

Advertisement calls of seven species of Sarawak frogs from the family Megophryidae

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ABSTRACT

The vocalization patterns of frogs in the family Megophryidae from Sarawak, Malaysia, play a crucial role in their behavioral ecology. This study aims to document and analyze the advertisement calls of seven Megophryidae species across diverse habitats in Sarawak. Using field recordings and acoustic analysis, distinct call characteristics, including frequency, duration, and temporal patterns, were identified. Advertisement calls were recorded and analyzed using SoundRuler Acoustic Analysis (ver. 0.9.6.0) and Praat Acoustic Software, allowing for species differentiation based on call parameters. The results revealed species-specific variations in vocalization, with pulse note count, note repetition rate, and dominant frequency emerging as the most distinguishing features. *Leptobrachium ingeri* exhibited the highest number of pulsed notes per call, while *Leptobrachella gracilis* demonstrated the highest note repetition rate, and *Leptobrachella mjobergi* produced the highest dominant frequency. These findings enhance our understanding of species-specific vocalizations and their ecological significance, particularly in mate selection, territorial defense, and environmental adaptation. This study underscores the importance of acoustic monitoring in biodiversity conservation and provides a foundation for future research on amphibian communication in tropical ecosystems.

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1. INTRODUCTION

Vocal communication in frogs is intricately shaped by sexual selection (Wilhite & Ryan, 2024), mechanisms of reproductive isolation (Santana et al., 2025), and specialized neural processes (Kelley, 2004). Male frogs emit species-specific advertisement and aggressive calls, serving the dual purpose of attracting potential mates and deterring rival males. These vocal signals are subject to intense sexual selection pressures, as females often select mates based on acoustic features (Santana et al., 2025). To locate and evaluate suitors, female frogs utilize a combination of auditory and visual cues, such as the inflation of the male's vocal sac (Elias-Costa, 2025). For example, the *Staurois latopalmaris* species, as observed by Preininger et al. (2009), exhibits foot-flagging, where males raise one or both hind limbs to display their brightly colored webbing as a mating strategy. This action occurred more frequently than advertisement calls and likely represents an adaptive strategy that supplements or replaces acoustic signals in environments with high ambient noise, such as near waterfalls, where sound transmission is compromised.

In dense choruses, accurate sound localization

becomes essential, as overlapping vocalizations can obscure signal perception. Inhibitory circuits within the auditory system act as filters, enhancing the ability to discriminate among calls. The auditory midbrain hosts neurons finely tuned to temporal elements such as pulse repetition rates and amplitude modulation, which are the key components for species-specific recognition (Kelley, 2004). Collectively, these distinct vocal patterns promote pre-mating isolation and play a pivotal role in frog speciation

In Malaysia, and particularly in the biodiverse rainforests of Borneo, research on anuran vocalizations remains relatively limited. Active monitoring (manual recording) was constrained by limited nighttime field hours and labor-intensive nature, and for passive recording, there is a need for a sound bank first, to compare the recorded calls to confirm the species. However, available studies have demonstrated the important role of bioacoustics data in distinguishing species. For instance, (Zainudin et al., 2010) reported significant differences in call characteristics among species in the genus *Pulchrana*, with variations in pulsed note numbers and repetition rates. Marly et al. (2017) further demonstrated that call parameters such as note duration,

pulse rate, call energy, frequency, and intensity effectively discriminated between *Pulchrana* species in Sarawak. Similarly, Amram et al. (2018) highlighted the importance of advertisement call traits in distinguishing species within Sarawak's Bufonidae family, with number of notes, note repetition rates, and pitch being the most apparent characters. Playback experiments conducted by Amram et al. (2020) also demonstrated species-specific responses among male *Pulchrana baramica*, *Pulchrana glandulosa*, and *Kurixalus appendiculatus*. Males were able to recognize conspecific advertisement calls and, in some cases, responded with aggressive vocalizations and behavior. These observations offer compelling behavioral evidence that acoustic signals play a critical role in facilitating reproductive isolation among sympatric frog species. Additional studies on *Microhyla* species in Borneo also reported interspecific differences in dominant frequency (Dehling, 2010).

Further supporting these findings, Deka & Zainudin (2025) identified pulse duration, call energy, and call frequencies as key parameters in differentiating frog species. Their research also demonstrated a strong correlation between dominant frequency, pulse duration, and body size, indicating that larger frogs typically produce lower-frequency calls. In addition to calling properties, vocal structure plays a significant role in shaping acoustic signals. A study by Deka et al. (2015) on the family Ranidae examined morphological variations in the vocal apparatus and found that closely related species possess similar vocal structures, which may enhance species recognition and contribute to reproductive success.

