small forested streams. During the day, they can be observed vocalizing on rocks close to the water, but are wary and when disturbed they escape into the water torrents (Lutz 1930; Haddad et al. 1996). *Hylodes heyeri* Haddad, Pombal, and Bastos, 1996 is a frog with restricted distribution. It occurs from southern São Paulo State to the southern limit of Paraná State in areas of the Atlantic Forest (Toledo and Lingnau 2002; Lingnau 2004). The main goal of our study was to provide a detailed description of the spectral and temporal parameters of the calls of *H. heyeri*, measurements of call intensity, and the influence of air temperature and male body size on variation of call parameters. Other aspects of the species, such as habitat use, distances to nearest vocalizing neighbour, and daily calling activity are also briefly assessed.

Materials and methods

Our study was conducted at Estação II of Instituto Agronômico do Paraná (25°26′59″S, 48°52′09″W), Municipality of Morretes, State of Paraná, in November 2001 and from January to April 2002. We studied a population of *H. heyeri* that inhabited a stream located on the east side of Serra do Marumbi, in the Serra do Mar mountains, approximately 150 m above sea level. The area around the stream was characterized by a humidity of 95–99% and numerous rocks, branches, and roots, which provided areas of difficult human access and good hiding places for individuals of *H. heyeri*. All observations were initiated between 6:00 and 8:00 h and lasted generally until 19:00 h. We monitored the study site for a total of 280 h over 39 days. Behavioural observations were conducted with focal animals (Lehner 1979; Martin and Bateson 1986). During focal observations, we counted the vocalizations emitted by a male for 5 min at intervals of 1 h, and recorded the air temperature for that period.

All vocalizations were recorded with a Sony ECM microphone coupled to a DAT TCD-D100 recorder. The vocalizations were digitized at a sampling frequency of 22 kHz and a resolution of 16 bits. The spectrograms were produced with Avisoft-SASLab Light with Fast Fourier Transformation (256 points), Overlap (75%), and Window (Hamming). The dominant frequencies, power spectrum, and oscillograms were obtained with Cool Edit using Fast Fourier Transformation (1024).

The peak sound pressure level (SPL) in dB was measured by a Minipa MSL-1352 sound level meter (fast setting of 125 ms and MaxHold), with a foam windshield held at a distance of 30 cm in front of the vocalizing male. The level of background noise at 30 cm was at least 20 dB below the level observed for each call. Only advertisement call intensities were measured, because territorial and courtship calls are not emitted so frequently. For each male, we measured the peak SPL for five successive advertisement calls, from which the mean for each male was determined.

For each recorded call sequence, the air temperature was measured with a thermometer (to the nearest 0.1°C). For description of the advertisement call parameters, such as call duration, number of notes per call, duration of notes and dominant frequency, we analysed five calls from 17 recorded males ($n=85$ calls); for interval between calls and SPL we used five calls from 15 recorded males ($n=75$ calls). Individuals that had their calls recorded or call intensities measured were immediately collected, fixed in 10% formalin, later preserved in 70% alcohol and measured for snout–vent length (SVL) to the nearest millimetre. Call data of individuals that could not be collected were not included in the analysis. Data for each acoustic parameter are reported as means ± SD. For comparisons between the acoustic parameters and SVL or air temperature we used Pearson's correlation test, with level of significance of $P<0.05$, according to Zar (1996). Voucher specimens were deposited at Museu Nacional do Rio de Janeiro, RJ (MNRJ) and Museu de História Natural Capão da Imbuia, Curitiba, PR (MHNCI). Recordings are stored at the Laboratório de Comportamento Animal, Universidade Federal de Goiás, Goiânia, GO.

Results

Males of *Hylodes heyeri* were found throughout the day vocalizing on rocks or in breaks among rocks ($n=21$), on the margin or very close to the stream. They were rarely observed vocalizing on branches ($n=2$), roots ($n=2$), leaves ($n=1$), or sand banks ($n=1$), although in these situations, they were close enough to the stream so that within one or two jumps they could reach the water. Two individuals were observed at night; they were both found on leaves of ground vegetation and were not vocalizing.

