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Effects of Body Size and Environmental Factors on the Acoustic Structure and Temporal Rhythm of Calls in *Rhacophorus dennysi*

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Abstract In anurans, the outcomes of male-male contests and female choice are often associated with body size. In some species, males evaluate an opponent's fighting ability and females evaluate male quality on the basis of male communication signals, which are thought to reflect information concerning male body size. Nevertheless, previous studies reveal that male call structure is not always correlated with body size. In the present study we investigated the relationships between body size and call structure in the large treefrog, *Rhacophorus dennysi*, as well as the relationship of its calling behavior with air temperature and humidity. The results show that both the dominant and fundamental frequencies are negatively correlated with body size, while inter-note intervals are positively correlated with body size, indicating that call characters could reflect body size in this species. Additionally, calling in this tropical species exhibits a circadian rhythm insofar as relatively high temperature and low humidity during the day is associated with less vocal behavior. Thus, individual variations in call structure are mainly dependent on body size while the temporal rhythm of calling activity is affected by environmental conditions in large treefrogs.

Keywords advertisement call, body size, rhythm, temperature, humidity, *Rhacophorus dennysi*

1. Introduction

Males compete directly or indirectly with each other for access to females and/or resources (Darwin, 1871). For anuran amphibians, male-male competition and female choice mainly depend on acoustic communication (Gerhardt and Huber, 2002; Narins *et al*., 2006). Although the temporal and spectral characteristics of advertisement calls are species-specific, they can vary among populations and individuals (Ryan and Wilczynski, 1988, 1991; Wagner, 1989 a, b; Keddy-Hector *et al*., 1992; Wilczynski *et al*., 1992). In anurans, body size also greatly affects the outcomes of male-male contests and female choice. Larger males usually defeat smaller ones (Emlen, 1976; Given, 1988; Howard, 1978; Wagner, 1989 a; Wells, 1978), while females often prefer relatively larger males (Morris and Yoon, 1989).

Previous studies have shown that some call characteristics of anurans reflect the body size of males (Duellman and Trueb, 1986; Martin, 1972; Gerhardt, 1994). The fundamental frequency of anuran acoustic signals is partially determined by the shape and mass of the laryngeal apparatus, which is in turn related to body size (Duellman and Trueb, 1986; Martin, 1972; Robertson, 1986; Bee and Gerhardt, 2001). Call spectral properties are negatively correlated with body size in many species (Gerhardt, 1994). However, there is also empirical evidence that call properties may not reflect body size. In our previous study, we demonstrated that the calls made by male *Babina daunchina* from male-built nests convey information concerning nest structure rather than body size to the females (Cui *et al*., 2012). Moreover, no significant relationship between body size and call characters has been found for other burrowing frogs, such as *Metaphrynella sundana*, which actively exploit resonance properties of tree holes to alter their note duration (Lardner and bin Lakim, 2002, 2004), and

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Eupsophus emiliopugini, *E. calcaratus* (Penna and Solis, 1999; Penna, 2004), *E. calcaratus* and *E. roseus* (Márquez *et al*., 2005) in which some call acoustic properties are affected by burrows.

It is important to note that some male frogs alter the spectral properties of their acoustic signals during interactions with other males (Bee and Perrill, 1996; Bee *et al*., 1999; Given, 1999; Howard and Young, 1998; Lopez *et al*., 1988; Wagner, 1989, 1992). Bee *et al*. (1999) suggested that male green frogs (*Rana clamitans*) lower the pitch of acoustic signals in defense of territories as a possible dishonest signal of size. This result strongly suggests that the relationship between call characters and body size needs to be assessed in more species and in diverse taxa which possess various habitats. The present study seeks to advance our understanding of vocalization by focusing on the relationship between call characteristics and male body size in large treefrogs (*R. dennysi*). These large treefrogs have relatively large body size and produce loud advertisement calls during the breeding season from February to May in Hainan, a Chinese tropical island (Wang *et al*., 2007). Nevertheless, until now no studies of call acoustics have been carried out on this species.