Despite this growing body of work, the vocalization patterns of leaf-litter frogs from the family Megophryidae remain poorly studied in Sarawak. This family includes cryptic species known for their remarkable camouflage, often resembling dead leaves on the forest floor to avoid predation (Inger & Stuebing, 2017). For example, *Pelobatrachus nasutus* exhibits highly specialized morphological adaptations, including skin folds that mimic leaf veins and sharp projections extending beyond the eyes and snout (Inger & Stuebing, 2017). As for vocalizations, the calls of Megophryidae frogs play a crucial role in their communication, mating behaviors, and territory establishment (Goutte et al., 2013; Xiong et al., 2015). Moreover, call characteristics can provide valuable insights into species-specific communication and serve as non-invasive tools for taxonomic clarification and biodiversity monitoring, especially in morphologically cryptic groups (Köhler et al., 2017).

The Family Megophryidae currently comprises four genera and 29 species in Borneo, with Sarawak alone hosting four genera. This study includes representatives from three genera, specifically seven species: *Leptobrachella juliandringi* (Dring's Dwarf Litter Frog), *Leptobrachella mjobergi*

(Mjoberg's Dwarf Litter Frog), *Leptobrachella gracilis* (Sarawak Slender Litter Frog), *Leptobrachella hamidi* (Whitebellied Slender Litter Frog), *Leptobrachium montanum* (Montane Large-eyed Litter Frog), *Leptobrachium ingeri* (Inger's Black-eyed Litter Frog), and *Pelobatrachus nasutus* (Bornean Horned Frog). Recent studies have highlighted the diversity and ecological significance of these species in their respective habitats. Conservation efforts are crucial for these frogs, as their unique adaptations and ecological roles contribute significantly to the biodiversity of Borneo (Goyes Vallejos et al., 2017).

Understanding the vocalization patterns of Megophryidae frogs in Sarawak is therefore essential, not only for filling taxonomic knowledge gaps but also for supporting conservation initiatives. Given the rapid rate of habitat loss in Borneo, documenting the bioacoustic profiles of these understudied species could significantly aid in monitoring population status and guiding conservation efforts (Goyes Vallejos et al., 2017), since acoustic surveys can reveal previously undocumented populations or range extensions. Acoustic monitoring allows researchers to identify species without physical capture or visual confirmation, which can reduce stress on animals and enables long-term monitoring in sensitive habitats (Sugai et al., 2019). Acoustic monitoring has emerged as a vital tool in biodiversity conservation, particularly for cryptic and nocturnal taxa such as Bornean frogs (Köhler et al., 2017).

By capturing species-specific vocalizations, researchers can detect presence, estimate population trends, and monitor habitat use with minimal disturbance to the ecosystem (Odom & Mennill, 2010). This method is especially valuable in regions like Borneo, where dense forest cover and high species richness pose challenges to traditional survey techniques (Inger & Stuebing, 2005). Moreover, bioacoustic data contribute to species identification and taxonomic clarification, as vocal traits often reflect evolutionary divergence, which is critical in areas with high rates of cryptic speciation (Köhler et al., 2017). As habitat loss and climate change accelerate, integrating acoustic methods into biodiversity assessments offers a scalable and cost-effective approach to safeguarding amphibian diversity (Gibb et al., 2019).

2. MATERIALS AND METHODS

The field surveys were conducted at various habitats across Sarawak, Malaysian Borneo, including Kubah National Park, Gunung Santubong National Park, Matang Wildlife Center, Ranchan Recreational Park, Kapit, Tanjung Datu National Park, and Bungo Range National Park (Table 1). These sites span a range of lowland to lower montane forest ecosystems, typical of the highly biodiverse rainforests of

Borneo. Kubah and Matang are characterized by lowland dipterocarp forests and include clear, rocky streams ideal for stream-breeding anurans. Gunung Santubong and Tanjung Datu feature coastal hill dipterocarp forests with steep terrain and high rainfall, supporting amphibians that depend on both terrestrial and aquatic microhabitats. Ranchan Recreational Park includes disturbed secondary forest and riparian zones. The Kapit and Bungo Range encompass more remote, mixed dipterocarp forests.

Table 1: Location of vocalisation field sampling.