Three vocalizations were documented in this study: an advertisement call (Figure 1), a territorial call (Figure 2), and a courtship call (not recorded). At sunrise, when males started to call, we could hear more territorial calls than advertisement calls. Throughout the day they emitted more advertisement calls (when not in aggressive interactions), and at sunset, the males again emitted more territorial calls.

When calling activity began, males showed high call repetition rates, decreasing slightly throughout the day, while air temperature increased. Repetition rates of the advertisement call increased again at sunset, after which males ceased calling (Figure 3).

The vocalization most frequently emitted by the males was the advertisement call, which consists of high-pitched whistled trills. The advertisement call has a harmonic structure, with the most amount of energy concentrated on the third harmonic (= dominant frequency). The power spectrum (Figure 1A) shows three initial peaks of increasing intensity, illustrating the fundamental frequency, the second harmonic, and the dominant frequency, respectively. The fundamental frequency, which is approximately 1.5–2.0 kHz, generally is obscured by the background noise of the torrents and waterfalls, while the dominant frequency in the third harmonic is more audible (Figure 1B). A slight frequency modulation within the dominant frequency occurs throughout the call. The oscillogram (Figure 1C) demonstrates clearly that the concentration of energy in notes increased throughout the beginning of the call, and the notes at the beginning of the call are emitted with less energy than in the second half of the call.

The mean distance to the nearest vocalizing neighbour was 5.08 ± 2.45 m ($n=15$), and varied from 2.0 to 11.0 m. When an intruding male approached to within 2.0 m of a resident male, the resident male or both individuals emitted the territorial call ($n=5$; Figure 2). This call has similar spectral properties to the advertisement call, but with a much shorter duration. The main acoustic parameters of the advertisement and territorial calls are listed in Table I.

Courtship interactions were also observed ($n=4$), during which males emitted a courtship call very similar to the advertisement call, but with a shorter time interval between the calls. Males emitted loud courtship calls approximately every 5 s.

Air temperature influenced the duration of the advertisement call, at higher temperatures males decreased the duration of the advertisement call (Table II). Temperature ranged from 20 to 25.2°C during our observations and male SVL average was 36 ± 0.9 mm, amplitude 33.9–37.9 mm ($n=17$ males). Despite the fact that the duration of the

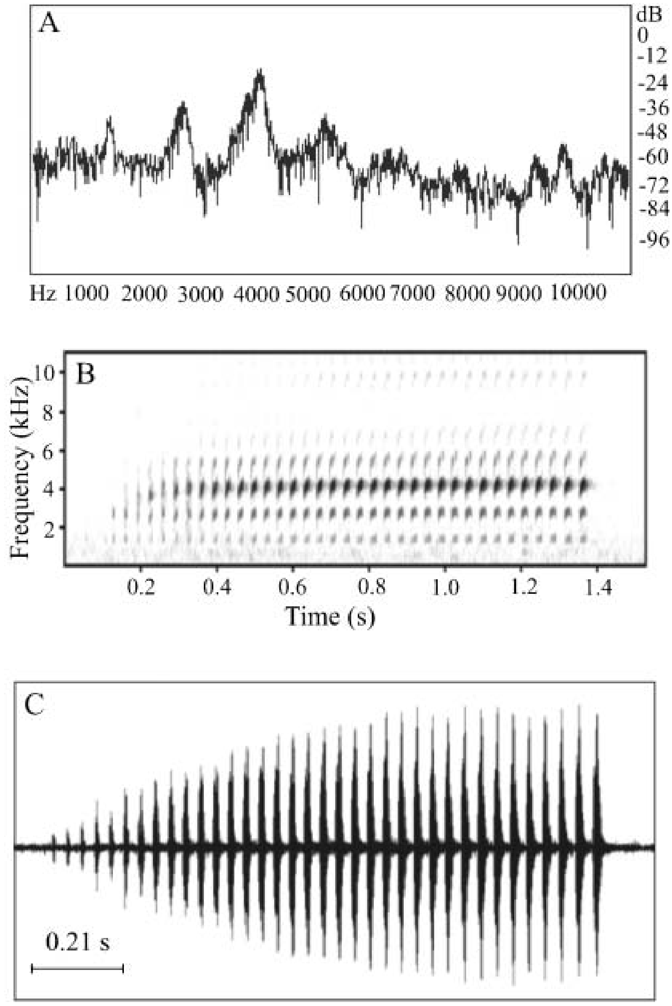

Figure 1. Advertisement call of *Hylodes heyeri* from the Municipality of Morretes, Paraná, Brazil. Recorded on 8 April 2002, at 21.7°C. (A) Power spectrum; (B) spectrogram; (C) oscillogram.

