



A male *Rhinophrynus dorsalis* Duméril & Bibron, 1841 (Anura: Rhinophrynidae) calling at an ephemeral pond (ca. 7 × 2 m, 0.50 m deep) in Tropical Dry Forest at Área de Conservación Guanacaste, Sector Santa Rosa, Costa Rica, elev. 298 m, on 25 May 2013. Compared with other amphibian species, this frog undergoes one of the shortest explosive breeding seasons, which lasts from one to a few nights. In the following study, breeding was a single night event that occurred in the study area after the first heavy rains of the year. 📷 © Gilbert Barrantes



Sexual size dimorphism and acoustical features of the pre-advertisement and advertisement calls of *Rhinophrynus dorsalis* Duméril & Bibron, 1841 (Anura: Rhinophrynidae)

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ABSTRACT: The interaction among natural selection, sexual selection, and species-specific ecological requirements is responsible for the evolution of complex courtship behaviors and breeding strategies. In some anurans, the breeding season is restricted to a short period each year (explosive breeders). *Rhinophrynus dorsalis* is a species with one of the shortest breeding seasons among amphibians, and this condition imposes some constraints on its courtship behavior and pair formation. Herein, we provide a quantitative description of the acoustic characteristics of calls produced by males, as well as the behavior of males and females displayed during the vocalization period. We also assessed the individual distinctiveness of the acoustic characteristics of the advertisement call, and measured the body size of males and females in amplexed pairs. Males produced two types of calls during their acoustical display: pre-advertisement and advertisement calls. We recorded and describe the pre-advertisement call for the first time in this species. Males can be identified by a unique combination of the spectral and temporal features of the advertisement call. Additionally, center frequency (the frequency where the energy interval of a sound is divided into two equal parts) correlates negatively with male size, and females might use this characteristic of male calls to select the size of males. We did not detect male-male aggressive interactions during pair formation or the vocalizing period, and thus female choice likely is based primarily on the acoustical features of the male call, as it occurs in other anuran species with explosive breeding. Females were larger than males, and larger females tend to be found in amplexus with larger males.

Key Words. Explosive breeders, individual call variation, *Rhinophrynus dorsalis*, sex dimorphism, vocalization descriptions

RESUMEN: Las interacciones entre selección natural, selección sexual, y los requerimientos ecológicos específicos de las especies son responsables de la evolución de comportamientos complejos de cortejo y estrategias reproductivas. En algunos anuros el periodo reproductivo está restringido a un periodo corto cada año (reproducción explosiva). *Rhinophrynus dorsalis* es una especie con una de las épocas reproductivas más cortas entre los anfibios y esta condición impone algunas restricciones sobre el comportamiento de cortejo y formación de la pareja. Aquí describimos cuantitativamente las características de las llamadas producidas por los machos y el comportamiento de los machos y hembras durante el periodo de vocalización. Adicionalmente, evaluamos la variación individual de las características de las llamadas de anuncio y medimos el tamaño del cuerpo de machos y hembras en amplexo. Los machos produjeron dos tipos de llamadas durante el cortejo: la llamada de pre-anuncio y la llamada de anuncio. Esta es la primera descripción de las llamadas de pre-anuncio en esta especie. Los machos pueden ser identificados

individualmente por una combinación de las características de la frecuencia y duración de la llamada de anuncio. Adicionalmente, la frecuencia central (frecuencia donde el intervalo de energía del sonido es dividido en dos partes iguales) se correlacionó negativamente con el tamaño del macho, y esta característica podría ser utilizada por las hembras para seleccionar el tamaño del macho. No detectamos interacciones agresivas entre machos durante el periodo de formación de parejas o de vocalización, y probablemente la elección de los machos por las hembras está basada en las características de las llamadas, como ocurre en otras especies de anuros con reproducción explosiva. Las hembras fueron más grandes que los machos, y las hembras más grandes fueron encontradas como machos de mayor tamaño en amplexo.

Palabras Claves: Descripción de vocalizaciones, dimorfismo sexual, reproductores explosivos, *Rhinophrynus dorsalis*, variación individual de llamadas

Citation: Sandoval, L., G. Barrantes, D. Ocampo, and C. Sánchez-Quirós. 2015. Sexual size dimorphism and acoustical features of the pre-advertisement and advertisement calls of *Rhinophrynus dorsalis* Duméril & Bibron, 1841 (Anura: Rhinophrynidae). *Mesoamerican Herpetology* 2: 154–166.

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Received: 21 May 2015; **Accepted:** 5 June 2015; **Published:** 18 June 2015.

INTRODUCTION

The evolution of courtship behavior and breeding strategies has been driven by multiple factors (Emlen, 2008). The role of intra- and inter-sexual selection on the evolution of complex courtship behaviors and breeding strategies is undeniable (Andersson, 1994). Ecological factors (e.g., seasonal distribution of resources, predation, and weather), however, may affect the access to mates (Clutton-Brock and Harvey, 1978). For instance, the particular ecological conditions that a large number of anuran species require for reproduction limit the range of possibilities within which intra- and inter-sexual interactions occur (Zamudio and Chan, 2008).

