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Advertisement calls of six species of anurans from Bali, Republic of Indonesia

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Abstract

We describe quantitatively the advertisement calls of six species of anurans from Bali and the release call of three of these. The advertisement calls of three of the species and the three release calls have not been described previously to the best of our knowledge. This is the first study that describes calls from anurans of the island of Bali. Advertisement call characteristics are discussed in light of within-individual and between-individual variation. For the three species with previously published accounts of their advertisement calls we compare the data obtained in Bali with other accounts. While *Bufo melanostictus* did not show a substantial difference in advertisement calls from Coorg (India), the calls of Balinese *Fejervarya* (*Limnonectes*) *limnocharis* show substantial differences with those recorded in Coorg (India). Furthermore, the Balinese recordings of *Polypedates leucomystax* are similar to recordings obtained by other authors in Negros (Philippines), the Malaysian part of Borneo, and from one of the morphs present in peninsular Malaysia, while being clearly different from recordings of populations from Thailand, Polillo (Philippines), and from the other morph recorded in Malaysia.

Keywords: *Anura, Bali, bioacoustics, Bufonidae, Indonesia, Ranidae, Rhacophoridae*

Introduction

Advertisement calls are generally recognized as being the main pre-mating reproductive isolating mechanism in anurans (Blair 1958; Gerhardt 1988; Ryan and Rand 1993). Since the development of sound analysis techniques, the comparison of advertisement calls of different populations has played a major role in the detection of cryptic species worldwide. This is particularly true in tropical regions, but also in more thoroughly explored regions like Europe and the Middle East. This way, many new taxa have been detected by variations in their advertisement calls before their genetics were studied (e.g. Schneider 1974; Schneider et al. 1984; Paillette et al. 1992; Schneider and Haxhiu 1994; Matsui 1997; Myers et al. 1997; Sánchez-Herraiz et al. 2000; Channing et al. 2002). In addition, the detailed description of anuran advertisement calls has proved to be a powerful tool for the determination of the taxonomic status of specimens collected in less explored areas (e.g.

García-Pérez and Heyer 1993; Márquez et al. 1995; Heyer et al. 1996; Narins et al. 1998; Heyer and Juncá 2003; Señaris and Ayarzagüena 2005). In order for the comparisons of calls to become a useful tool, a quantitative description of the characteristics of the advertisement calls of anuran species is needed.

The Indonesian island of Bali is located between the islands of Java and Lombok, 8° south of the equator. It is part of the Indo-Australian archipelago which is known to be the most geologically complex group of islands in the world and to support the highest degree of biological endemism ever recorded (Brown and Guttman 2002). Currently, 12 species of anurans from three different families are known from Bali (Iskandar 1998). In this paper we describe the calls of six species, including release calls for three of them, and compare the advertisement calls with previous studies, when possible. The advertisement calls of three of the species and the three release calls had not been described previously to the best of our knowledge, and this is the first study that describes calls of the anurans from the island of Bali.

The species encountered and recorded during the fieldwork were the following:

Bufo melanostictus Schneider, 1979 is a bufonid with an extremely wide distribution that covers most of SE Asia, from India to the islands of Bali and Sulawesi, where it has been recently introduced (Iskandar 1998). *Bufo melanostictus* is normally found in human habitats throughout its distributional range.

Bufo biporcatus Gravenhorst, 1829 is another bufonid species with a relatively wide distribution that includes the islands of Sumatra, Sulawesi, Java, and Bali. Its habitat is primary and secondary forest although in Bali and Lombok it also occurs in human habitats (Iskandar 1998).

Fejervarya limnocharis Gravenhorst, 1829 is a ranid frog that is distributed from India to the west, to Flores archipelago of Indonesia to the east, and all the way north to Japan. It is normally found in paddy fields and grasslands at low altitude, rarely up to 700 m, although in some regions it can be found at higher altitudes in rice fields (Iskandar 1998).

Occidozyga sumatrana Peters, 1877, another ranid frog, is very similar to the widely distributed *O. laevis* but differs from this one in being significantly smaller. Besides Bali, the distribution of this species includes the Malay Peninsula, Sumatra, Borneo, and perhaps Indochina (Iskandar 1998). The animals are normally found in puddles in the forest or in secondary clearings, never in large numbers.

Rana chalconota Schlegel, 1837, a small ranid species that inhabits southern Sumatra, Java, and Bali, is always associated with bodies of stagnant or nearly stagnant water (Iskandar 1998). Normally individuals can be found perching on the vegetation surrounding the pond or in the pond on leaves of lotus or water hyacinths.

Polypedates leucomystax Gravenhorst, 1829 is a rhacophorid frog with an extremely wide distribution throughout SE Asia. It occurs in India, southern China, Indochina, Philippines, and some islands of Indonesia such as Java, Bali, Lombok, and Irian Jaya (western New Guinea) where it has been introduced (Iskandar 1998). It is frequently found among low vegetation or around marshes and secondary clearings. This species often approaches human habitation, attracted by insects around lamps.

Materials and methods

Recordings were obtained between 1 and 16 December 2000 with a Sony WM D6C cassette recorder and a M-80 Sennheiser directional microphone. The recordings were later digitized and edited at a sampling frequency of 44.1 kHz and 16 bit resolution in a

Macintosh computer with a Delta 66 audio card and Peak 2.5 software (Bias Inc.). Signalyze 3.12 software (Infosignal Inc.) was used to analyse sounds. Temporal data were obtained from the oscillograms and frequency information was obtained using fast Fourier transforms (FFTs) (frame width, 1024 points). The terminology used for the description of the calls is based on Heyer et al. (1990) and the oscillograms and audiospectrograms presented follow the format of Bosch et al. (2000). The species captured were identified morphologically. The nomenclature follows Iskandar (1998) and is in agreement with Frost (2004).

Various call characteristics were measured from the different calls of each species: call duration, number of pulses within calls, pulse rate (pulses per second) within calls, intercall duration, dominant frequency, relative location of maximum amplitude within the call (in order to define the point within each call in which the amplitude is maximum we define the beginning of the call as 1 and the end as 100; this value provides some information about intensity modulation) and other frequencies with substantial energy. In addition, frequency amplitude (difference between maximum frequency and minimum frequency) was measured in *Rana chalconota*, which produced different short calls with a substantial variation in frequency amplitude. It was measured with Raven 1.0 software after filtering (high pass 100 Hz) and normalizing all calls to the same peak amplitude.