advertisement call and the number of notes per call was highly correlated (r=0.9421; n=16; P<0.0001), there was no correlation between air temperature and number of notes (Table II). There was also no correlation between air temperature and interval between calls or dominant frequency of the advertisement call (Table II). In addition, there was no correlation between SVL and call intensity (r=−0.059; n=15; P=0.833), or with dominant frequency of the advertisement call (r=−0.4023; n=17; P=0.1093).

Discussion

All *Hylodes* species, for which advertisement call descriptions are available, have the dominant frequency in the third harmonic (Haddad and Giaretta 1999; Haddad and Pombal 1995; Haddad et al. 1996, 2003; Heyer and Cocroft 1986; Nascimento et al. 2001; Pavan et al. 2001; Pombal et al. 2002; Vielliard and Cardoso 1996; Wogel et al. 2004; present study). According to Haddad and Giaretta (1999), the advertisement calls of some

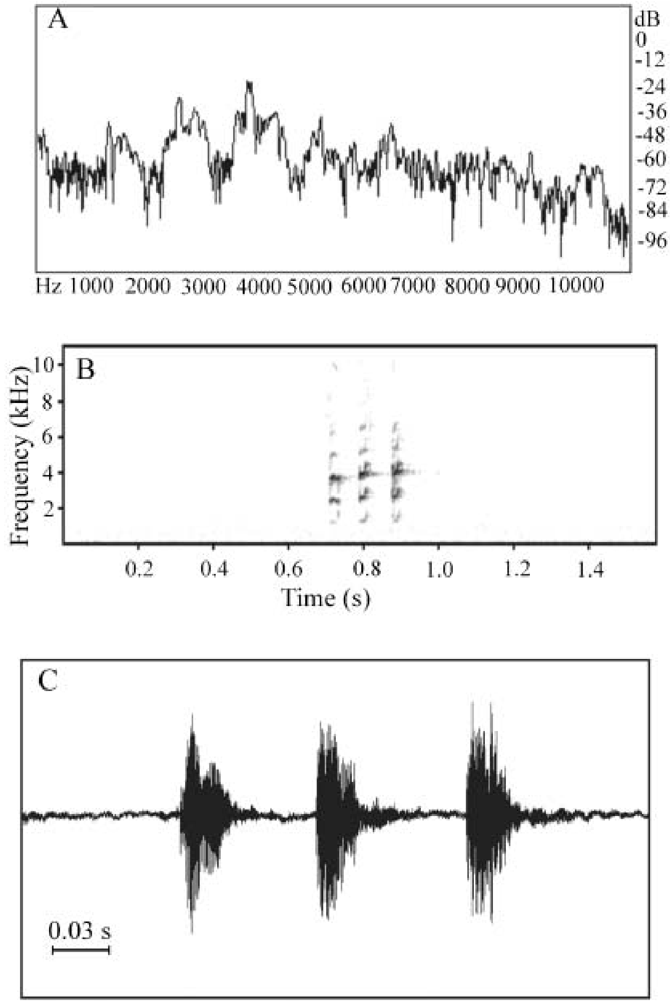

Figure 2. Territorial call of *Hylodes heyeri* from the Municipality of Morretes, Paraná, Brazil. Recorded on 11 January 2002, at 22.4°C. (A) Power spectrum; (B) spectrogram; (C) oscillogram.

species of *Hylodes* possess the following characteristics: numerous short notes with harmonic structure; energy concentrated on the third harmonic that is free from the low noise frequencies of the environment; notes rhythmically spaced within the sequences that are separated by long periods of silence.