The breeding season of a large number of anurans is reduced to a short period each year (i.e., explosive breeders), but even within explosive breeders the length of the short reproductive period often determines the strategy followed by females to select males, and that of males to access females (Licht, 1976; Davies and Halliday, 1979; Woolbright, 1983). In males of explosive breeding species, access to females is expected to decrease with the number of individuals and the time involved in physical agonistic interactions, reducing the reproductive success of those individuals that more often engage in such interactions. Therefore, anuran males with explosive and very short breeding seasons tend to be involved in fewer agonistic interactions with other males (Emlen and Oring, 1977), and female choice is based on the information conveyed by the acoustical displays of males (Licht, 1976; Ramer et al., 1983) rather than by male-male physical combats or territorial characteristics (Berven, 1981), although some exceptions are known, e.g., *Pyxicephalus* frogs (Shine, 1997).

The operational sex ratio (OSR) at the moment of reproduction may change the intensity of male-male competition in explosive breeders (Lodé et al., 2005; Zamudio and Chan, 2008). Wells (1977) proposed that male-male competition is relatively low in anuran explosive breeders. The available data for a few anurans, however, is contradictory (Ryan, 1985). The intensity of male-male competition in explosive breeders is expected to be high if the OSR is strongly male-biased, but competition would decrease as the OSR levels off. Male-male competition in explosive breeders also might be intensified by female choice, e.g., selection of large males (Gatz, 1981), although sexual selection in explosive breeders is thought to be low (Emlen and Oring, 1977).

In numerous anuran species some features of the male advertisement call (e.g., fundamental frequency) are correlated with male size (Ryan, 1980; Morris and Yoon, 1989; Andersson, 1994), and females prefer larger males for mating (Gerhardt and Huber, 2002). Growth in anurans is indeterminate, and therefore large males tend to be older and their size may reflect a better capability to survive and/or to obtain better resources (Flowers and Graves, 1995), or the capability to fertilize more eggs (Ryan, 1980). Thus, although in most explosive breeders females are larger than males (Woolbright, 1983), it still is advantageous for females to choose larger males. Females also might select male size in proportion to their own body size, to closely match the position of the two cloacae during spawning (Robertson, 1990).

In the literature, *Rhinophrynus dorsalis* often has been referred to as a frog or a toad, and popular common names for this species include Burrowing Toad, Cone-nosed Frog, and “El Sapo Borracho” (The Drunken Toad). In Costa Rica, this anuran inhabits Tropical Dry Forest, where it remains underground practically year round. This species emerges for breeding with the first heavy rains of the year, when large numbers of individuals gather in ponds. Males then call while floating on water or sitting partially submerged in shallow water, and within a few hours most males in the pond engage in pelvic amplexus with females (Foster and McDiarmid, 1983). The annual breeding event lasts from one to a few nights in a given pond, after which individuals burrow and remain underground until the next breeding event (Leenders, 2001; Savage, 2002). Other aspects of courtship and reproductive biology (e.g., pair formation, female choice, and acoustic characteristics of male calls) of *R. dorsalis* are unknown. Within anurans, *R. dorsalis* undergoes a short and explosive breeding season, comparable to that of such species as *Anaxyrus americanus*, *Incilius luetkenii*, and *Lithobates sylvaticus*, which have a breeding season that lasts only for a few days (Woolbright, 1983; Savage, 2002). Thus, considering that *R. dorsalis* is one of the most unusual and relatively unknown anuran species in Mesoamerica, herein we provide a quantitative description of the acoustic characteristics of male calls, including a previously unknown type of call. Additionally, we question if the spectral and temporal features of the advertisement call can provide enough information for male identification and discrimination among males of different sizes. Attaining both of these conditions would suggest the possibility of female choice (e.g., larger males) based on acoustical features of the advertisement call (Ryan, 1985). Finally, we evaluate the body size relationship between amplexant males and females.

MATERIALS AND METHODS

Recording Methods

We recorded the vocalizations of *Rhinophrynus dorsalis* on 25 May 2013, from 1920 to 2030 h, in a single pond (ca. 7 × 2 m, 0.50 m deep) located in the Tropical Dry Forest at Área de Conservación Guanacaste, Sector Santa Rosa, Provincia de Guanacaste, Costa Rica (10°50'N, 85°37'W; WGS 84; elev. 298 m). We recorded a total of 12 males using a Marantz PMD 661 digital recorder and a shotgun microphone Sennheiser ME66/K6 (recording format: WAVE; sampling rate: 44.1 kHz; accuracy: 16 bits). We captured and measured six males (snout–vent length; SVL); the other six males swam into deeper water after we recorded their vocalizations, and in order to avoid disturbing the other calling males at the site we did not attempt to capture them. No temperature or humidity corrections were conducted in the analysis, because the weather conditions were constant (22.7°C and 98% of humidity during the recording period; Instituto Meteorológico Nacional de Costa Rica). We recorded the vocalizations by placing the microphone 5–10 cm in front of the snout of each male, to avoid acoustic interference from other calling individuals; often, however, some males were calling within 10 cm from the focal individual. The clipping and distortion that this approach might produce in the recordings due to saturation of the microphone membranes was negligible when visually comparing the structure of the vocalizations in the spectrograms recorded at different distances (5–10 m) from the focal individual. To reduce saturation on the recordings, we manually adjusted the recording volume in the field. Each male was recorded continuously for 1.1–5 min. All the recordings were deposited in the Laboratorio de Bioacústica, Escuela de Biología, Universidad de Costa Rica.

Body Size

We captured all the amplexed pairs ($n = 15$) pairs of *R. dorsalis* from a single pond, and in both sexes measured their SVL to evaluate sexual dimorphism.

