



The calls of the poorly known Philippine Flat-headed frog, *Barbourula busuangensis* (Anura: Bombinatoridae)

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Abstract. We describe the call of *Barbourula busuangensis*, a peculiar and elusive fully aquatic frog endemic to the Palawan archipelago of western Philippines. This species is so poorly known that most of its basic natural history characteristics (reproductive mode and seasonality, diet, age structure, lifespan) remain to be discovered. Contrary to the calls of other frog species adapted to life in fast-flowing streams, the call of *B. busuangensis* has a very low fundamental frequency around 250 Hz, with an average duration of 1.2 seconds. Additionally, its pulsed, amplitude modulated structure differs from the tonal calls of all known species in its most closely-related (sister) clade, the genus *Bombina*.

Key words. Amphibia, bioacoustics, Palawan, torrent species, vocalizations.

Introduction

Barbourula TAYLOR & NOBLE, 1924, together with *Bombina* OKEN, 1826 are the living representative genera of the family Bombinatoridae GRAY, 1825, a group of basal frogs distributed from temperate Europe and East Asia to tropical Southeast Asia (FROST 2023). While the six species of *Bombina* occur, with disjunct distributions, in the continental Europe and Asia, the two species of *Barbourula* exhibit insular distributions. Whereas *B. kalimantanensis* ISKANDAR, 1978 is endemic to the Indonesian portion of Borneo (Kalimantan), *B. busuangensis* TAYLOR & NOBLE, 1924 (Fig. 1) occurs in the Philippine island of Palawan and some adjacent islands, both in the north (Busuanga and, perhaps, Culion, in the Calamian archipelago), and offshore the southernmost tip of Palawan (Balabac; FIDENCI [2007], FROST [2023]).

Barbourula represents a very old clade (BLACKBURN et al. 2010), and it is distinguished as one of the remaining, least-studied anuran groups (AmphibiaWeb 2022), despite the many characteristics that make the genus of particular interest to anuran systematists, ecologists, and natural historians. These fully aquatic and nocturnal frogs inhabit

clear, rocky, well oxygenated forest streams (Fig. 2), from sea level to moderate elevations, and show some particularly odd features. For example, *B. kalimantanensis* is the only anuran species purportedly lacking functional lungs (BICKFORD et al. 2008), and from this assumption we infer that its oxygen intake might be entirely cutaneous; in contrast, *B. busuangensis* has fully functional lungs. Perhaps the most remarkable gap in our knowledge about *Barbourula* is how these frogs reproduce. This void of information is especially interesting due to the presence of large, unpigmented oviductal eggs in females of at least *B. busuangensis* (Fig. 3), and the fact that small juveniles have been readily observed and collected (e.g., AFUANG & CIELO 2010), whereas tadpoles have never been reported. These data suggest the possibility that *Barbourula* may have evolved a unique mode of reproduction not yet described for aquatic anurans (INGER, 1954, BROWN & ALCALA 1983, ALCALA & BROWN 1987).

Although comprehensive and exhaustive information has been published on the osteology and myology of *B. busuangensis*, mostly in a context of comparative and evolutionary anatomy (CLARKE 1987, ROČEK et al. 2016), very little is known about its distribution, ecology, and natural

history. Nonetheless this species is considered of conservation priority in Palawan (ALCALA & CUSTODIO 1995) and has been recently tagged with the IUCN's category "Near Threatened" (NT: IUCN 2022), whereas the National Philippine government's Red List, using non-IUCN methodology, classifies the species as "Vulnerable" (GONZALEZ et al. 2018). Both assessments, however, highlight the need for base-line information on its natural history and distribution in order to implement proper management and conservation policies.

Among the components of the reproductive biology of most anuran species, the advertisement calls (if present) have an important role. Their characteristics are tightly related to the type of environment, behavior, mate recognition, and courtship, and, ultimately, sexual selection and fitness (RYAN 1992). Herein we describe vocalizations of *B. busuangensis* obtained in two different circumstances. Although with some limitations, our description represents an important step forward towards our goal to understand the biology of this elusive and poorly known species.