Various studies have suggested that the rushing water from the streams creates a noisy environment in which a vocal signal might be less easily heard than in most habitats (Heyer et al. 1990; Lindquist and Hetherington 1996). Wogel et al. (2004) suggested that, at least for species of the genus *Hylodes*, vocal signals are not significantly obscured by background noise as previously suggested, because it seems there is not a deficit related to the acoustic channel. We agree with Wogel et al. (2004) that there is no deficit in the acoustic communication in species of *Hylodes*, because the dominant frequency of advertisement calls is in the third harmonic, above the frequencies from the rushing water of the streams. According to Hödl and Amézquita (2001), the higher the frequency, the better the contrast to the low-frequency-dominated noise produced by the turbulent waters. The calls of

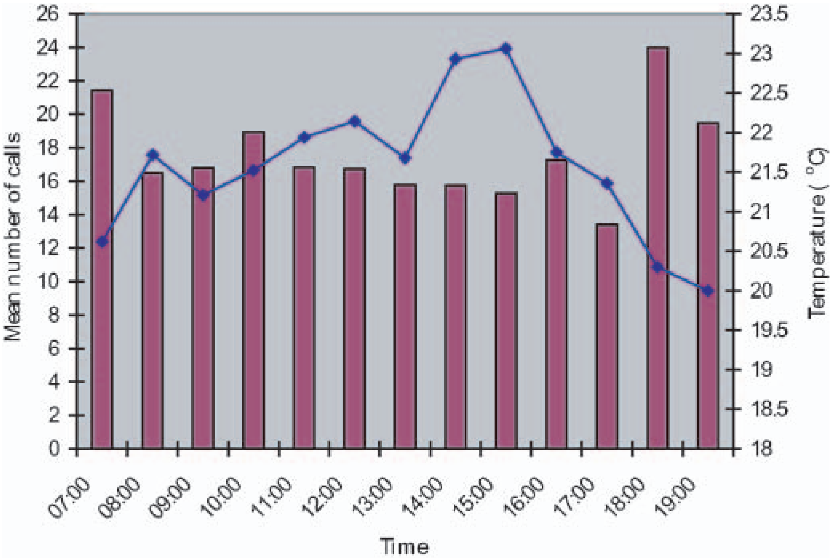

Figure 3. Mean number of advertisement calls (bars) emitted by males of *Hylodes heyeri* during 5 min of monitoring each hour, and air temperature (line).

Hylodes therefore appear to be shaped by evolutionary forces to minimize interference of the acoustic conditions of the environment (Vielliard and Cardoso 1996).

The acoustic communication of *H. asper* (Müller, 1924) was thoroughly studied by Haddad and Giaretta (1999). Males of *H. heyeri* have a similar behaviour to males of *H. asper*, in that they both emit more territorial calls at sunrise and sunset than during midday. It is possible that males emit more territorial calls during sunrise and sunset because at that time they are moving between calling sites and nocturnal shelters. In nocturnal anurans, aggressive calls are produced primarily at the beginning of a night's chorus and are believed to be important in establishing spacing between calling males (Rose and Brenowitz 1997). When Haddad et al. (1996) described *H. heyeri*, they included the advertisement call and the encounter call. In this study we used "territorial call" instead of "encounter call", since we demonstrated more accurately the territorial function of this call (see also Lingnau 2003).

Table I. Main acoustic parameters of the advertisement and territorial call of *Hylodes heyeri* at the municipality of Morretes, Paraná, Brazil.

	Advertisement call			Territorial call		
	Mean ± SD	Minimum–maximum	Calls analysed/♂ recorded	Mean ± SD	Minimum–maximum	Calls analysed/♂ recorded
Call duration (s)	1.11 ± 0.25	0.69–1.86	85/17	0.19 ± 0.02	0.09–0.27	22/4
Number of notes per call	32.58 ± 5.87	20–48	85/17	2.77	2–4	22/4
Duration of notes (s)	0.03 ± 0.002	0.02–0.04	85/17	0.03 ± 0.002	0.02–0.04	22/4
Interval between calls (s)	13.97 ± 7.45	8.98–38.75	75/15	3.8 ± 0.17	1.61–11.01	22/4
Dominant frequency (kHz)	4.22 ± 0.12	3.90–4.61	85/17	3.77 ± 0.15	3.36–4.88	22/4
Sound pressure level (dB)	89.55 ± 2.49	85.64–95.58	75/15	Not recorded		

Table II. Correlation coefficients between the acoustic parameters of the advertisement call and air temperature in *Hylodes heyeri*.