Vocalization Measurements

We classified the vocalizations of *R. dorsalis* visually by using the anurans' appearance on sound spectrograms and the behavioral context in which they vocalized. We took all measurements by using a combination of the spectrogram screen, the power spectrum, and the waveform screen in the Raven Pro 1.4 sound analysis software (Cornell Lab of Ornithology, Ithaca, New York, United States). This approach allowed us to obtain more accurate measurements of the sounds (Redondo et al., 2013), because the power spectrum and the waveform screen are not affected by the settings on the gray-scale in the spectrogram screen (Charif et al., 2004). We used the following settings in Raven to obtain the measurements: a temporal resolution of 5.8 ms, frequency resolution of 188 Hz in a Hann window with 256 kHz sampling and 50% overlap. We counted the total number of vocalizations produced by each male during the recording time to estimate the vocalization rate.

We took seven fine-structural measurements in 490 vocalizations (464 advertisement calls and 26 pre-advertisement calls) that were not overlapped by other sounds. This large sample size reduces the possible effect of differences between recording conditions in the values of minimum and highest frequency. All acoustic measurements were taken by one of us (LS) with experience measuring vocalization in different animal groups. In each vocalization we measured the following: (1) the duration in s; (2) the standardized peak time in s (the time when the first maximum amplitude frequency occurred); (3) the minimum frequency in Hz; (4) the highest frequency in Hz; (5) the maximum amplitude frequency in Hz; (6) the center frequency in Hz (the frequency where the energy interval of a sound is divided into two equal parts); and (7) the average entropy in μ (this describes how the energy in a sound is distributed, and provides basic information of the transmission properties of the sound; sounds with low entropy values transmit better than sounds with high entropy values; Bradbury and Vehrencamp, 2008). Additionally, we measured the duration of inter call intervals.

We randomly selected a subset of four calls per minute in each male recording, and in the event that within one minute there were four or less calls, we used all the calls to trace the maximum amplitude frequency of each vocalization over time (pitch tracking; Charif et al., 2004). For pitch tracking we used segments of 0.05 s. We estimated the relative position where the first change in the frequency occurred proportionally to the total duration of the call (values close to 0 indicate that the inflexion occurred close to the beginning of the call, and values close to 1 indicate that it occurred close to the end of the call).

Statistical Analyses

We conducted a backwards stepwise discriminant function analysis (DFA) to compare the vocalization characteristics across males. We used this analysis to select the least number of the seven fine-structural measurements that explained the largest amount of variation between males (Sandoval and Escalante, 2011). We reported the explained variance using jackknife cross-validation in SYSTAT (version 11.00.01; SYSTAT Software, Chicago, Illinois, United States). To describe the individual distinctiveness based on the fine-structural measurements of advertisement calls, we used the potential for individual coding method (PIC; Vignal et al., 2004). This method has been used to describe individual distinctiveness in bird songs (e.g., Vignal et al., 2004; Seddon and Tobias, 2009; Sandoval et al., 2014), and also in frogs (e.g., Gasser et al., 2009; Bee et al., 2013). For this method, we compared the variation in the fine-structural measurements within (CV_w) and between males (CV_b), and then estimated the ratio between both coefficients of variation ($PIC = CV_b/CV_w$); PIC scores > 1.0 have a potential for individual discrimination. We used a student's t -test to compare the variability between CV_b and CV_w . We conducted a linear regression between the sizes of captured males versus the mean of the fine-structural measurements of advertisement calls produced by each male. We estimated if the change in the trace of the maximum amplitude frequency is related to the call duration by using a linear model in which male identity was included as a random factor to consider the effect of using several calls from the same male.

We compared the size of males and females in amplexed pairs by using a paired *t*-test, and correlated the body size of the female and male in amplexing pairs with a Spearman correlation test. Finally, we compared the size between calling males (single males) and amplexed males using a student's *t*-test. We conducted statistical analyses in SYSTAT and JMP (version 7.0; SAS Institute, Cary, North Carolina, United States), and reported all results as mean \pm SD.

RESULTS

Behavior in *Rhinophrynus dorsalis*

We counted ca. 50 *Rhinophrynus dorsalis*, 15 *Hypopachus variolosus* (Microhylidae), four *Smilisca baudinii* (Hylidae) and two *Incilius luetkenii* (Bufonidae) in the small pond. Most (if not all) of the male *R. dorsalis* were calling when we arrived at the pond (1920 h), so they dominated the acoustical environment. This reproductive event occurred after the first heavy rains of the year, which occurred after an extremely long dry season that lasted more than six months. At least two-thirds of the males were calling while floating on the water (Figs. 1A, B), and the remaining males called from near the edge of the pond while partially submerged. The body of the males quivered in slow motion from the nose to the vent as they released the air and produced the call; additionally, when males produced their calls the water surrounding their body vibrated (Fig. 1C).

When we arrived at the site, only three pairs of *R. dorsalis* were observed in amplexus (pelvic amplexus), but the number of amplexant pairs increased over the next hour. Several mating pairs swam underwater for a few minutes (Fig. 1d), presumably for the female to lay eggs (Foster and McDiarmid, 1983). During our recording period, we did not observe any agonistic interaction between males that were calling or with those engaged in amplexus. On one occasion, however, we observed two males swimming in the same direction but the smaller male changed direction and made contact with the larger male, but we saw no further interactions. In a second instance, we observed a pair in amplexus when a second male tried to amplex the same female. The following day it did not rain, and that night we did not see or hear a single *R. dorsalis* in the studied pond or in nearby ponds. Females were larger (= longer in SLV; 81.0 ± 6.0 mm, $n = 15$) than males (72.1 ± 6.0 mm, $n = 21$), and amplexed females were larger than the males in all pairs (paired *t*-test: $t_{14} = 6.66$, $P < 0.001$). For amplexed pairs, on average the females were 14% ($\pm 8\%$) larger than males and larger females were amplexed by larger males (Spearman correlation: $r = 0.57$, $P = 0.027$, $n = 15$ pairs). Male size was similar between calling males (74.5 ± 5.7 mm) and amplexed males ($t_{20} = -1.38$, $P = 0.18$).