Calling rhythm is an important behavioral characteristic which varies substantially among different species of anurans (Bevier, 1997; Bridges and Dorcas, 2000). For this reason, study on the initiation and maintenance of group calling behavior can provide insights into the factors affecting the evolution of such displays. Nevertheless, the factors affecting calling rhythms in anuran species are still not well understood. For anurans, climatic factors such as ambient temperature and humidity are often associated with the timing and intensity of reproductive activity which in both males and females are subject to energetic constraints and availability of water for laying eggs (Gerhardt and Huber, 2002). Thus, in the present study, we also investigated the diurnal rhythms of calling behaviors in male large treefrogs, and the possible relationship of their calling behaviors with air temperature and relative humidity.

2. Materials and Methods

2.1 Vocalization recording and body size measurement The experiments were conducted in the Mt. Diaoluo National Nature Reserve in Hainan, China (18.44° N and 109.52° E, elevation of 933 m a.s.l.) during April, 2011. The vocalizations of male *R. dennysi* were recorded using a directional microphone (Sennheiser ME66 with K6 power module) connected to a digital recorder (Marantz PMD 660, 16 bit, 44.1 kHz) about 1 m from the subjects from 20:00 to 24:00 h. To investigate possible relationships between vocalization characters and body size, the animals were captured, and their body mass and snout-vent length (SVL) were measured after the calls were recorded. The peak sound pressure levels (SPLs) of some calls were measured (A-weighted) with a sound level meter (AWA 6291, Hangzhou Aihua Instruments Co., Hangzhou) held about 1 m from the subject. To investigate the rhythm of the call activities, the vocalizations of male frogs were recorded continuously for 24 h per day from 25 to 29 April, 2011, using an Aigo R5518 recorder with internal microphone (Aigo Digital Technology Co. Ltd., Beijing). The recorder was placed in 5 different sites located approximately 500 m apart on each of 5 different days to ensure adequate sampling of different males. The animal treatment procedures were approved by the Animal Care and Use Committee of the Chengdu Institute of Biology, Chinese Academy of Sciences.

2.2 Measurements of temperature and relative humidity Ambient temperature and relative humidity were sampled automatically every half hour using a TP220 temperature and relative humidity recorder (Beijing Anfu Electronic Technique Co., Beijing), which was placed close to the sound recorder. These data were then stored on the hard drive of a computer after all the experiments were completed.

2.3 Analysis and statistics Three clean calls (no overlap with or contamination by other animal sounds) for each male were obtained from the recordings and the acoustic properties of these calls were measured for statistical analysis. The amplitude modulated waveforms (oscillograms) and sonograms of calls were prepared using free PRAAT software (Boersma and Weeninkk, Version 5.1.11, University of Amsterdam). The calls consisted of 3–5 notes which are short discrete sounds produced in succession. The notes and call renditions were enumerated manually using Adobe Audition 3.0 (California, USA) software, and the numbers of calls/30 min and notes/30 min were enumerated.

Data were statistically analyzed using Sigmaplot 11.0 software (Systat Software Inc., Chicago, USA). Prior to the statistical analyses, all data were examined for assumptions of normality and homogeneity of variance, using the Shapiro-Wilk and Levene tests, respectively. Pearson or Spearman's correlation analysis was used to detect possible relationships among the variables.

One way repeated measures ANOVA was employed to evaluate the differences in dominant frequency (DF), fundamental frequency (FF), and note duration (ND) among call notes, and the Holm-Sidak method was used for *post hoc* comparisons between different notes. Wilcoxon Signed Rank Test was used to evaluate the differences in inter-note intervals (IVs). The data were expressed as mean ± SD, and $P < 0.05$ was considered to be statistically significant.