No.	Location	Forest Type	Coordinate
1	Tanjung Datu National Park	Coastal hill dipterocarp	N 01°42.943' E 110°26.752'
2	Matang Wildlife Centers	Lowland Dipterocarp	N 01° 36'40.4" E 110° 09'49.7"
3	Kubah National Park	Lowland Dipterocarp	N 01° 36'19.3" E 110° 11'30.3"
4	Santubong National Park	Coastal hill dipterocarp	N 01° 73.163' E 110° 33243'
5	Ranchan Recreational Park	Disturbed secondary forest	-
6	Wilmar Plantation, Miri	Modified agricultural landscape	N03° 16.00' E113° 40.0'
7	Kapit	Mixed Dipterocarp	-
8	Bungo Range National Park	Mixed Dipterocarp	-

Visual and auditory surveys were conducted during the night, when anuran activity and vocalizations are at their peak. The data collection was conducted between 2015 to 2019. Each site was surveyed for a duration ranging from one to four weeks, with two to three researchers conducting the surveys per session. Anuran vocalizations were recorded opportunistically upon encounter, ensuring minimal disturbance to the animals. Recordings were done using a TASCAM DR-40 Linear PCM Recorder in .wav format, with a 44.1 kHz sampling rate, 16-bit depth, and in stereo mode. The use of a higher sampling rate enabled accurate recording of a wide frequency range. For each species, calls from two to three individual males were recorded for durations ranging from two to ten minutes, depending on individual availability (Leong et al., 2003). The total number of anurans recorded in this study is summarized in Table 2.

After recording, individuals were identified in the field based on morphological characteristics, using identification keys and descriptions provided by Inger & Stuebing (2005) and Inger et al. (2017). Voucher photographs were taken when necessary for reference. For call analysis, samples were extracted as 60-second segments from the recordings. Sample size (n) was determined by the number of calls or notes analyzed within this period.

Acoustic parameters were analyzed using SoundRuler Acoustic Analysis Software version 0.9.6.0 and

Praat Software. Terminology and classification of acoustic variables followed established guidelines by Littlejohn (2001), repurposed later by Deka & Zainudin (2025), ensuring consistency in call description and comparison.

Table 2: Species and Number of Individuals of Megophryidae Recorded.

Species	Field No.	Location
<i>Leptobrachella juliandringi</i> (n=2)	KPT01	Kapit
	KPT02	Kapit
<i>Leptobrachella mjobergi</i> (n=4)	TD02	Tanjung Datu NP
	TD03	Tanjung Datu NP
	KNP02	Kubah NP
	MWC06	Matang WC
<i>Leptobrachella gracilis</i> (n=7)	RC02	Ranchan RP
	RC03	Ranchan RP
	RC04	Ranchan RP
	TD04	Tanjung Datu NP
	TD05	Tanjung Datu NP
<i>Leptobrachella hamidi</i> (n=3)	KNP03	Kubah NP
	KNP04	Kubah NP
	RC05	Ranchan RP
	RC06	Ranchan RP
	RC07	Ranchan RP
<i>Leptobrachium ingeri</i> (n=3)	GS 01	Gunung Santubong NP
	GS 02	Gunung Santubong NP
	GS 03	Gunung Santubong NP
<i>Leptobrachium montanum</i> (n=1)	BR01	Bungo Range NP
<i>Pelobatrachus nasutus</i> (n=4)	KNP06	Kubah NP
	KNP07	Kubah NP

3. RESULTS

All seven species of Megophryidae investigated exhibited distinct advertisement call characteristics, indicating species-specific vocal signatures. Among the call parameters analyzed, only note repetition rate appeared significantly different among species (Table 3).

Table 3: Summary of call characteristics of selected Sarawak Megophryidae.

Species	Call Characters		
	No. of notes	Note repetition/ 60 sec	Dominant frequency (kHz)
<i>Leptobrachella juliandringi</i>	2	100	8.1
<i>Leptobrachella mjobergi</i>	2	168	9.8
<i>Leptobrachella gracilis</i>	3	364	2.67
<i>Leptobrachella hamidi</i>	1	300	7.3
<i>Leptobrachium ingeri</i>	13	5	1.9
<i>Leptobrachium montanum</i>	7	4	0.8
<i>Pelobatrachus nasutus</i>	1	2	2.1

Below are detailed descriptions of the advertisement calls for each species, accompanied by representative acoustic oscillograms and spectrograms illustrating their temporal and spectral features.