Material and methods

Recordings of the species' calls were obtained by JB, LA and AL between 16–21 June 2005 at Kalinawnaw River (Barangay Quezon, Busuanga, $12^{\circ}13'56.0''$ N, $119^{\circ}56'49.4''$ E) with a Sennheisser ME-66 directional microphone and a Sony WM D6C recorder. One animal was recorded calling in the field (see below), and additional calls were recorded from selected individuals in captivity, placed in plastic containers $60 \times 40 \times 50$ cm, filled with water 10 cm deep (Fig. 4). In the tanks, calls were recorded under water, using a SEIS miniature hydrophone YS-3000. An attempt to make experiments of phonotaxis was carried out inside the tanks, but responses were too weak and no data amenable of further analyses were obtained. Recordings were digi-



Figure 1. Adult individual of *Barbourula busuangensis* from Bulaalacao River, North Palawan (Photo: IDLR).

tized at 44.1 kHz sampling frequency and 16-bit resolution, and analyzed with Raven 1.1 (Cornell University, Ithaca, New York). Figures were produced with the R package See-Wave (SUEUR et al. 2008). Temporal data were obtained from the oscillograms and frequency information was obtained using fast Fourier transforms (FFTs) (frame width, 1024 points). For call parameters, we follow the definitions proposed by KÖHLER et al. (2017): a call being the main acoustic unit in a frog vocalization, notes being smaller

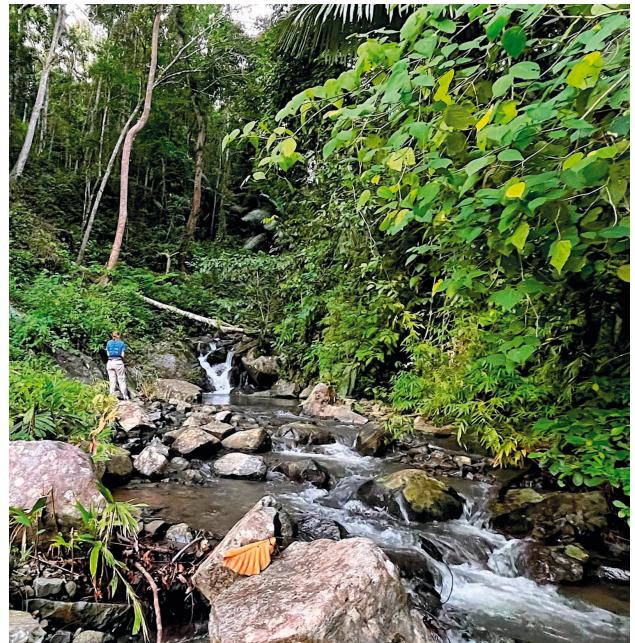


Figure 2. Characteristic habitat of *Barbourula busuangensis* in Banon creek, central Palawan (Photo: MM).



Figure 3. Adult female of *Barbourula busuangensis* showing mature, unpigmented eggs through the ventral skin (Photo: IDLR).

subunits, separated by silence of short duration, pulses being sound bursts within calls or notes, fundamental frequency being the base frequency produced by the vocal cords (lowest harmonic), and dominant frequency being the frequency where more power is concentrated within the whole power spectrum. Recordings are deposited in the Fonoteca Zoológica of the Museo Nacional de Ciencias Naturales (www.fonozoo.org) with the access numbers 14316 (field) and 14317 (tanks), and are available in the web checklist 'Frog Calls of the World'.

Results

During several nights of fieldwork in 2005, many individuals (juveniles and adults) were observed in the Kalinawnaw River. Some large individuals (SVL > 80 mm) were seen on the shore, partially submerged. Only one individual – presumably a male – was recorded in natural conditions when it was calling from the river bank, perhaps on a rock wall approximately 2 m above water. However, the individual was not detected, and we attribute the recorded call (15 calls in total) to *B. busuangensis* based on its general similarity to the calls recorded in the tanks. Furthermore, a moderately-sized (~70 mm SVL) female (but mature, showing eggs through the abdominal skin) approached the location where the individual was vocalizing, albeit additional interaction, courtship and anticipated amplexus was not observed. At the time of recording, between 21–23 h, water temperature was 26°C.