3. Results

3.1 Acoustic structure of advertisement calls All the frogs recorded in this study lived on shrubbery, banana tree or grass (*Andropogon chinensis*) during the breeding season. The males usually produced loud advertisement calls antiphonally (Figure 1). The mean peak SPL of the advertisement calls of 4 males was 77 ± 2 dB (weighted, re 20 µPa measured 1 m from the subjects) and the background noise was 47 ± 9 dB (Measured with an AWA 6291 sound level meter). Occasionally, when two males approached closely the males produced relatively low amplitude aggressive calls which were composed of fast clicks (Figure 1). Since the aggressive calls did not occur frequently and the amplitude was very low compared to the relatively higher background noise in the field (47 ± 9 dB), we failed to record enough samples of aggressive calls for analysis. The advertisement calls of 27 males were recorded successfully. The call properties of the advertisement calls are summarized in Table 1. Most male advertisement calls were composed of 3–5 notes, with the average note number being 3.5 ± 0.6. The durations of the notes varied substantially among calls ranging from 19.7 ms to 83.3 ms ($F_{2,52} = 43.2$, $P < 0.001$). The duration of the first note was 40.6 ± 6.9 ms, which is much shorter than that of the second (54.9 ± 11.5 ms, $P < 0.001$) and the third notes (55.5 ± 11.5 ms, $P < 0.001$), while the inter-note interval (IV) between the first and second notes (IV1) was longer than that between the second and third notes (IV2) (Z-Statistic = –4.337, $P < 0.001$)). In the frequency domain, there were significant inter-note differences for both the DF ($F_{2,52} = 63.2$, $P < 0.001$) and FF ($F_{2,52} = 8.14$, $P < 0.001$). The DF of the first note was 1266.9 ± 75.9 Hz which was significantly lower than that of the second (1360.6 ± 77.9 Hz, $P < 0.001$) and the third notes (1337.8 ± 64.6 Hz, $P < 0.001$). The FF of the first, second and third notes were 625.8 ± 64.6 Hz, 638.2 ± 19.7z and 641.4 ± 18.2 Hz, respectively (Table 1).

3.2 Relationship between body size and call structures Correlation analysis was used to determine if male call characteristics including FF, DF, ND and IV were associated with body size. The mean male body mass and SVL of *R. dennysi* were 39.5 ± 6.9 g and 87.6 ± 5.3

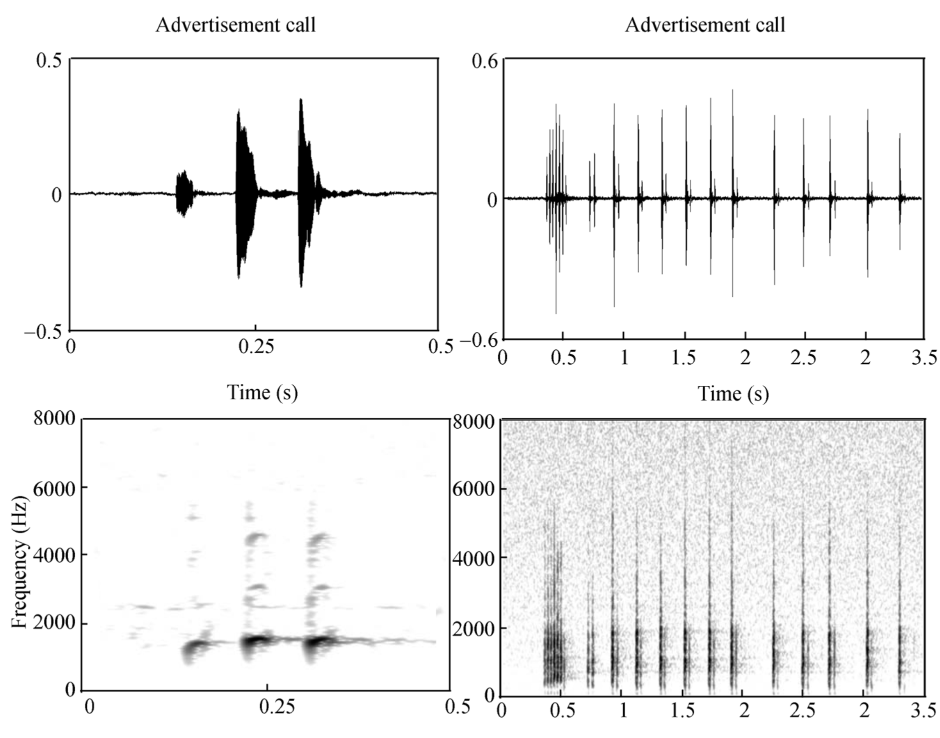

Figure 1 Amplitude-modulated waveform and spectrogram of a typical male advertisement call and aggressive call of *R. dennysi*. The FFT (faster fourier transformation) frame is 1024.

mm, respectively (n = 27) (Table 1). The DF and FF were negatively correlated with body mass and SVL (Table 2). The IV was positively correlated with body mass, while there was no significant correlation between body mass or SVL and ND (Table 2; Figure 2).