Acoustical Analyses

We recorded two types of vocalizations produced by male *R. dorsalis*. Porter (1962) named the main vocalization type a "mating call," which was renamed by Wells (2007) as an "advertisement call," but since then no additional spectrographic analysis of this vocalization or of the calling behavior has been published. All the males recorded produced this vocalization; in total, we analyzed 464 advertisement calls. The second type of vocalization we observed has not been reported, and thus we named it a "pre-advertisement call" because some males produce it just before they produced the advertisement call. We recorded this vocalization in four males, and analyzed 26 pre-advertisement calls (6.5 ± 5.9 pre-advertisement calls per male).

Description of Advertisement Call

The advertisement call consisted of a single tone with an upward modulation having an inflexion near the midpoint of the call duration (0.49 ± 0.12 s) (Fig. 2). Advertisement calls had a duration of 1.36 ± 0.12 s, peak time of 1.33 ± 0.13 s, minimum frequency of 171.61 ± 17.75 Hz, highest frequency of 775.61 ± 136.39 Hz, maximum amplitude frequency of 401.15 ± 66.83 Hz, center frequency of 396.7 ± 43.30 Hz, and average entropy of 1.69 ± 0.20 μ . Males produced 11.78 ± 5.01 advertisement calls per minute. The interval between advertisement calls was 4.03 ± 7.44 s.

The maximum amplitude frequency increased 86.1 Hz or by a multiple of that value over time. Eleven males started all the advertisement calls analyzed at 344.5 Hz, and one male started five of the 16 analyzed advertisement calls at 258.4 Hz and the rest at 344.5 Hz; it then increased up to 775.2 Hz; this change in frequency averaged 225.11 ± 142.37 Hz. The duration of the call, after controlling by the effect of the singing male, did not show a significant correlation with the frequency change on the advertisement call ($r^2 = 0.46$, $F_{1,150} = 2.61$, $P = 0.11$).