The recordings were obtained from three different sites on the island. Table I summarizes the exact locations, the species, and number of specimens recorded at each site. All individuals captured for identification or after recording their calls were immediately released once finished, as no collecting permit was available. The release calls recorded were made by some of the captured males while being manipulated for measurement. The numerical parameters of the advertisement calls are shown in Table II. Average values are included together with between-individual and within-individual coefficients of variation ($CV_{between}$ and CV_{within}) that were calculated in order to determine which are "static" and which are "dynamic" (*sensu* Gerhardt 1991). Static parameters are presumably those that better characterize the species-specific call, because they remain fairly constant among individuals of a population, at least within a calling session. Considering that calling temperature variation in the lowland tropical environment where the recordings were obtained is extremely constant in all the recordings considered in this study (24.5–29°C), for the advertisement calls, the ratio of between-individual coefficient of variation to within-individual coefficients of variation ($CV_{between}/CV_{within}$) is a measure of relative between-male call variability. Thus call variables where $CV_{between}/CV_{within} > 1.0$

Table I. Localities, species encountered, and number of males recorded (the presence of *Polypedates leucomystax* was confirmed during the fieldwork in West Bali National Park, but unfortunately no recordings from this species were obtained).

Localities	Family	Species	Males recorded
Nusa Dua (08°47′53.7″S, 115°14′01.9″E)	Bufonidae	*Bufo melanostictus*	6
Recording date: 1–3 December 2000	Rhacophoridae	*Polypedates leucomystax*	5
Tirtagganga (08°25′05.2″S, 115°35′13.3″E)	Bufonidae	*Bufo biporcatus*	12
Recording date: 5–10 December 2000	Ranidae	*Occidozyga sumatrana*	8
	Ranidae	*Rana chalconota*	7
	Rhacophoridae	*Polypedates leucomystax*	1
West Bali National Park (08°08′30.0″S, 114°39′12.3″E)	Ranidae	*Fejervarya limnocharis*	3
Recording date: 16 December 2000	Rhacophoridae	*Polypedates leucomystax*	0

Table II. Mean, standard deviation (SD), range and coefficient of variation (CV) of call parameters of all the species recorded.

	Duration (ms)	Number of pulses	Pulse rate (pulses/s)	Intercall duration (ms)	Dominant frequency (Hz)	Relative location of maximum amplitude[a]	Other frequencies (Hz)	Frequency amplitude[b] (Hz)
Bufo biporcatus ($n_{individuals}$=12; n_{calls}=235)								
Mean (SD)	506.9 (100.6)	4.2 (0.8)[c]	9.1 (2.5)[c]	1362.7 (678.2)	1737.7 (148.7)	48.3 (11.1)		
Range	329.7–641.0	2.8–4.9	7.7–16.7	781.1–3058.1	1359.2–1961.4	21.4–61.2		
$CV_{between}$ (CV_{within})	19.9 (17.5)	18.6 (14.9)	27.2 (6.0)	49.8 (55.3)	8.6 (2.5)	22.9 (65.4)		
CV ratio	1.14	1.25	4.6	0.90	3.44	0.35		
B. biporcatus (release call) ($n_{individuals}$=3; n_{calls}=111)								
Mean (SD)	16.0 (1.4)			499.4 (261.3)	1553.5 (361.0)			
Range	14.5–17.2			318.8–798.9	1152.5–1852.8)			
$CV_{between}$ (CV_{within})	8.6 (13.0)			52.3 (168.9)	23.2 (8.8)			
B. melanostictus ($n_{individuals}$=5; n_{calls}=57)								
Mean (SD)	771.6 (97.5)	46.6 (4.4)	62.1 (5.9)	4239.0 (3122.9)	1555.2 (112.5)	71.9 (9.1)		
Range	678.9–933.0	40.6–51.4	40.6–51.4	2006.2–10478.7	1433.5–1684.5	12.6–20.1		
$CV_{between}$ (CV_{within})	12.6 (18.9)	9.4 (13.5)	9.5 (11.6)	73.7 (71.7)	7.2 (3.7)	12.6 (20.1)		
CV ratio	0.66	0.70	0.81	1.03	1.95			
B. melanostictus (release call) ($n_{individuals}$=4; n_{calls}=53)								
Mean (SD)	456.6 (129.2)	4.3 (0.75)	11.9 (3.8)	1010.3 (174.3)	1059.6 (387.7)			
Range	284.8–558.7	3.7–5.4	9.2–17.5	786.4–1202.2	482.7–1320.9			
$CV_{between}$ (CV_{within})	28.3 (55.1)	17.5 (52.4)	31.8 (40.9)	17.3 (50.3)	36.6 (14.8)			
Fejervarya limnocharis (Type I) ($n_{individuals}$=3; n_{calls}=71)								
Mean (SD)	202.0 (34.7)	3.0 (0.3)	15.2 (1.4)	944.7 (104.4)	2119.0 (86.0)	19.9 (22.3)	1037.0 (27.3)	
Range	163.4–230.6	2.6–3.2	13.9–16.7	836.6–1044.9	2044.4–2213.1	6.2–45.8	1018.4–1068.3	
$CV_{between}$ (CV_{within})	17.2 (19.5)	10.4 (17.2)	9.1 (16.0)	11.1 (43.1)	4.1 (4.1)	111.7 (76.0)	2.6 (5.2)	
CV ratio	0.88	0.60	0.56	0.26	1.00	1.47	0.5	
Occidozyga sumatrana ($n_{individuals}$=8; n_{calls}=93)								
Mean (SD)	165.6 (19.9)	22.9 (3.5)	143.2 (18.3)	9293.3 (7160.1)	2741.5 (113.7)	67.4 (2.9)		
Range	126.9–194.4	16.7–28.6	115.6–177.5	2521.7–25,768.8	2593.8–28,76.9	64.1–72.5		
$CV_{between}$ (CV_{within})	12.0 (10.4)	15.4 (7.9)	12.8 (9.1)	77.1 (83.3)	3.8 (4.3)	4.4 (8.7)		
CV ratio	1,15	1.95	1.41	0.93	0.88	0.51		
Rana chalconota (Type A) ($n_{individuals}$=7; n_{calls}=73)								
Mean (SD)	24.7 (17.2)	2.0 (0.5)	117.6 (35.6)	5569.3 (5132.8)[d]	1596.5 (330.4)	18.7 (4.9)		3480.5 (564.9)
Range	11.8–62.1	1.6–3.0	48.3–156.3	1618.2–15,438.6	1149.9–2055.9	13.4–27.1		2889.8–4444.0
$CV_{between}$ (CV_{within})	69.8 (61.2)	24.5 (44.6)	30.3 (34.7)	92.2 (156.5)	20.7 (18.0)	26.6 (75.1)		16.2 (12.6)
CV ratio	1.14	0.55	0.87	0.59	1.15	0.35		1.29

Table II. (*Continued.*)