The call of the individual recorded in the field was a single pulsed note with a very low emphasized (fundamental) frequency centered about 250 Hz, and substantial power at 630 Hz (Table 1, Fig. 5A). The average duration was 1.2 s, and the number of pulses per call was 10–18 (N=15). The call was repeated at relatively regular intervals (averaged interval between calls was 37 s). The peak amplitude value inside the call was positioned at the end of the call, most

Table 1. Parameters of the calls of *Barbourula busuangensis* (mean, SD in parenthesis and range).

	Field recordings	Tank recordings
Sample size	15 calls from a single individual	12 calls from at least 3 different individuals
Call duration (s)	1.227 (0.213) 0.944–1.716	0.658 (0.092) 0.355–1.037
Intercall interval (s)	37.2 (8.6) 25.8–48.0	–
Number of pulses per call	13 (2.5) 10–18	11 (1.1) 6–16
Pulses/second	10.6 (0.8) 9.9–13.5	18 (0.8) 14.5–20.0
Pulse duration (s)	0.044 (0.009) 0.029–0.067	0.024 (0.002) 0.022–0.027
Pulse period (s)	0.103 (0.009) 0.084–0.129	0.042 (0.002) 0.022–0.027
Dominant frequency (Hz)	254 (13) 216–264	535 (61) 405–676
Other frequency (Hz)	635 (32) 598–671	–

often at the second to last pulse (Fig. 5A). Pulses were regularly distributed within the call, but the inter-pulse interval preceding the final pulse showed a greater period (Fig. 5A).

Recordings inside the water-filled tanks (water temperature 26°C) were obtained on three different nights from at least three different individuals. Individual frogs were replaced daily and, of the nine individuals used, four were females, identified by the presence of eggs visible through the ventral skin. Frogs called occasionally, with only 12 calls registered in about four total hours of recording time. Calls recorded inside the tanks exhibited a pulsed structure (Fig. 5B) and low emphasized/fundamental frequencies similar to those of the field-recorded individual (Fig. 5A), but some temporal and structural differences were evident.



Figure 4. Plastic tanks with hydrophone and individuals of *Barbourula busuangensis*.

Call duration was shorter (0.658 vs 1.227 s in average), the number of pulses was lower (11 vs 13 in average), and the pulse rate was higher (18 vs 11 in average) (Fig. 5B). Contrarily to calls recorded in the field, calls recorded inside the tanks exhibited greater variation in amplitude. Also, calls obtained from the tanks presented higher dominant frequencies, perhaps as a result of an enhancement of the second harmonic due to resonance within our experimental enclosure chambers.

Discussion

The fact that similarly structured vocalizations were obtained from individuals calling both (1) from presumably above water, at an elevated position on the river bank, with acoustic signal transmission through common atmospher-

ic air; and also, (2) from other individuals, recorded by hydrophones, vocalizing perhaps under water (inside experimental water-filled enclosures), with signal transmission through water, indicates that *B. busuangensis* might vocalize both outside and from the water, partially or totally submerged. Although spectral differences between calls registered in the field (likely airborne) and those registered inside the tanks (likely subaquatic) could be expected, differences in the temporal- and amplitude-related characteristic domains could be more difficult to explain. We cannot discard that the differences in vocalizations are due to having recorded calls from both males and females, which might vary. An alternative explanation is that placing several individuals together in the tank could have triggered biased or artifactual social interactions, and their vocalizations could represent generalized agonistic or encounter calls (aggressive signals to establish spacing between call-