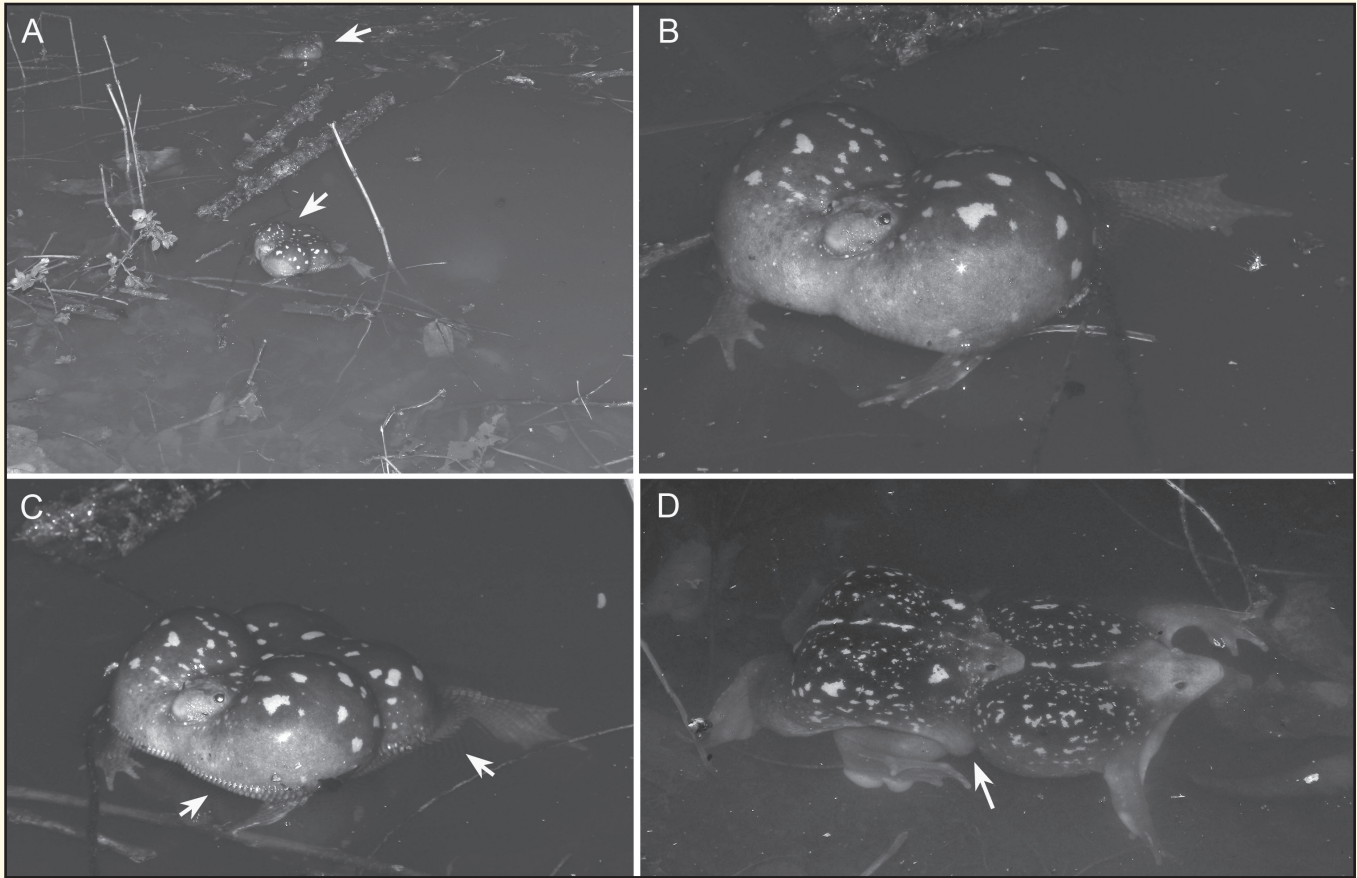


Fig. 1. Behavior of *Rhinophrynus dorsalis*. (A) Two males calling while floating in a small ephemeral pond; (B) male with the vocal sacs fully inflated before initiating a call; (C) male releasing the air as it calls (arrows depict the vibration of water around the body); and (D) pair in amplexus swimming underwater (note the right arm of the male grabbing the female around her pelvis).

Description of Pre-advertisement Call

The pre-advertisement call consisted of a single short sound without modulation, shorter and with higher frequencies than the advertisement calls (Fig. 3). The pre-advertisement calls had a duration of 0.25 ± 0.09 s, peak time of 0.24 ± 0.09 s, minimum frequency of 365.93 ± 67.63 Hz, highest frequency of 1014.53 ± 176.29 Hz, maximum amplitude frequency of 616.19 ± 90.16 Hz, center frequency of 626.12 ± 62.40 Hz, and average entropy of 2.04 ± 0.30 μ . Males produced 28.44 ± 15.40 pre-advertisement calls per minute. The interval between the pre-advertisement calls was 2.46 ± 7.10 s, based on two males with 10 and 13 vocalizations of this type recorded. Both males produced a series of pre-advertisement calls prior to switching to the advertisement calls, or to stop vocalizing.

Individual Variation

The advertisement calls of male *R. dorsalis* varied widely among individuals (Wilks' $\lambda = 0.02$, $F_{44,1723} = 68.45$, $P < 0.001$, Fig. 4) with a cross validation of 61%, using four of the fine-structural measurements: highest frequency, center frequency, maximum amplitude frequency, and average entropy. All the fine-structural measurements of advertisement calls showed PIC scores ≥ 1.0 , suggesting a potential for individual distinctiveness (Table 1). After correcting for multiple comparisons, only four variables showed high individual variation (highest frequency, maximum amplitude frequency, center frequency, and average entropy).