	Mean ± SD	Correlation coefficient	*n*	*P*
Call duration (s)	1.13 ± 0.25	−0.6338	16	0.0084*
Number of notes per call	32.82 ± 5.98	−0.4032	16	0.1214
Dominant frequency (kHz)	4.22 ± 0.12	0.0839	16	0.7575
Interval between calls (s)	13.97 ± 7.45	−0.1624	15	0.5631

*Significant correlation.

There are various applications for information on call intensity. Values of SPL are important for guiding the choice of playback levels in behavioural studies, make possible estimation of the maximum distance over which intraspecific communication may occur, and as a first step in estimating the sound power output of the animal (Gerhardt 1975). The SPLs of calls determine spacing patterns of males in chorusing assemblages of various anurans (Brenowitz 1989; Penna and Solís 1998). The values obtained here for SPLs of *H. heyeri* are similar to those obtained by Penna and Solís (1998) and Guimarães and Bastos (2003) for other anuran species.

The duration of the advertisement call of *H. heyeri* showed a negative correlation with air temperature. A strong influence of temperature on acoustic patterns has been documented in many species of anurans (Sullivan and Malmos 1994; Giacoma et al. 1997; Navas and Bevier 2001). Guimarães and Bastos (2003) found a correlation of two temporal parameters (number and duration of the notes) with air temperature in *Hypsiboas raniceps* Cope, 1862. It is common to find relationships between repetition rate or interval between calls and air temperature (Sullivan and Malmos 1994; Giacoma et al. 1997; Navas and Bevier 2001), but we did not find this in *Hylodes heyeri*. Nevertheless, temperature seems to have a strong influence on the activity of *H. heyeri*, with males decreasing the duration of their calls at higher temperatures, probably to avoid increase of metabolic costs and greater energy expenditure.

In several species of anurans there is a positive correlation between the call intensity and body size of the vocalizing male (Arak 1983; Given 1988). According to Brenowitz (1989), the variability in the intensity of the call can reflect differences in the size of the body or other aspects of the condition of the males. This correlation was not apparent in other species (Ryan 1983; Penna and Solís 1998), including *H. heyeri*. The failure to detect an effect of body size on advertisement call intensity in this study may be the result of small sample size available or other complex variables that could be influencing call intensity. Among the difficulties involved in creating adequate measurements of call intensity is the potential for degradation of sound transmission caused by differences in the environment through which it is transmitted (Penna and Solís 1998; Kime et al. 2000).

Among anurans the dominant frequency of the advertisement call is generally inversely correlated to male size (Giacoma et al. 1997; Márquez and Bosch 2001). Sullivan and Hinshaw (1990) considered dominant frequency to be the only variable of the call that really provides any potential information about size of vocalizing males, and males in some species use this information to determine the fighting capability of opponents (Hoglund and Robertson 1988; Wagner 1992). However, in our study we found no correlation between dominant frequency and SVL for *H. heyeri*.

Within the genus *Hylodes*, our study is the second one to show the influence of air temperature on some aspects of acoustic communication. In *Hylodes phyllodes* Heyer and

Cocroft, 1986 a negative relationship between the number of calling males per hour and air temperature was demonstrated (Hatano et al. 2002). The same study also found that mean light intensity in the habitat was positively correlated with the mean number of calls per male. Apparently temperature could affect the acoustic activity of *Hylodes* species in various ways. More studies on acoustic activity of *Hylodes* are necessary to better understand the influence of biotic and abiotic factors on vocal patterns within this genus.

Acknowledgements

We thank José P. Pombal Jr and Luis M. Bini for helpful comments on an earlier version of the manuscript. Marcos Gridi-Papp helped with comments on methodology. Megan E. Gibbons helped with the English on an earlier version. Carina M. Lingnau and Rafael Costa helped occasionally with the fieldwork. R.L. acknowledges CAPES for a graduate fellowship. R.P.B. acknowledges CNPQ for a research fellowship. We are grateful to the Instituto Brasileiro do Meio Ambiente (IBAMA) for collecting permits (licence number 155/2001).

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