3.1 *Leptobrachella juliandringi*

Leptobrachella juliandringi (Dring's Dwarf Litter Frog) produces a continuous, repetitive high-pitched advertisement call characterized by approximately 100 notes per 60 seconds under natural conditions, where frogs vocalize spontaneously in the wild, at natural calling sites, and in the presence of conspecifics, without experimental interference or artificial stimuli. Each call consists of a series of two short, pulsed notes (Figure 1). Interestingly, occasional variations in the call structure are observed, where the first note is sometimes omitted and only the second note is emitted, indicating a degree of call plasticity. Spectrographic analysis reveals that *L. juliandringi* exhibits among the highest dominant frequencies of the examined Megophryidae species, with a peak frequency reaching up to 8.1 kHz. Additionally, the call displays harmonic structures extending beyond 20 kHz, with some harmonics reaching the ultrasonic range (>20 kHz). The production of such high-frequency calls may be an adaptation for communication in fast-flowing stream environments, where low-frequency background noise is prevalent (Chen et al., 2020). Ultrasonic communication has been documented in several anuran species and is thought to play a crucial role in mate attraction and species recognition, particularly in acoustically complex habitats (Feng et al., 2006; Zhang et al., 2015).

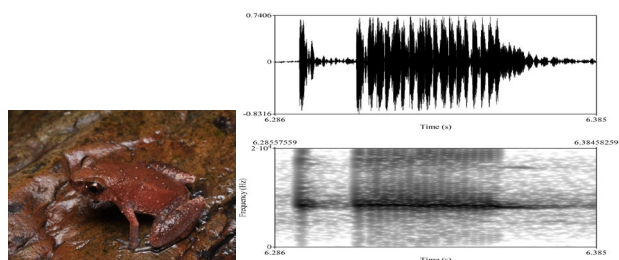


Figure 1: *Leptobrachella juliandringi* photographed in situ, accompanied by the oscillogram and spectrogram of a representative advertisement call illustrating its vocal characteristics.

3.2 *Leptobrachella mjobergi*

Leptobrachella mjobergi (Mjöberg's Dwarf Litter Frog) produces a continuous, repetitive series of high-pitched advertisement calls, averaging approximately 168 notes per 60 seconds under natural field conditions. Each call typically consists of two distinct notes (Figure 2). Similar to *L. juliandringi*, variation in call structure is observed, with occasional omission of the first note, resulting in sequences where only the second note is produced. Notably, *L. mjobergi* exhibits two distinct call types, characterized by a 'short second note' and a 'long second note'. Calling sequences often begin with a series of short notes, which, after approximately 55 seconds, transition to a mix of short and long

notes, eventually becoming dominated by the long notes. This cyclical pattern continues, with the call reverting to short notes after roughly another 55 seconds, suggesting a rhythmic modulation in call behavior potentially linked to male display strategies or calling stamina (Larter & Ryan, 2024).

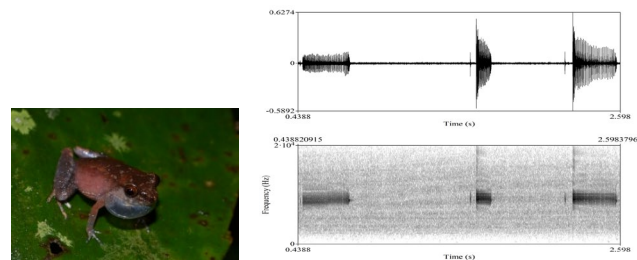


Figure 2: *Leptobrachella mjobergi* photographed in situ, accompanied by the oscillogram and spectrogram of a representative advertisement call illustrating its vocal characteristics.

Spectrographic analysis reveals that *L. mjobergi* produces some of the highest frequency calls among Bornean Megophryidae, with dominant frequencies reaching up to 9.8 kHz, which is notably higher than that of *L. juliandringi* in this study, and surpassing *L. gracilis* and *L. maurus* studied by Sukumaran et al. (2010), whose calls exhibit notably lower dominant frequencies and simpler temporal structures. Sukumaran et al. (2010) also reported slightly lower dominant and fundamental frequency for *L. mjobergi*, with each pulse being about 9.3 kHz. The calls also exhibit well-developed harmonic structures extending well beyond 20 kHz into the ultrasonic range (>20 kHz). Such high-frequency and ultrasonic calls are thought to confer adaptive advantages in noisy stream habitats, allowing males to reduce masking by low-frequency background noise and potentially enhancing female localization and species-specific recognition (Feng et al., 2006; Chen et al., 2020). The presence of alternating short and long note patterns may further aid in individual recognition or territorial signaling (Narins et al., 2006; Fang et al., 2019).