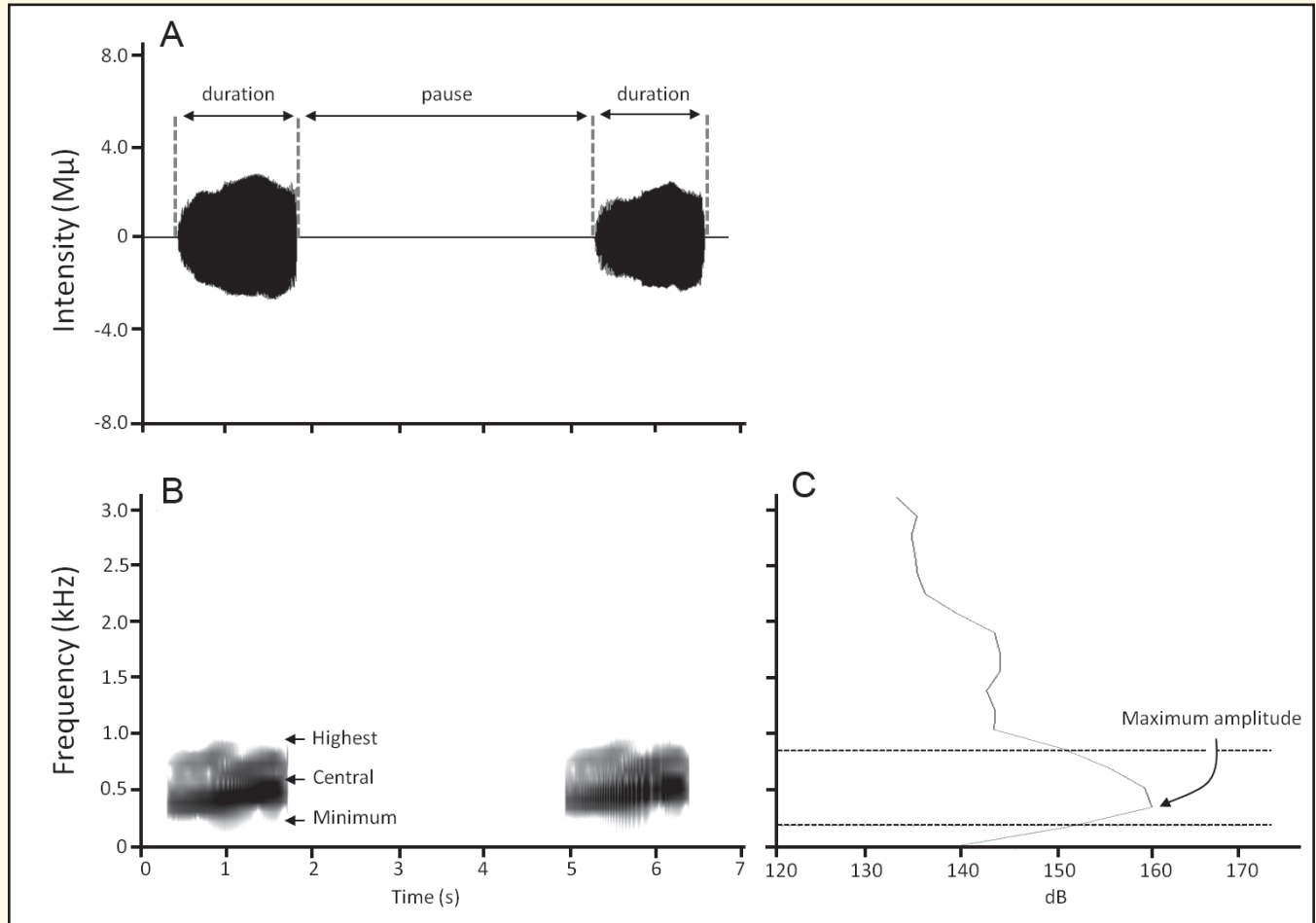


Fig. 2. Oscillogram (A), spectrogram (B), and power spectrum (C) of mating calls of male *Rhinophrynus dorsalis*. Fine acoustic measurements are indicated by arrows.

The values of the center frequency decreased as body size increased ($r^2 = 0.75$, $t_4 = -3.48$, $P = 0.02$; $Y = -63.81x + 875.74$). The call duration showed a positive tendency related with body size ($r^2 = 0.60$, $t_4 = 2.47$, $P = 0.07$). The frequency measurements (minimum: $r^2 = 0.02$, $t_4 = 0.25$, $P = 0.81$; highest: $r^2 = 0.09$, $t_4 = -0.63$, $P = 0.56$; maximum amplitude: $r^2 = 0.51$, $t_4 = -2.02$, $P = 0.11$), peak time ($r^2 = 0.15$, $t_4 = 0.84$, $P = 0.45$), and the average entropy ($r^2 = 0.06$, $t_4 = -0.53$, $P = 0.62$) were not associated with the body size of males.

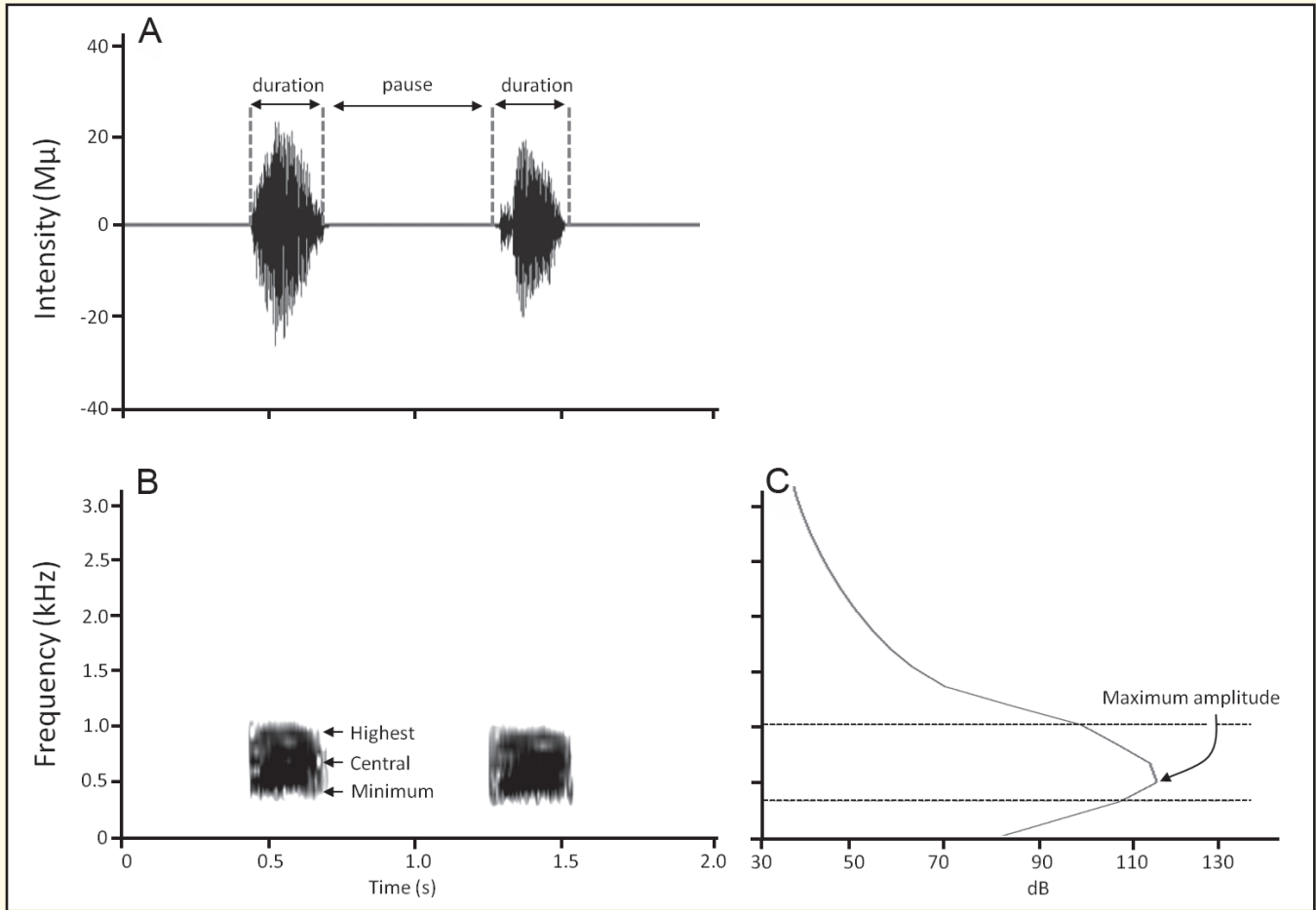


Fig. 3. Oscillogram (A), spectrogram (B), and power spectrum (C) of pre-mating calls of male *Rhinophrynus dorsalis*. Fine acoustic measurements are indicated by arrows.