Table 1 Body size and call properties of male *R. dennysi*.

	Sample size	Mean	Std dev	Max	Min
Body mass (g)	27	39.5	6.9	52.0	27.5
SVL (mm)	27	87.6	5.3	96.0	76.0
Note number	27	3.5	0.6	5.0	3.0
DF1 (Hz)	27	1266.9	75.9	1392.3	1090.3
DF2 (Hz)	27	1360.6	77.9	1521.3	1248.0
DF3 (Hz)	27	1337.8	64.6	1492.7	1233.7
FF1 (Hz)	27	628.5	22.7	645.0	559.0
FF2 (Hz)	27	638.2	19.7	674.3	587.7
FF3 (Hz)	27	641.4	18.2	674.3	587.7
ND1 (ms)	27	40.6	6.9	53.3	19.7
ND2 (ms)	27	54.9	11.5	83.0	37.3
ND3 (ms)	27	55.5	11.5	83.3	37.7
IV1 (ms)	27	47.5	9.5	63.3	17.3
IV2 (ms)	27	37.0	11.4	54.0	12.3

Note: DF1, DF2 and DF3 represent the dominant frequencies of the first, second and third notes of the calls; FF1, FF2 and FF3 represent the fundamental frequencies of the first, second and third notes of the calls; ND1, ND2 and ND3 represent the note durations of the first, second and third notes of the calls; and IV1 and IV2 represent the intervals between the first and second notes and between the second and third notes, respectively. The same below.

3.3 Calling behavior and environmental factors Call rate (i. e., calls per 30 min and notes per 30 min) varied across 24 h (Figure 3 A, B). Male *R. dennysi* called from 18:30 h to the next 06:30 h, and ceased calling during the period from 07:00 h to 18:00 h. The peak call activity occurred at about 19:30 h. Air temperature varied significantly during the day (Figure 3 C), with relatively high air temperatures apparently occurring during the period from 07:00 h to 20:30 h. The air temperature increased continually from 07:00 h to 10:00 h, where it remained relatively stable till 14:00 h before rapidly decreasing at 20:30 h. Relative humidity varied inversely with temperature and also varied significantly within 24 h cycle (Figure 3 D). Relative humidity usually approached 100% from 18:30 h to 06:30 h, during which calling occurs.

4. Discussion

Three hundred and eighty nine different amphibian species have been identified in China, reflecting the vastness of the territory and highly diverse landforms, of which 262 species are endemic to China (Hu *et al*., 2012). However, surprisingly few studies have investigated the