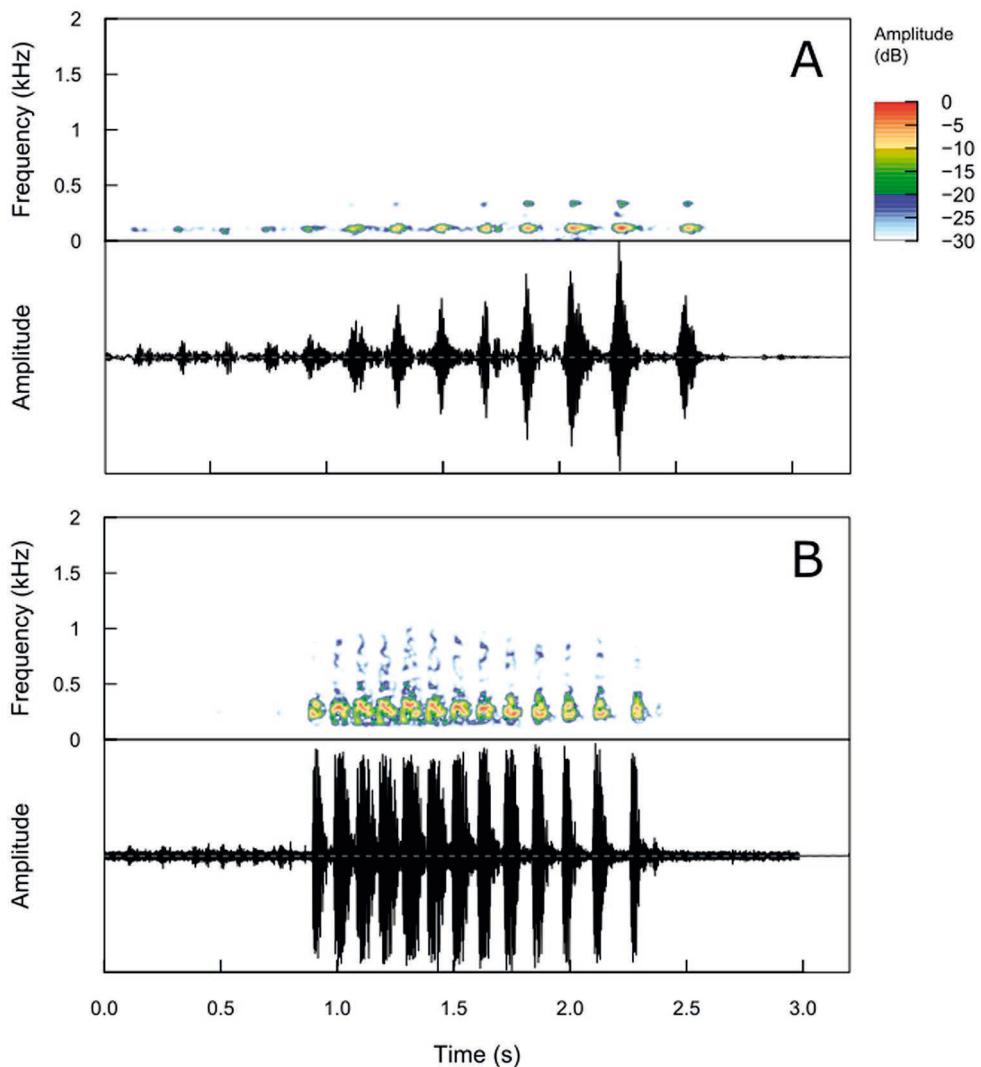


Figure 5. Audiospectrogram (above) and oscillogram (below) of calls of *Barbourula busuangensis*: A) Advertisement call recorded in the field; B) call recorded with hydrophone inside plastic tanks.

ing individuals sensu TOLEDO et al. [2015]). In contrast, we find it more likely that the call emitted by the individual on the shore above the river was an advertisement call (Fig. 5A).