Table 1. Fine acoustic measurements of the advertisement call of 12 male *Rhinophrynus dorsalis*. Coefficient of variation between males (CV_b) and within males (CV_w), potential for individual coding (PIC), and result of two samples *t*-student test comparing the coefficient of variation by call measurement.

	CV_b	CV_w , mean	PIC	<i>t</i>	df	<i>P</i>
Duration (s)	10.82	8.16	1.33	1.51	21	0.15
Peak Time (s)	11.81	6.56	1	-4.67	21	0.64
Minimum frequency (Hz)	11.22	9.49	1.18	0.95	21	0.35
Highest frequency (Hz)	18.95	8.03	2.36	6.05	21	< 0.001
Maximum amplitude frequency (Hz)	18.97	6.97	2.72	3.95	21	0.001
Central frequency (Hz)	10.02	3.14	3.19	6.51	21	< 0.001
Average Entropy (u)	12.33	6.72	1.83	5.2	21	< 0.001

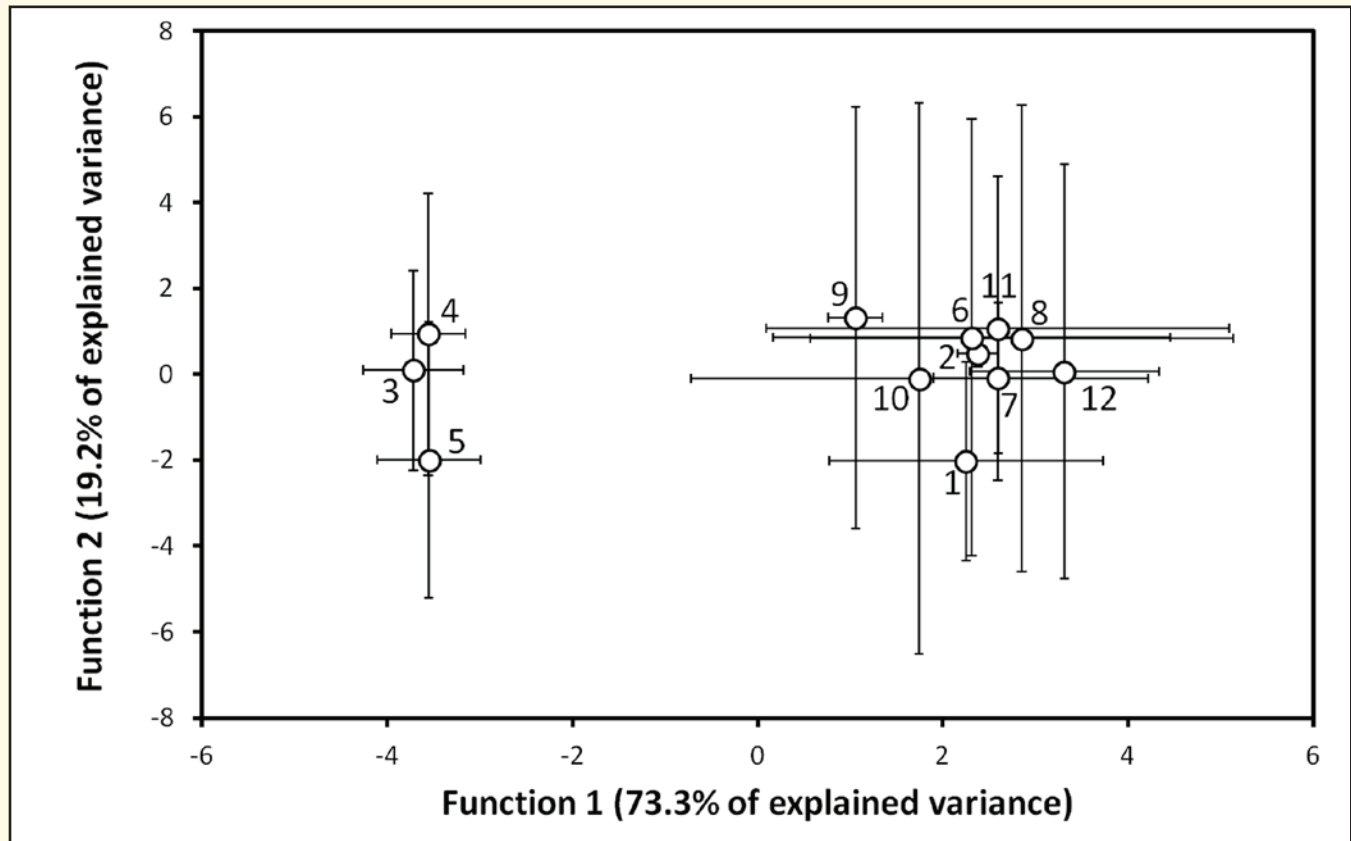


Fig. 4. Discriminant function analysis plot of the first two discriminant functions (total explained variance = 90.7%) that separate 12 males of *Rhinophrynus dorsalis* according to four fine acoustic measurements (highest frequency, central frequency, maximum amplitude frequency, and average entropy) of their mating calls. Points represent the centroid means (numbers indicate individual males) and the error bars are the standard deviation for each function.