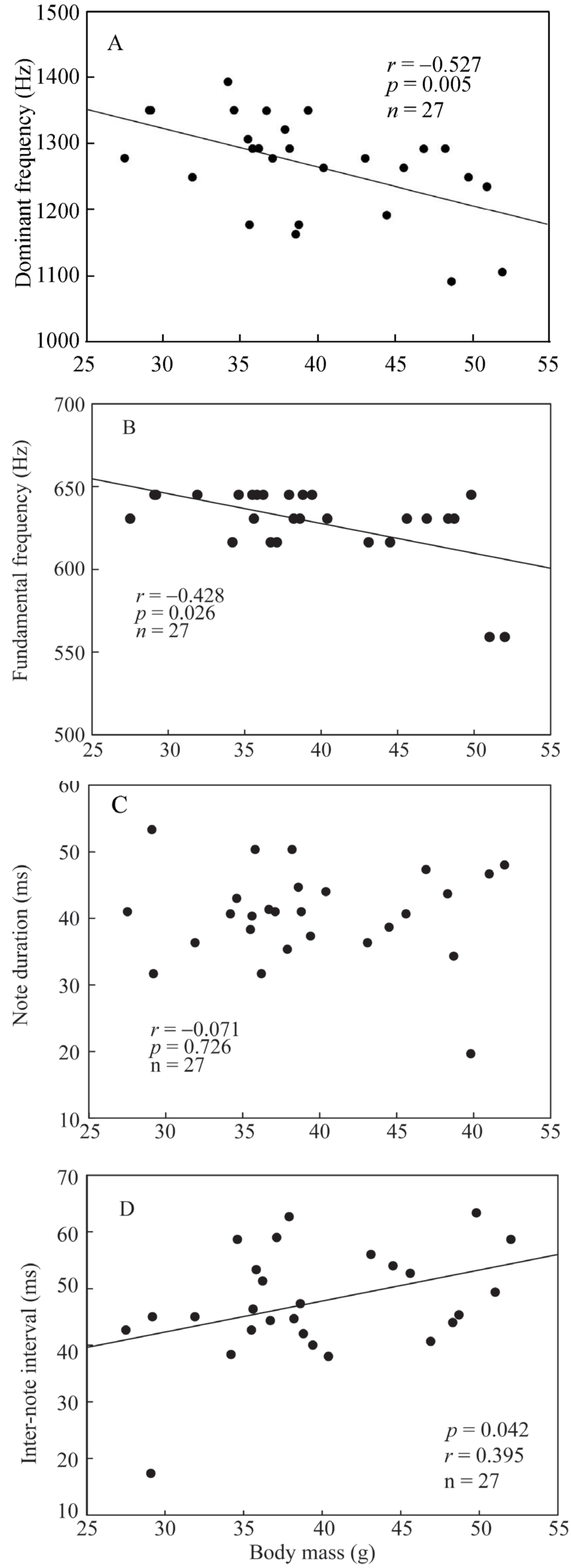

Figure 2 Relationship between body mass and dominant frequency (A), fundamental frequency (B), note duration (C) and inter-note interval (D) for *R. dennysi.*

Table 2 Results of a correlation analysis between call properties and body size.

	BM	SVL	ND1	ND2	ND3	IV1	IV2	DF1	DF2	DF3	FF1	FF2	FF3
BM		0.86	0.07	0.11	0.23	0.40	0.42	0.53	0.44	0.42	0.43	0.48	0.28
		< 0.001	0.73	0.57	0.25	0.04	0.03	0.01	0.02	0.03	0.03	0.01	0.16
SVL			0.13	0.25	0.36	0.13	0.33	0.55	0.53	0.58	0.37	0.60	0.12
			0.51	0.20	0.07	0.52	0.09	0.00	0.00	0.00	0.06	0.00	0.54
ND1				0.44	0.35								
				0.02	0.07								
ND2					0.89								
					< 0.0001								
IV1							0.54						
							0.00						
DF1									0.85	0.80			
									< 0.001	< 0.001			
DF2										0.85			
										< 0.001			
FF1												0.67	0.63
												< 0.001	< 0.001
FF2													0.59
													< 0.001

Note: Upper values in each row show correlation coefficients (*r* values), and the numbers below the coefficients are *P* values. BM: Body mass; SVL: snout-vent length.

call characteristics of Chinese frog species (Jiang *et al*., 2002; Xu *et al*., 2005; Shen *et al*., 2008, 2010; Yu and Zheng, 2009; Cui *et al*., 2010, 2011, 2012; Wei *et al*., 2012; Xu *et al*., 2012). More such studies on acoustic communication in Chinese anuran species are needed to investigate the evolution of calling behavior. In the present study, we explored the detailed characters of male advertisement calls and analyzed the relationships between call characters and body size, as well as the relationship between calling rhythms and climate factors in *R. dennysi* in Hainan, China. The results show that the FF and DF of the first note of *R. dennysi* calls are about 628 Hz and 1267 Hz, respectively. These values are apparently lower than those of the other two studied species, *R. omeimontis* and *R. chenfui*, in the same genus, with the FF and DF being about 1050 Hz and 2300–2900 Hz for *R. omeimontis* and 1250 Hz and 2000–2349 Hz for *R. chenfui*, respectively (Matsui and Wu, 1994).