Aquatic frogs living in noisy, fast-flowing streams (where cascades are common), usually have calls adapted to be heard by congeners also inhabiting conditions characterized by high levels of ambient noise. Developing adaptations to overcome the noise implies that the calls must not only be heard, but must also be properly decoded by conspecifics and, importantly, not confounded with calls of other sympatric/syntopic anuran species. Calls of torrent species can be variable in duration and structure, either tonal or pulsed, but are frequently high-pitched, that is, they have high dominant frequency; often, such species also exhibit pronounced frequency modulation (GOUTTE et al. 2018). As an extreme adaptation, ultrasonic vocalizations and a modified tympanum have been described in at least two species of Asian torrent frogs in the family Ranidae, *Huia cavitympanum* (BOULENGER, 1893) and *Odorrana tormota* (WU, 1977) (ARCH et al. 2008, SHEN et al. 2008). High-pitched frog vocalizations propagate well, contrast with (and, thus “overcome”) a noisy background, and do not appreciably degrade or attenuate when transmitted through open air, from elevated perches, as has been documented in some species of glass frogs (Centrolenidae; see GUAYASAMIN et al. 2020) and other tree frogs (Hylidae, e.g., *Hyloscirtus armatus*; see DUELLMAN et al. 1997). However, vocalizing from perches on vegetation above a stream is quite different, acoustically, from calling at the level of the stream itself or from rocks on a running riparian water course’s bank, immediately adjacent to water. In such microhabitats and corresponding, localized, acoustic environments, the source of ambient environmental background noise is much more proximate to vocalizing animals and potentially much more intense as a potential selective agent. In conditions like these, attenuation (loss of sound power or amplitude with distance from the source), degradation (loss of sound quality or signal fidelity), and/or distortion (environmentally induced loss of spectral components, filtering of specific frequencies by environmental heterogeneities, etc.) of the sound over short distances can be severe, making it inaudible or unrecognizable by conspecifics. In such cases, some anuran lineages appear to have evolved compensatory communications systems or switched to other signal modalities – such as, for example, external vocal sacs that are used for visual communication, as is the case of the Brazilian large, torrent species *Phantasmarana apuana* (POMBAL, PRADO & CANEDO, 2003) (AUGUSTO-ALVES et al. 2018). However, other species of this genus like *P. boticariana* (GIARETTA & AGUIRA 1998) seem to vocalize using low frequency calls (MUSCAT et al. 2020) and the same has been reported for the large riverine species *Mantidactylus guttulatus* (BOULENGER, 1881) from Madagascar (VENCES et al. 2004). Visual signaling has been reported in numerous other diurnal, non-arboreal frogs, representing a different way of social and sexual communication; visual mate-recognition, ad-

vertisement, and courtship has evolved several times independently (e.g., *Atelopus* spp. [Bufonidae], *Staurois* spp. [Ranidae]; see HÖDL & AMÉZQUITA 2001). Visual signaling seems to be absent in *B. busuangensis* and no related structures or observed behaviors indicate that such way of communication is present. Still, the call of *B. busuangensis*, with its remarkable low frequency (potentially subject to low-frequency ambient environmental noise interference from running water) and general low amplitude (similarly vulnerable to being masked by sounds associated with cascading, or generally flowing streams and rivers), would appear to be of low performance for the general environment where this species occurs, unless their communication takes place only underwater; in this case, lower frequencies would be favored.

In addition, it must be considered that *B. busuangensis* lacks an external tympanum, although they have a complete middle ear including columella and tympanic annulus (ROČEK et al. 2016). This is also the case in the bufonid *Atelopus franciscus* LESCURE, 1974, studied by BOISTEL et al. (2011) in French Guiana. Like *B. busuangensis*, males of this species lack external vocal sac and have a complete middle ear, but no external tympanum, and still they are able to communicate in their noisy riverine habitat by means of calls of low intensity and low frequency (~800 Hz; although much higher than those of *B. busuangensis* this difference is partly due to the interspecific disparity in body size between the two lineages). Anatomical pathways for low-frequency sound transmission to the inner ear, other than the middle ear, like the opercularis system or bones and other tissues from the sides of the head (BOISTEL et al. 2011), must be considered as potential pathways for sound conduction that may result in effective communication in noisy environments and through water.