	Duration (ms)	Number of pulses	Pulse rate (pulses/s)	Intercall duration (ms)	Dominant frequency (Hz)	Relative location of maximum amplitude[a]	Other frequencies (Hz)	Frequency amplitude[b] (Hz)
R. chalconota (Type B) ($n_{individuals}$=6; n_{calls}=38)								
Mean (SD)	41.5 (8.2)				2648.2 (417.1)	9.2 (2.9)		2360.9 (418.4)
Range	33.1–55.2				2005.9–3090.2	4.4–12.2		1695.8–2753.8
$CV_{between}$ (CV_{within})	19.6 (27.8)				15.8 (16.3)	31.7 (46.9)		17.7 (19.5)
CV ratio	0.71				0.97	0.68		0.91
R. chalconota (Type C) ($n_{individuals}$=4; n_{calls}=9)								
Mean (SD)	25.8 (6.0)				3021.8 (232.4)	25.7 (13.9)		1132.2 (373.7)
Range	19.6–31.9				2726.6–3254.2	13.9–45.9		740.7–1505.6
$CV_{between}$ (CV_{within})	23.4 (33.1)				7.7 (10.3)	54.5 (21.3)		33.0 (18.9)
CV ratio	0.71				0.75	2.56		1.75
R. chalconota (release call) ($n_{individuals}$=1; n_{calls}=4)								
Mean (SD)	14.9			5981.8	1265.5		2758.2	
Range								
CV_{within}	54.7			78.6	43.0		9.2	
Polypedates leucomystax ($n_{individuals}$=6; n_{calls}=69)								
Mean (SD)	218.5 (96.9)	16.5 (3.7)	84.7 (28.8)	48,554.9 (82,304.2)	2550.1 (135.7)	47.8 (15.8)		
Range	148.0–408.3	12.6–23.2	43.8–129.4	6209.5–125,817.5	2320.6–2677.7	25.7–62.8		
$CV_{between}$ (CV_{within})	44.4 (17.4)	22.3 (11.9)	34.1 (10.1)	169.5 (53.7)	5.3 (4.5)	32.94 (29.8)		
CV ratio	2.55	1.87	3.37	3.15	1.18	1.10		

$CV_{between}$, measure of between-individual variability and is calculated with the coefficients of variation of the mean values of the individual males; CV_{within}, measure of the within-individual within-calling period variation, calculated as the average of the individual coefficients of variation of each recording; $n_{individuals}$, number of individuals; n_{calls}, total number of calls analysed. For the advertisement calls: CV ratio, ratio ($CV_{between}$/CV_{within}) where the largest numbers indicate high potential for inter-individual discrimination. [a]Relative location of maximum amplitude is a dimensionless unit with a value from 0 (beginning of the call) to 100 (the end of the call). [b]Frequency amplitude=maximum frequency − minimum frequency. [c]For *Bufo biporcatus*, the number of pulses is actually the number of pairs of pulses and the pulse rate is the rate at which pairs of pulses are emitted. [d]For *Rana chalconota*, the inter-call duration is calculated including the three types of call.

are more likely to be used in sexual selection while call variables with low values of $CV_{between}$ are more likely to be used for species recognition.

Results

Bufo biporcatus was recorded in Tirtagganga, around a temple known as the Water Palace and in a nearby rice field. The average snout-to-vent length (SVL) of the males captured was 53 mm (range 42–67 mm, *n*=5) with an average weight of 14 g (range 13.5–17.5 g, *n*=5). Females on average were larger [SVL 57.2 mm (range 54–63 mm), weight 19.2 g (range 16–26 g), *n*=6]. Males were always found inside the water, calling from the edge in groups of two or three males, separated by approximately 1–1.5 m. The recordings were obtained between 22:00 and 00:00 h with air temperatures ranging from 26 to 28°C. Only one type of advertisement call was heard for this species. It was normally composed of 8–10 paired pulses (Figure 1A) although some calls of only six and even four pulses were recorded. Martin (1971) made a classification of the type of pulses in the genus *Bufo* based on the amplitude modulation within pulses. Following his definitions, *B. biporcatus* has Type II pulses, which are complex pulses with a repetitive amplitude modulation within each pulse. The calls were easily heard from a distance of more than 20 m. The release call of this species was also recorded (Figure 7A). It was a series of pulses with an average duration of 16 ms and average fundamental frequency around 1.5 kHz, which was also the dominant frequency, and two or three harmonics every 0.5–0.6 kHz. The numerical data of the advertisement calls and release calls are summarized in Table II. To the best of our knowledge this is the first description of the advertisement call and release call of this species.

The recordings of *Bufo melanostictus* were obtained in a garden in Nusa Dua, a locality of Bali, in a highly developed environment, between 18:00 and 20:00 h. Males were found calling on land and sitting on rocks at the edge of the water in the fountains of the garden; the air temperature was 28–29°C. The average SVL of the males captured was 64.2 mm (range 56–72 mm, *n*=5). The calls were loud and could be heard from a distance of more than 50 m. Most of the recordings obtained were from isolated males, although a large chorus was heard from a distance. The calls heard from the chorus (Figure 1B) were much longer in duration and seemed to be a succession of the calls emitted by isolated males (Figure 1C). The release call of *B. melanostictus* was a series of groups of 2–14 pulses with an average duration of 456 ms and an average dominant frequency around 1.0 kHz (Figure 7B). The amplitude modulation within pulses would correspond to Type III pulses with a relatively slow rise-time, *sensu* Martin (1971). The numerical data of the advertisement calls from single males and of the release calls are summarized in Table II. We believe that the release call of *B. melanostictus* has not been described previously.