Differences in DF and FF values for *Rhacophorus* species might be due to the inter-species differences in body size. The mean body sizes of male *R. omeimontis* and *R. chenfui* are 52–66 mm and 33–41 mm, respectively (Fei *et al*., 2010), which are much smaller than *R. dennysi* (ranging between 76–96 mm, 87.6 ± 5.3 mm). Notably, the weak frequency modulation within notes (Figure 1) and increasing frequency among the notes (Figure 1; Table 1) were observed in *R. dennysi* and have also been reported for *R. omeimontis* and *R. chenfui* (Matsui and Wu, 1994). These features may, therefore, reflect the common male call characteristics of the genus *Rhacophorus*.

As described above, DF and FF were significantly negatively correlated with body size in *R. dennysi* (Figure 2, Table 2). This is consistent with the results from many anuran species, indicating that FF is correlated with the body size of individual males (Keddy-Hector *et al*., 1992; Gerhardt, 2005). Our results showed that the IV was positively correlated with the body size in *R. dennysi* (Figure 2). Given that the note duration is relatively stable in this species, increased IV will result in longer calls which may be metabolically costly reflecting greater body size. Thus, the correlation between size and IVs reported here suggests that IV may be an important signal facilitating male-male competition and mate choice. In male cricket frogs (*Acris crepitans*), both the spectral and temporal call parameters are biomechanically related to laryngeal size which is, in turn, largely determined by body size (Mcclelland *et al*., 1996). These results support the idea that the call characters of anuran males can provide information about body size which would enhance the ability of males to evaluate an opponent's fighting ability (Arak, 1983; Bee *et al*., 1999; Davies and Halliday, 1978; Given, 1987; Ramer *et al*., 1983; Robertson, 1986; Wagner, 1989) and the ability of females to evaluate the potential mate's quality on the basis of the acoustic features of male communication signals (Morris and Yoon, 1989). However, in some species, male frogs can alter spectral properties of their acoustic signals