While there is no information about whether the only congeneric species, *B. kalimantanensis*, has any vocalizations, the advertisement calls of species in the only other bombinatorid genus, *Bombina* (the extant sister clade of *Barbourula*; BLACKBURN et al. [2010]), are well documented. Their calls are single tonal notes of relatively high, non-modulated frequency, which corresponds with the advertisement call classified as “Guild A” by EMMRICH et al. (2020). This is markedly different from the call described herein for *B. busuangensis*, which is pulsed and clearly fits the most common guild characterized in anurans, i.e., “Guild C” (EMMRICH et al. 2020). Unlike most vocalizing frogs, sound production in *Bombina* is made during inspiration (ZWEIFEL 1959, LÖRCHER 1969), but we have no information on the mechanism involved in *Barbourula*. Although in the same family and thus phylogenetically related, these two genera have a very old divergence date, estimated around 47.1 mya (BLACKBURN et al. 2010); hence, similarity in call structure due to phylogenetic relatedness might not actually be expected. Additionally, *Bombina* and *Barbourula* species are highly ecologically dissimilar (see DUELLMAN & TRUEB 1986). Likewise, in Alytidae, the sister group of Bombinatoridae, some taxa have tonal calls (species of *Alytes* WAGLER, 1830) and other possess pulsed calls

(members of *Discoglossus* OTTH, 1837 and *Latonia* MEYER, 1843). Given the antiquity of Archaeobatrachia, disentangling the evolution of call types (spectral and temporal parameters and their ancestral character conditions) is challenging.

Since advertisement calls are heavily subjected to both sexual selection and natural selection (DUELLMAN & TRUEB 1986), we might predict that non-closely related frog taxa with similar morphology, microhabitats, and environmental constraints may converge on a similar call structure (see BRADBURY & VEHRENCAMP 2011, GOUTTE et al. 2018). Perhaps the best example to compare with *Barbourula* would be that of the South American, Andean genus *Telmatobius* WIEGMANN, 1834. *Telmatobius* frogs are remarkably similar to *Barbourula* in ecology (aquatic), overall morphology and appearance, including absence of an external ear. For most *Telmatobius* species, advertisement calls are unknown (or believed to be absent), but some species emit vocalizations. In the case of the riverine species *T. hintoni* PARKER, 1940 and *T. oxycephalus* VELLARD, 1946, calls can be emitted both airborne and underwater and they are considered poorly adapted for transmission in noisy aquatic environments (BRUNETTI et al. 2017). Their calls are structurally similar to those of *B. busuangensis* described herein and also exhibit remarkably low emphasized frequencies (mean 482 Hz in *T. hintoni*, 637 Hz in *T. oxycephalus*; BRUNETTI et al. [2017]). It is noteworthy that, although nuptial excrescences and/or keratinized spicules are common features in males of *Telmatobius* spp. (see DE LA RIVA [2005]) and in other aquatic frogs inhabiting fast-flowing streams, *B. busuangensis* apparently lacks these structures and other as of yet surveyed phenotypic indications of sexual dimorphism.

The fact that our only individual recorded in natural conditions might be well above the flowing water on a rocky wall may indicate a way to mitigate the potential acoustic interference from high ambient background cascading water noise, although admittedly such an assertion on our part is based on a single observation. However, climbing on large stones, boulders, and rock walls surrounding cascades has been observed by us during fieldwork on multiple occasions. Individuals of *B. busuangensis* are particularly common in pools at the base of such cascades, waterfalls, and seeps – and our frequent observations of various stages of maturation (including tiny juveniles; specimens deposited in KU) perhaps indicate that these are preferred sites for breeding and development. Clearly, additional habitat-, seasonal-, and life stage-targeted fieldwork is sorely needed. Our experience with this work strongly suggests to us that such studies, necessarily conducted in natural field settings, will be required to document the most basic natural history of *B. busuangensis*. Wholly absent from the literature of the past three decades, field-based observational documentation of naturally occurring life history parameters are the only means of arriving at a better understanding of the reproductive mode, mating and courtship behaviors, socially-variable communication, and development of this secretive and most enigmatic Philippine anuran species.

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