The individuals of *Fejervarya limnocharis* were found near Taman Sari in West Bali (Bali Barat) National Park between 20:00 and 22:00 h. Advertisement calls were recorded inside a temporary pond with the males calling from inside the water, typically less than 30 cm away from the shore and with their bodies partially submerged in the water. The water temperature ranged from 26.5 to 28.1°C. Only a single male was captured with a SVL of 49.5 mm and a weight of 10 g. The captured females were larger and much heavier with average SVL of 61.5 mm (range 60–63 mm, *n*=2) and an average weight of 23.2 g (range 20.5–26.0 g, *n*=2). The advertisement call (Type I) of *F. limnocharis* was composed of two to four different pulses. The first pulse was always different, of higher intensity, and normally it was followed by one to three (typically two) less intense and shorter duration
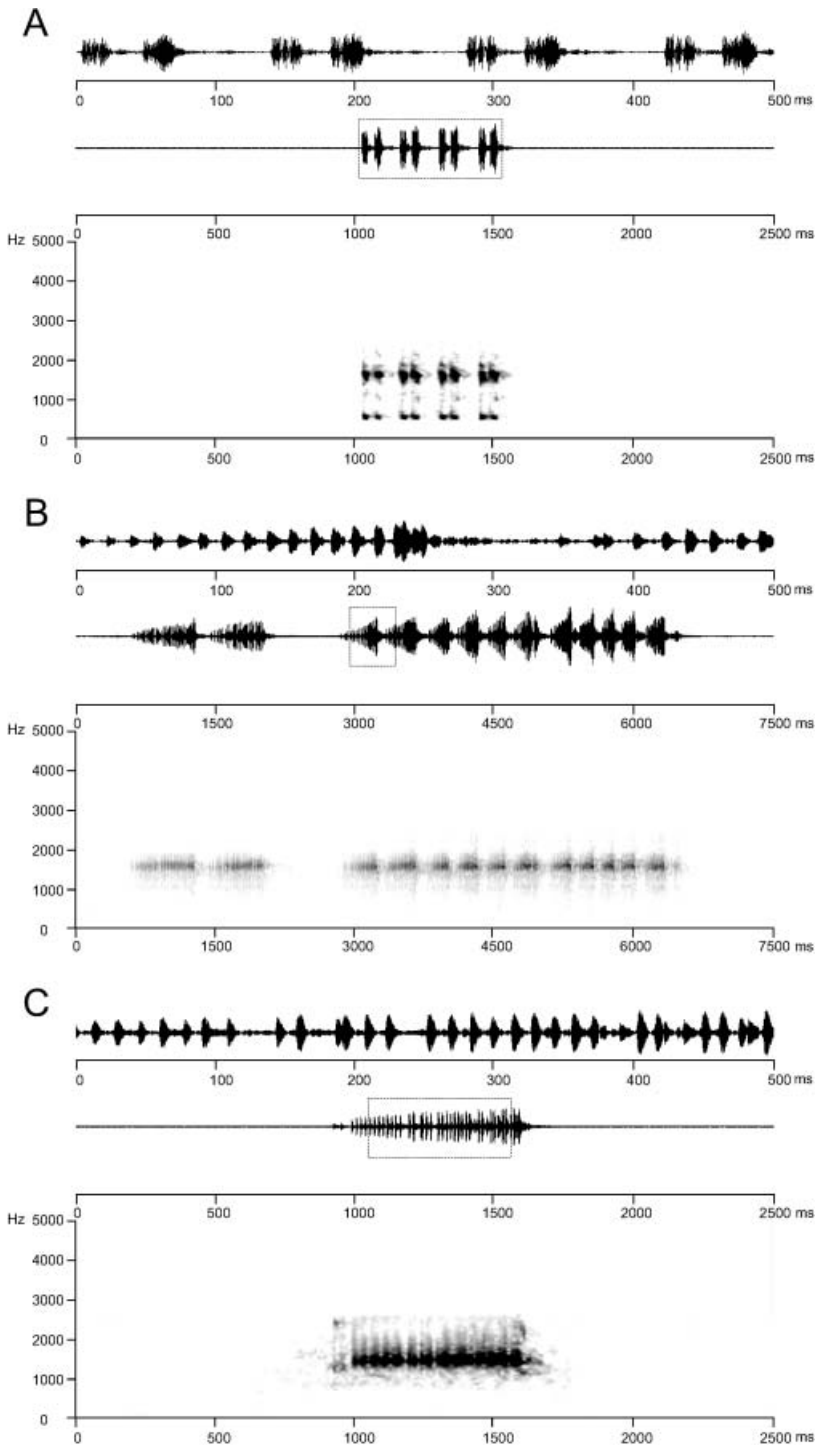
Figure 1. Expanded oscillograms, full-scale oscillograms, and audiospectrograms of the advertisement calls of the bufonids *Bufo biporcatus* (A) and *B. melanostictus* in a chorus (B) and an isolated male (C). The boxes in the full-scale oscillograms indicate the time shown in the expanded oscillograms.
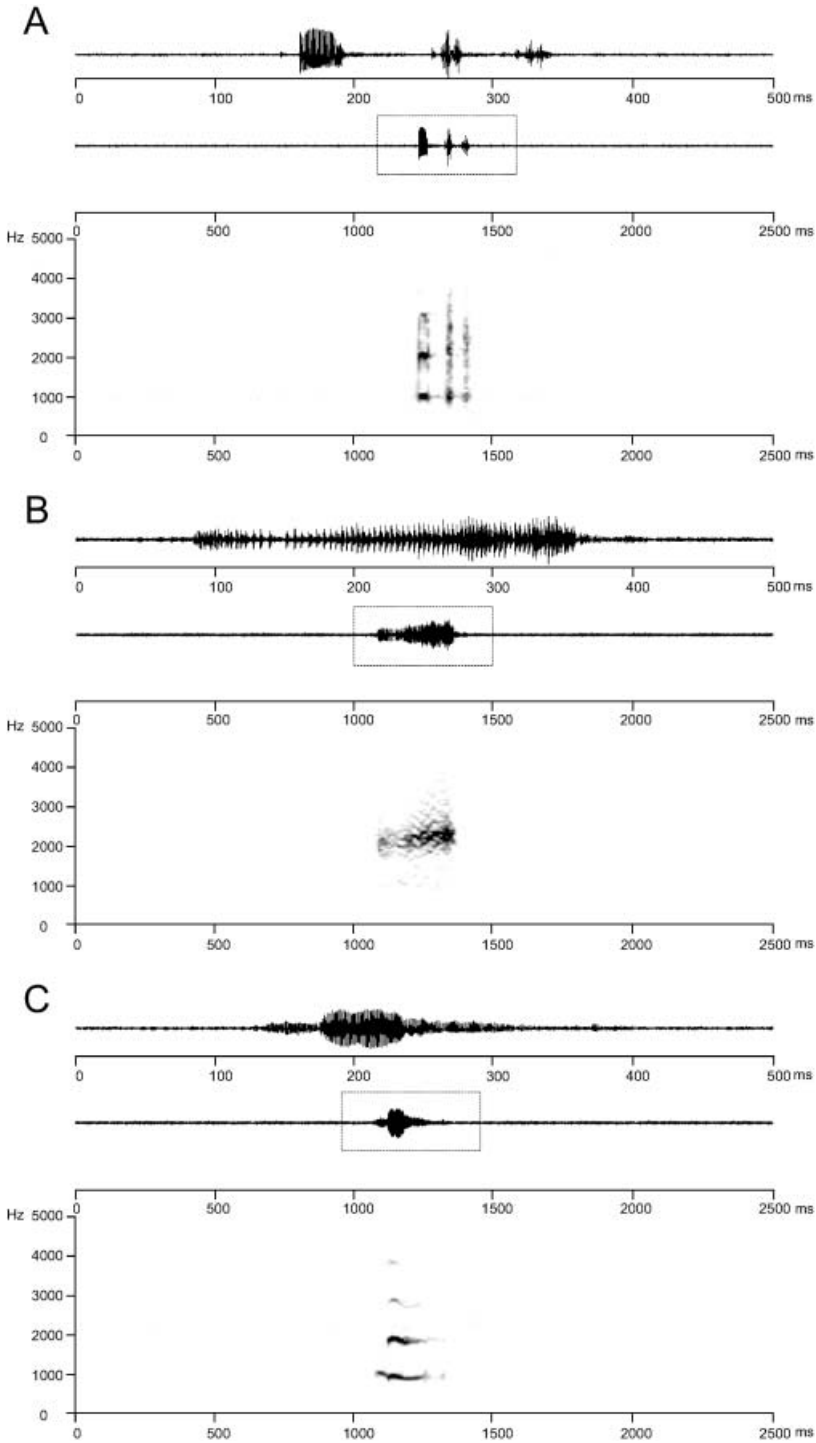
Figure 2. Expanded oscillograms, full-scale oscillograms, and audiospectrograms of the advertisement call (Type I) (A) and calls Type II (B) and Type III (C) of the ranid *Fejervarya limnocharis*. The boxes in the full-scale oscillograms indicate the time shown in the expanded oscillograms.

clicking pulses (Figure 2A). The numerical data for call Type I are summarized in Table II. Two more types of calls were recorded from only one of the individuals (Figure 2B, C). Both sounded like squeaks and normally appeared alternatively. The most common of these two other types of calls (Type II; Figure 2B) had an upward frequency modulation between 2.0 and 2.5 kHz and an average dominant frequency of 2.4 kHz. Type III (Figure 2C) was always emitted between two Type II calls although a Type II was not always followed by a Type III call. This last call sounded like a descending squeak and had a dominant frequency of 1.8 kHz and a second frequency of 0.9 kHz. The duration of the three types of call was very similar (range 203.0–283.3 ms). The calls of this species could easily be heard from a distance of more than 20 m.