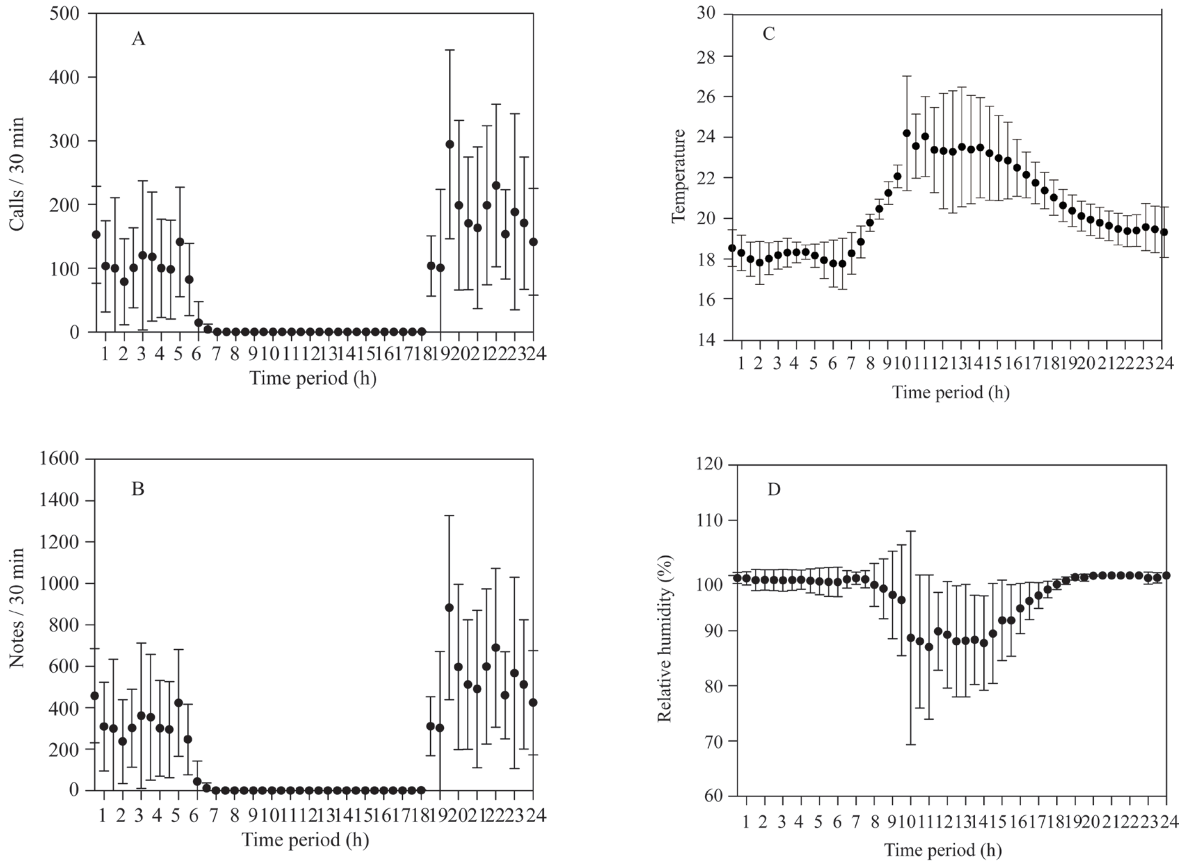

Figure 3 Diurnal variations in calls/30 min (A), notes/30 min (B), temperature (C), and relative humidity (D) (Mean ± SD).

during interactions with other males (Bee and Perrill, 1996; Bee *et al*., 1999; Given, 1999; Howard and Young, 1998; Lopez *et al*., 1988; Wagner, 1989, 1992) or alter the spectral properties of their acoustic signals by exploiting the resonant properties of the tree hole or burrow they inhabit (Lardner and bin Lakim, 2002; Cui *et al*., 2012). Future work using playback experiments would be required to determine if male *R. dennysi* can alter the spectral properties of calls.

Comparatively, little is known about the ecology and calling behavior in *R. dennysi* (Wang *et al*., 2007). In the present study, the circadian pattern of calling behavior and the relationship of male calling with temperature and humidity were investigated. We found that the calling behavior of male *R. dennysi* showed typical day-night circadian rhythms. Male *R. dennysi* called at night from 18:30 h to the next 06:30 h, and ceased calling at day time from 07:00 h to 18:00 h, with peak call activity occurring at about 19:30 h (Figure 3 A, B). This calling pattern is consistent with diurnal variations in air temperature and relative humidity (Figure 3 C, D). These results suggest that the calling behavior of large treefrogs is strongly affected by air temperature and relative humidity, as has been found for other frog species (Navas, 1996; Wong *et al*., 2004; Saenz *et al*., 2006; Cui *et al*., 2011).

In many anuran species, calling behavior exhibits distinctive circadian patterns across the 24-h cycle and the patterns differ substantially among species. Bevier (1997) found considerable variation in tropical anurans in Panama, and Runckle *et al*. (1994) found that the calling of *Hyla versicolor* peaked in early evening. Given (1987) reported that the calling activity of *Rana virgatipes* peaked around midnight, and Shimoyama (1989) reported that *R. porosa* called more frequently after midnight than before midnight. In a temperate species, *Babina daunchina*, vocal activity continues for 24 h on most days and the peak of calling activity is closely associated with the temperature peak (Cui *et al*., 2011). In contrast, for the tropical species *R. dennysi*, relatively higher temperature and lower humidity inhibit calling behavior. Based on our results, together with those from previous studies, we propose that in tropical environments, temperature can be an ecological constraint for continuous signaling during the day, so that signaling commences in the evening when temperature falls (Gerhardt and Huber, 2002), while in some temperate species relatively higher temperature and lower humidity facilitate the chorus (Cui *et al*., 2011). Additional work is needed to test the generality of this hypothesis by comparing the calling behaviors of different populations of the same species dwelling in temperate and tropical areas. Moreover, other factors such as photoperiod and light intensity are also likely to affect the rhythm of calling behavior, which also deserves further study.

In conclusion, in large treefrogs the DF and FF are negatively correlated with body size, while the IV is positively correlated with body size. These results support the idea that call characters reflect information concerning body size, which could facilitate decision making related to male-male competition and female selection. Furthermore, call activity reflects an apparently circadian rhythm in which relatively higher temperature and lower humidity may inhibit calling in the tropical species *R. dennysi*. These results support the general conclusion that the variations in call structures are mainly dependent on body conditions, while the temporal rhythm of calling activity in frogs is affected by environment conditions.

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