DISCUSSION

The reproductive season of *Rhinophrynus dorsalis* lasts only a few days (sometimes a single day), and its beginning is unpredictable because it depends on the first heavy rains of the year (Leenders, 2001; Savage, 2002). This particular condition makes it difficult to obtain information on courtship behavior and vocalizations from more than a single pond in a single year or across years. Our results provide quantitative information on the characteristics of male calls and male-male interactions, and suggest that female choice is based on individual acoustic characteristics of advertisement calls.

In anuran species in which males do not establish territories and male-male contests are absent (or nearly so), female choice is based on the characteristics of behaviors displayed by males (Forester and Czarnowsky, 1985; Bee et al., 1999; Gerhardt and Huber, 2002), though in some species female choice seems to be absent (Davies and Halliday, 1979; Arak, 1988; Bruning et al., 2010). Females also have a strong tendency to prefer larger males to father their progeny, based on male calling features (Wells, 1978; Davies and Halliday, 1979; Katsdaros and Shine, 1997; Tsuji and Matsui, 2002). In all the mating (amplexed) pairs of *R. dorsalis*, females mated with smaller males, but larger females mated with larger males. This suggests that there might be a dual selection because females prefer larger males (higher quality males), but it may be advantageous for males to reproduce with larger females because larger females usually carry more eggs (Kupfer, 2007). Larger females might be found in amplexus with larger males, however, in the absence of active selection by females (Bruning et al., 2010). By inflating their bodies,

females reduce the ability for smaller males to maintain amplexus and resist attacks from other males. Although we did not evaluate this mechanism in female *R. dorsalis*, this body-inflating mechanism possibly is widespread across anuran females and deserves future investigation in this species. A final possibility for the correlation between female and male body size is that females may select the males' size in relation to their own body size to facilitate the match between the two cloacae during spawning (Robertson, 1990).

We found that one of the characteristics of the male advertisement call (center frequency) in *R. dorsalis* was negatively correlated with male size. This agrees with reports for numerous species of anurans, where low frequencies or other acoustic features were correlated with the male body size (Bee et al., 1999; Gingras et al., 2013). In this particular case larger males produce calls with lower minimum frequencies and with the maximum energy carried by low frequencies, when compared with calls of smaller males. The information carried by calls with these characteristics (lower frequencies) travels longer distances and experiences less attenuation and degradation by environmental obstacles (Forrest, 1994; Gerhardt and Huber, 2002; Slabbekoorn and Smith, 2002; Slabbekoorn, 2004; Boncoraglio and Saino, 2007; Ey and Fisher, 2009), allowing them to reach potential receivers at greater distances.

Males of *R. dorsalis* may rely on a single or a combination of different call features for individual identification and male size assessment, given that four (highest frequency, maximum amplitude frequency, center frequency, and average entropy) of the seven fine-structural measurements of the advertisement calls of males showed substantial between-male variation, and one of them also was associated with male body size (center frequency). These acoustical and temporal characteristics of the advertisement call convey enough information to identify most males individually (61%). This level of potential individual recognition is higher or similar in *R. dorsalis* than in other anuran species (Bee et al., 2001; Gasser et al., 2009) and will favor the individual's recognition, possibly reducing the aggressive interaction between males and facilitating the selection of males by females as it occurs in other frog species (Tibbetts and Dale, 2007), but playback experiments will be necessary to test this hypothesis.

The pre-advertisement call of *R. dorsalis* previously had not been described and its function is unclear. The acoustical and temporal characteristics of the pre-advertisement call are similar to distress and aggressive calls of other animals (reduce frequency modulation, wide frequency range, and short duration; Ryan, 1980; Hödl and Gollmann, 1986; Given, 1999; Marler, 2004), but in this anuran pre-advertisement calls being distress calls seems unlikely because no potential danger was perceived. The pre-advertisement call likely has an aggressive function or is a close range signal for other males, but this deserves more investigation. We also noted that the water vibrates as the sound is produced, and cannot discard the possibility that these vibrations convey some information on the male's quality and/or position in the pond (Christensen-Dalsgaard and Jorgensen, 1988; Narins, 1990; Halfwer et al., 2014).

In conclusion, the extremely short and explosive reproductive events and the ecological conditions of the habitat (dry seasonal forests) possibly have influenced the evolution of the courtship behavior, female choice, and male-male competition of *R. dorsalis*. Females in this species are larger than males, which is typical of anuran species with explosive reproduction and in which male-male contests are scarce or absent (Shine, 1979; Bee et al., 1999). Considering the absence of territoriality and male-male contests, females of *R. dorsalis* possibly select their mates based on the characteristics of their advertisement call, which potentially allows the identification of a large percentage of males in the population and conveys information on male size.

Acknowledgments.—We thank Louis W. Porras, D. Fenolio, and B. Kubicki for copy-editing work that largely improved this manuscript. LS was supported by scholarships and grants from the Ministerio de Ciencia y Tecnología (MICIT) and the Consejo Nacional para Investigaciones Científicas y Tecnológicas (CONICIT) of Costa Rica, the Government of Ontario, and the University of Windsor.

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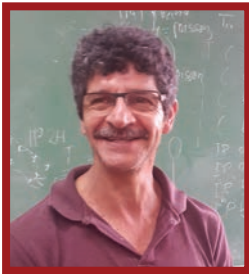
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