The individuals of *Occidozyga sumatrana* recorded were found floating on the surface of the water in a rice field in Tirtagganga between 22:00 and 00:00 h, when the air temperature was 24.5–25°C. The males we found had an average size of 32.7 mm (range 31.5–39.5 mm, $n=3$) and an average weight of 3.7 g (range 3.0–4.5 g, $n=3$). The typical advertisement call was a short, pulsed call with an average dominant frequency of 2.7 kHz (Figure 3A). The numerical data for this call are summarized in Table II. This call could be heard from more than 20 m distance. One of the males recorded was found in amplexus and the female was removed for measuring. After a short period of time the male started calling again towards another nearby male floating approximately 5 cm away, although no aggression or attempt to get close was observed. During this interaction three different types of call were recorded besides the advertisement call. The first of these calls was a three-part call composed of a pulse train preceded and followed by a single, longer pulse of similar dominant frequency (Figure 3B). The last pulse was always more intense than the others. The pulse rate of the pulse train was much lower than the average pulse rate of the advertisement call (40–66 pulses/s) and the average dominant frequency was much lower (1.2–1.4 kHz). This call was also recorded previously in another calling male but we could not confirm if it was interacting directly with other individuals. The second call recorded from the male separated from amplexus was also a pulsed call with a highly variable duration (range 15.4–585.7 ms), slightly lower average pulse rate (103.14 pulses/s), and also a lower average dominant frequency (1.3–1.7 kHz) (Figure 3C). Finally, this male occasionally emitted a short whistle with an average dominant frequency of 1.9 kHz (Figure 3D). To the best of our knowledge this is the first description of the calls of this species.

Calling individuals of *Rana chalconota* [average SVL 40 mm (range 34–44 mm), average weight 3.9 g (range 3–5 g), $n=4$] were found in a garden pond at Tirtangganga, between 22:00 and 00:00 h; the air temperature was 27°C and the humidity relatively low due to the lack of rain for 2 days. The frogs called with a very low intensity and it was very difficult to distinguish individual calls in a single recording session. The calls were so quiet that they could not be heard from more than 1–2 m away. The calls consisted of what seemed like a random series of chirps and chucks, as it was impossible to identify any pattern of repetition (Figure 4D). From our recordings we identified three different call types. The most commonly heard sounds (Type A) were the chucks with very wide frequency amplitude (3.4 kHz), which could have from one to four pulses (normally two; Figure 4A). The second most common kind of call (Type B) had a very short frequency modulation and sounded similar to the first call although higher pitched and relatively higher in intensity volume. This call also had relatively wide frequency amplitude (2.0 kHz) (Figure 4B). Finally, the last type of call (Type C) were chirps with a variable dominant frequency but a shorter frequency amplitude (1.1 kHz) (Figure 4C). Due to the high variation in the acoustic characteristics of the calls of *R. chalconota*, we tested our subjective classification of
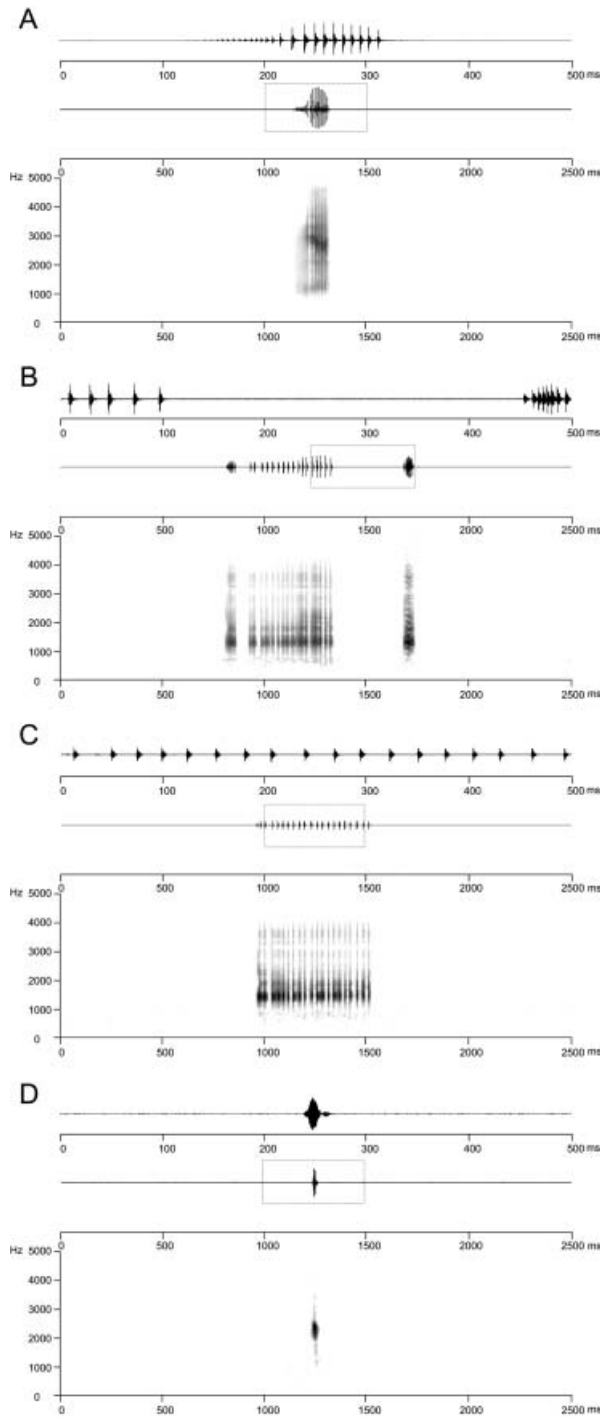
Figure 3. Expanded oscillograms, full-scale oscillograms, and audiospectrograms of the advertisement call of the ranid *Occidozyga sumatrana* (A) and of other calls (B–D) recorded from a single male after being separated from amplexus with a female. The boxes in the full-scale oscillograms indicate the time shown in the expanded oscillograms.
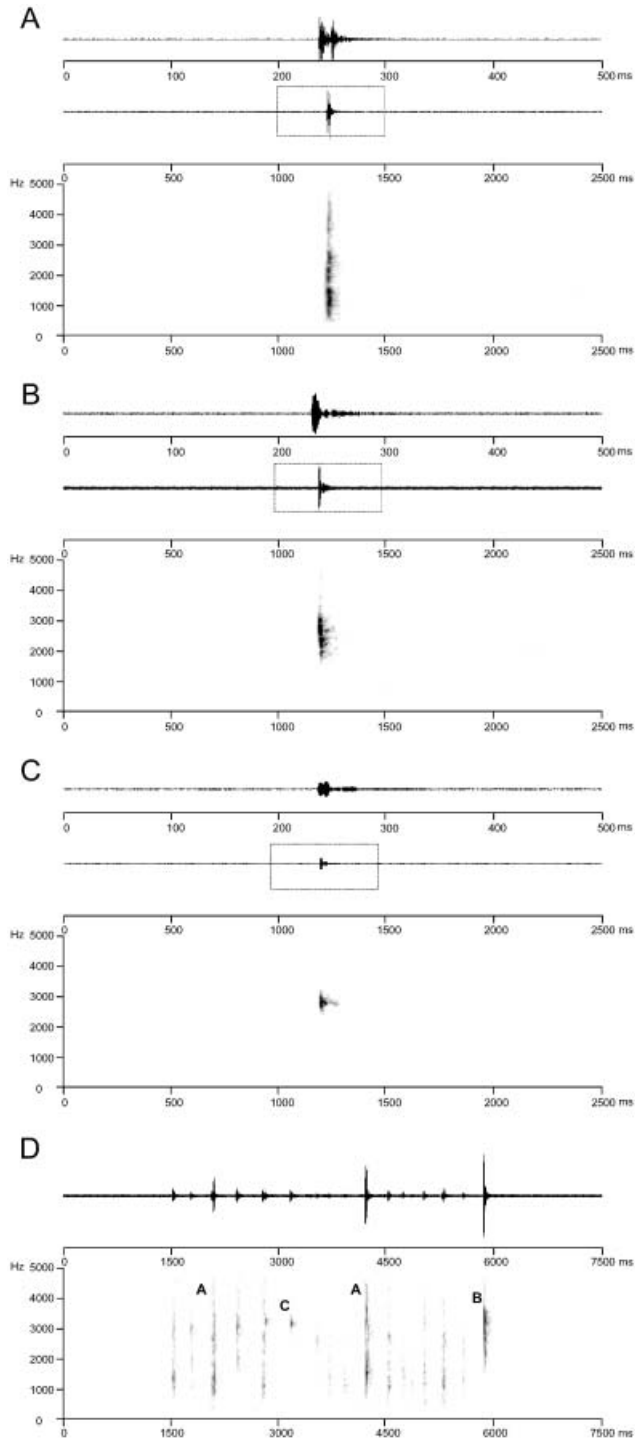
Figure 4. Expanded oscillograms, full-scale oscillograms, and audiospectrograms of the three different call types of the ranid *Rana chalconota*. The boxes in the full-scale oscillograms indicate the time shown in the expanded oscillograms.
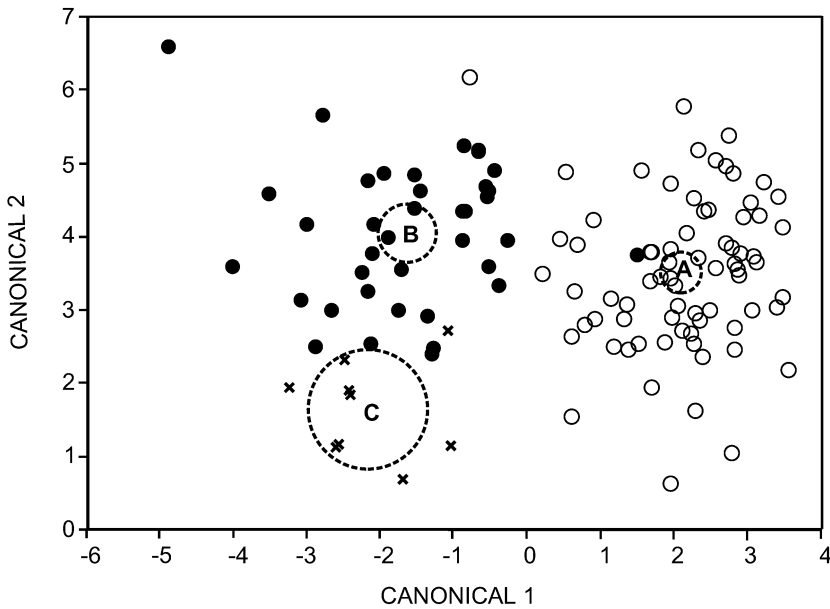
Figure 5. Discriminant analysis performed with five sound parameters (duration, number of notes, dominant frequency, relative location of maximum amplitude, and frequency amplitude) for the call types of *Rana chalconota*. Open circles are Type A calls, filled circles are Type B calls, and crosses are Type C calls. The size of the dotted circle corresponds to a 95% confidence limit for the mean.

call types with a discriminant analysis. Using five sound parameters (duration, number of notes, dominant frequency, relative location of maximum amplitude, and frequency amplitude), more than 93% of the calls were classified correctly (Figure 5). One of the captured animals emitted a short series of release calls, which were pulses with an average dominant frequency of 1.5 kHz (Figure 7C). The numerical data for all the calls are summarized in Table II. To the best of our knowledge, the calls of *R. chalconota* have never been described before.

We found *Polypedates leucomystax* in all three localities, although no recordings were obtained in West Bali National Park. A single individual was captured and had a SVL of 48 mm, weighting 5.5 g. Males were always calling from emergent vegetation perched 1.5–2 m over the surface of the water. The advertisement call was a single, short, pulsed call (Figure 6). The numerical data are summarized in Table II. The advertisement calls of the animals from the three localities did not seem to be significantly different from each other but unfortunately, as the sample size is small and most of the animals could not be captured, it is not possible to do any statistical comparison.

Discussion

Following the results of Gerhardt's (1991) extensive study of the vocalizations of three species of North American anurans, where the characteristics of ''static'' and ''dynamic'' call characteristics were first discussed, we investigated the coefficients of variation (CV) for the advertisement calls. The data obtained for within-individual variation (CV_{within} in Table II) can provide some insight as to which of the variables of the advertisement call measured are less variable within individual and within calling bout (static parameters), and
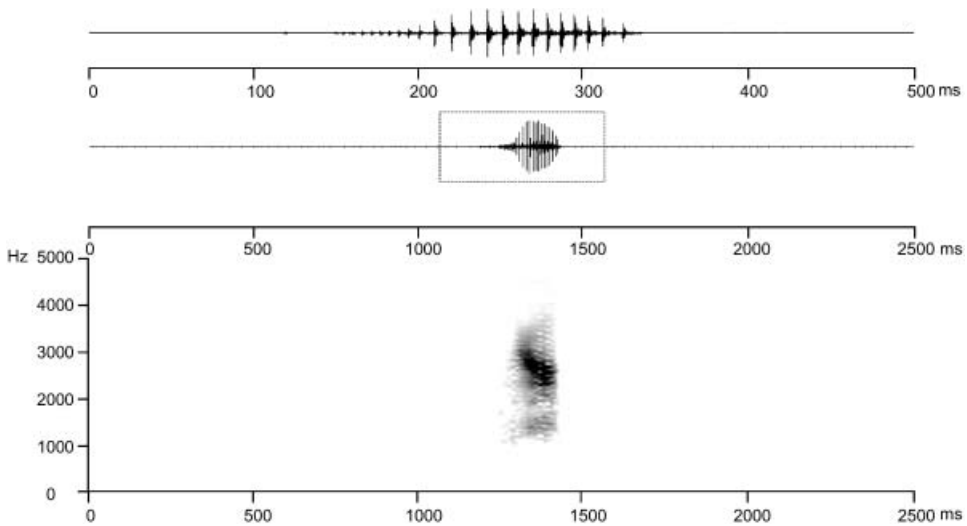
Figure 6. Expanded oscillogram, full-scale oscillogram, and audiospectrogram of the advertisement call of the rhacophorid frog *Polypedates leucomystax*. The box in the full-scale oscillogram indicates the time shown in the expanded oscillogram.

which are more variable (dynamic parameters). The data obtained for relative between-individual variation (CV ratio in Table II or $CV_{between}/CV_{within}$) indicate which call characteristics are more likely to be involved in inter-individual recognition or sexual selection. Furthermore, we can determine which variables are more likely to be involved in species recognition [those that show low inter-individual variation in absolute terms ($CV_{between}$ in Table I), and have low intra-individual variation as well (CV_{within} in Table II)]. In the advertisement call of *B. biporcatus*, pulse rate and dominant frequency appear to have high potential for conveying information about individual male status in a sexual selection context, while only the dominant frequency appears to have low between-individual variation. In *B. melanostictus*, only dominant frequency appears to have a relatively high relative between-individual variation, while three call characteristics (dominant frequency, number of pulses, and pulse rate) have values below 10, indicating some potential for species recognition. However, the calls emitted in the dense chorus (which were only recorded once) may have additional potential for sexual selection, although the sample size is too limited to confirm this point. In *F. limnocharis*, in Type I calls, only the relative location of maximum amplitude showed some potential for individual recognition or sexual selection. However, it is likely that the use of different note types and the sequence of emission of these may play a role. The very low between-individual coefficient of variation in call dominant frequency suggests that this parameter may be important for species recognition. In *O. sumatrana*, only call duration (and to a lesser extent pulse rate) show some potential for inter-individual recognition. The low absolute CV values for both dominant frequency and relative location of maximum amplitude suggest that these characteristics may have the highest potential for species recognition. In *R. chalconota*, the existence of three call types suggests that call sequence may play a role in inter-individual selection, but this may not be properly addressed here because not enough observations of individual calling sequences were recorded. Among the variables measured, only the relative location of maximum amplitude of call Type C and the width of the frequency range show high CV ratios, indicating that these characteristics
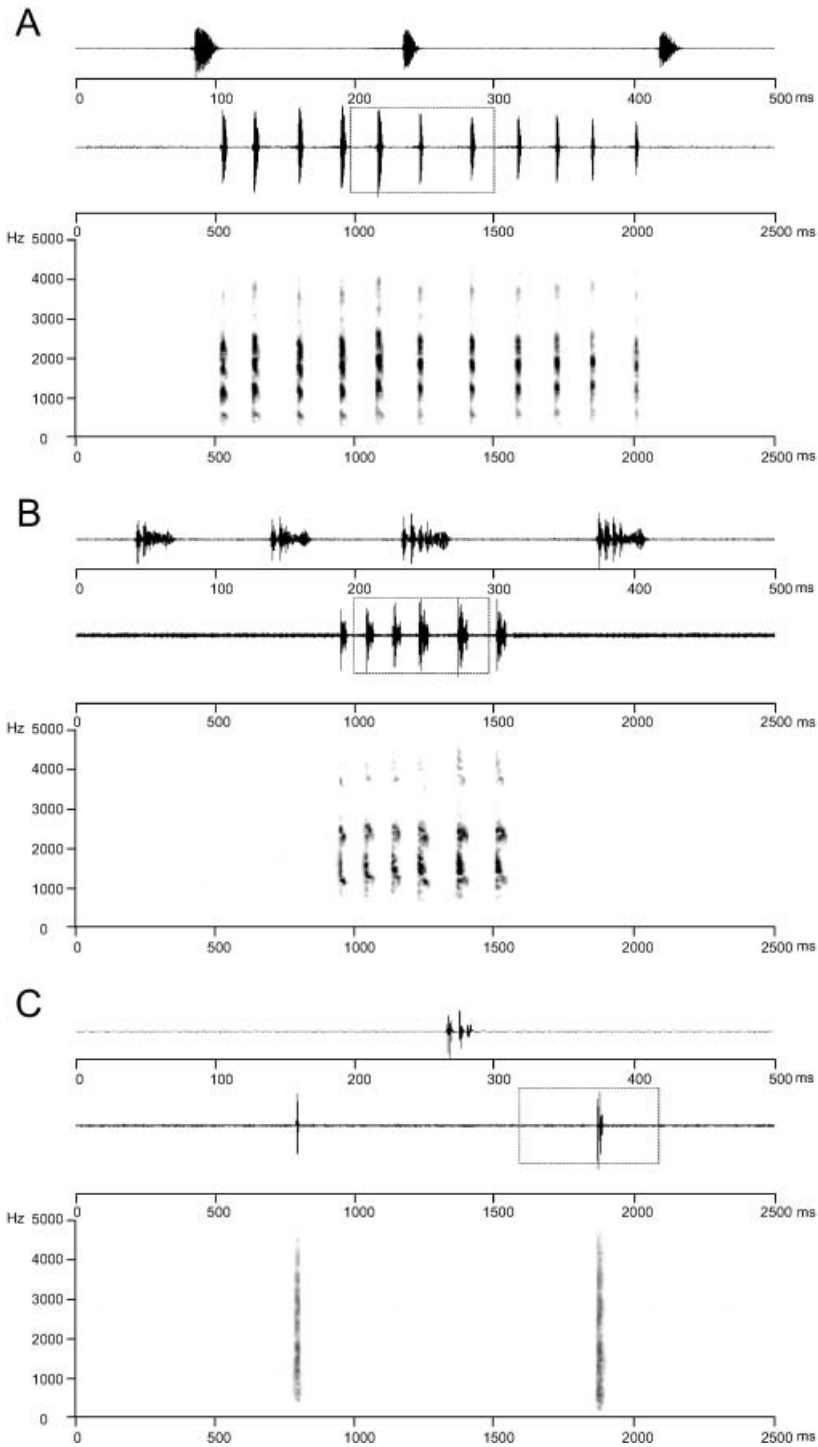
Figure 7. Expanded oscillograms, full-scale oscillograms, and audiospectrograms of the release calls from (A) *Bufo biporcatus*, (B) *Bufo melanostictus*, and (C) *Rana chalconota*. The boxes in the full-scale oscillograms indicate the time shown in the expanded oscillograms.

may play a role in individual recognition or sexual selection. Of all the variables measured only the dominant frequency of the Type C note shows low inter-individual variation indicating some potential for species recognition. Finally, in *P. leucomystax* most measured characteristics have high CV ratios and thus may play a role in sexual selection or individual recognition (all except for the relative location of maximum amplitude). On the other hand, only dominant frequency shows a low absolute between-individual CV, suggesting that this characteristic may be used for species recognition. Of course, amplitude call characteristics may also play a role for both intra- and inter-individual recognition but these characteristics could not be measured with the equipment available in the field.

The advertisement calls of *Bufo biporcatus*, *Occidozyga sumatrana*, and *Rana chalconota* were previously undescribed and thus no comparison with previous recordings is possible. The advertisement call of *Bufo melanostictus* from the state of Coorg, India, has been previously described by Hampson and Bennet (2002). They reported that the average duration of the calls of the specimens of India was 40 s and the average dominant frequency 1.6 kHz. The average pulse rate was not given. Compared with our recordings, the dominant frequency is very similar but the duration is extremely different. This is probably because the call described by Hampson and Bennet (2002) refers to the calls we only recorded from a single chorus from a distance, and that most of our recordings were from isolated males. In any event, the comparison of the call characteristics does not suggest a clear difference between the populations recorded. The fact that this species is always found tightly related to anthropogenic and highly disturbed habitats and never in primary forest throughout its distribution (Iskandar 1998), suggests that this species is probably introduced indirectly by human activities, and that all the toad populations may belong to the same species.

The advertisement call of *Fejervarya* (*Limnonectes*) *limnocharis* has been recently described in individuals from Coorg, India, as a pulsed call with an approximate duration of 70 ms and 1.4 kHz of dominant frequency (Hampson and Bennet 2002). This description is extremely different from our results. Veith et al. (2001) have proposed that some populations of *F. limnocharis* from Java are different species based on morphological and molecular characters; thus, rather than a single species, *F. limnocharis* is actually a complex of species. Our results support this view and we recommend further study of the taxonomic status of this species, including recording and analysis of the advertisement calls.

The advertisement call of *Polypedates leucomystax* has been previously described in individuals from other populations. The comparison of the acoustic characters suggests that there is high variation among populations (Sánchez-Herráiz et al. 1995). Heyer (1971) described two different call types in individuals from Sakaerat in Thailand. The Thailand calls had a slightly longer duration (230–380 ms), were made up of only four to five pulses, and had similar dominant frequency (2.5–2.6 kHz) compared with the calls of the individuals from Bali. In summary, these calls recorded from Thailand are quite different from those recorded from Bali. In addition, we did not record any call types other than the advertisement call, while Matsui (1982) described different types of call for *P. leucomystax* from Sabah, in the Malaysian part of Borneo. What the author described as the primary mating call is somewhat similar to our recordings (average duration 130 ms, an average of 12.8 pulses per call, and average dominant frequency of 2.5 kHz) although he described a series of harmonics which we did not find. This difference could be due to the different equipment with which the recordings were made, or to different analysis techniques. The other type of call he describes is a tonal note that does not resemble anything from our

recordings. Kuramoto (1986) described the advertisement call of *P. leucomystax* from Taiwan but these populations were later classified as a distinct species, *P. megacephalus*, by Matsui et al. (1986). In this case, the advertisement calls were composed of short pulses with a complex spectral structure (range 0.0–3.0 kHz). The number of pulses in each call varied between one and five. This call is somewhat similar to the longer calls described by Heyer (1971). The calls of *P. leucomystax* from Negros, Philippines, were described by Brzoska et al. (1986) as pulsed calls with an average duration of 192 ms and an average pulse number of 16.2 per call. The dominant frequency was around 2.5 kHz. This type of call is very similar to our results but Brzoska et al. (1986) also describe a second type of call, which is less intense, that we did not record. More recently, Hampson (2000) also described the call of *P. leucomystax* from another population in the Philippines. In this case the call is described as very variable with a variety of ''clicks, gurgles and croaks''. The croaks had a dominant frequency around 0.7 kHz. The description of the calls suggests they are very different from our results. Sánchez-Herráiz et al. (1995) described the calls of individuals from Sarawak, Borneo. The main type of call described is very similar to our recordings (average duration 143.5 ms, 10–16 pulses per call, and an average frequency of 2.6 kHz), although they found sometimes supranumerary pulses of similar dominant frequency in some calls. They also found a second type of call with lower intensity, average duration of 40 ms, three to five pulses per call, and an average frequency of 2.4 kHz. Narins et al. (1998) compared different characteristics, including the calls, between two morphs of *P. leucomystax* found in a pond near Kuala Lumpur in peninsular Malaysia, and his results strongly suggested that the two morphs were not the same species. Both morphs had three different types of call. What he defined as ''morph A'' had two types of advertisement call (A1 and A2) and a third call defined as ''staccato call''. A1 call was very similar to the calls recorded by us from *P. leucomystax* in Bali. This call had an average duration of 174.3 ms, a mean dominant frequency of 2.2 kHz, and a mean 13.2 pulses per call. The calls from the other morph are completely different from the calls we recorded in Bali. In summary, the main calls described from populations of the Malaysian part of Borneo (Matsui 1982; Sánchez-Herráiz et al. 1995), from Negros, Philippines (Brzoska et al. 1986) and from one of the morphotypes of peninsular Malaysia (Narins et al. 1998) are somewhat similar to our recordings and we expect them all to be one taxon. Although we did not record any other type of call from the individuals of Bali as in the previously mentioned studies, this could be due to the small sample size ($n=6$) and to the fact that all males recorded by us were calling isolated, not in a chorus aggregation. On the other hand, the call descriptions of *P. leucomystax* from Thailand (Heyer 1971) as well as the descriptions from Polillo (Philippines) (Hampson, 2000) and from the ''morph B'' of peninsular Malaysia (Narins et al. 1998) are all quite different from our calls, and among them. The duration and dominant frequency described from the individuals of Thailand (Heyer 1971) are similar to our results, but the pulse structure is completely different. In the case of the specimens from Polillo (Hampson 2000), the description of the call in the manuscript is not very detailed but differs very much from our results. Finally our results, as well as those from other populations of *P. leucomystax* (Matsui 1982; Brzoska et al. 1986; Sánchez-Herráiz et al. 1995), agree with the suggestion made by Narins et al. (1998) that ''morph B'' described in their article is probably a different species from ''morph A''. This high variation in the acoustical characteristics of the calls of *P. leucomystax* between different locations of SE Asia agrees with the high morphological variability found by Inger (1966), who proposed *P. leucomystax* to be a complex of species. Further studies of the taxonomic status of this species will be welcomed.

Acknowledgements

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