3.3 *Leptobrachella gracilis*

Leptobrachella gracilis (Sarawak Slender Litter Frog), formerly assigned to the genus *Leptolalax*, produces a distinctive advertisement call consisting of a long series of rapid, ticking notes. The calling rate is remarkably high, ranging from 360 to 364 notes per 60 seconds, making it the highest call rate among all Megophryidae species in this study (Figure 3). The initial notes of the advertisement call of *L. gracilis* consist of three pulses, which subsequently transition into a four-pulse pattern, resulting in a characteristic rhythmic ticking sound. Spectrographic analysis reveals that *L. gracilis* produces calls of medium pitch relative to other *Leptobrachella* species, with a dominant frequency centered around 2.67 kHz. Specimens from all three localities exhibited

comparable dominant frequencies. However, Sukumaran et al. (2010) reported that *Leptolalax cf. gracilis* from Tawau Hills Park, Sabah, produced advertisement calls with a downward frequency sweep ranging from 8.3 to 6.7 kHz—noticeably higher than the values observed in the present study. This discrepancy suggests that the Tawau Hills specimens may not represent *L. gracilis*, but rather a morphologically similar, potentially distinct species.

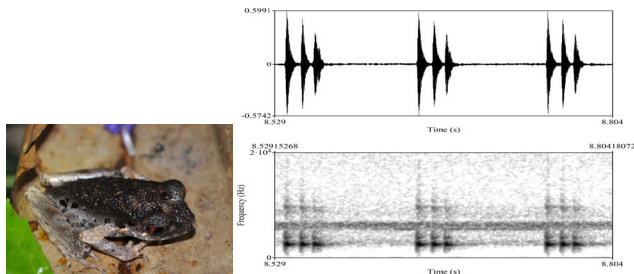


Figure 3: *Leptobrachella gracilis* photographed in situ, accompanied by the oscillogram and spectrogram of a representative advertisement call illustrating its vocal characteristics.

In addition to the dominant frequency, a clear harmonic band is visible in the spectrogram, indicating the presence of energy at multiple frequency levels. This moderate frequency range may be adaptive for effective sound transmission in dense leaf-litter environments, where both high- and low-frequency signals can be attenuated (Köhler et al., 2017; Chen et al., 2020). The exceptionally high call rate of *L. gracilis* may play an important role in reproductive isolation and species recognition within sympatric communities.

3.4 *Leptobrachella hamidi*

Leptobrachella hamidi (White-bellied Slender Litter Frog), formerly classified under the genus *Leptolalax*, produces a continuous and repetitive high-pitched advertisement call characterized by approximately 300 notes per 60 seconds (Figure 4). Each call consists of a single short, tonal note. Spectrographic analysis reveals a dominant frequency around 7.3 kHz, with a slight downward frequency modulation visible within individual notes. This high-frequency call, combined with a rapid note repetition rate, produces an intense acoustic output that may sound piercing or uncomfortable to human listeners, an effect likely adaptive for enhancing detectability in noisy stream environments (Feng et al., 2006; Grafe et al., 2012).

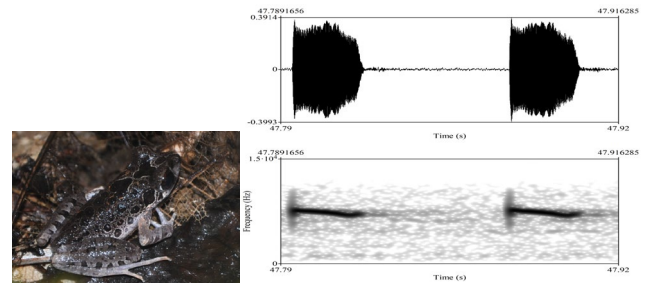


Figure 4: *Leptobrachella hamidi* photographed in situ, accompanied by the oscillogram and spectrogram of a representative advertisement call illustrating its vocal characteristics.

When compared to other *Leptobrachella* species in this study, *L. hamidi* exhibits one of the highest note repetition rates, almost as high as *L. gracilis*. However, *L. hamidi* demonstrates a significantly shorter calling session duration, with individual calling bouts lasting up to 14 seconds, whereas *L. gracilis* maintains calling bouts of up to 30 seconds. This suggests that *L. hamidi* alternates between brief, intense calling periods and longer rest intervals within a one-minute timeframe. Such a calling strategy may reflect a balance between maximizing mate attraction through rapid, high-energy signals while reducing energy expenditure and predation risk during prolonged calling bouts (Narins et al., 2006; Wells, 2007; Peignier et al., 2022).

Additionally, the combination of high frequency and rapid repetition may serve as a key mechanism for species recognition, particularly in habitats where multiple *Leptobrachella* species occur sympatrically. Acoustic differentiation characterized by temporal and spectral properties has been widely recognized as an important driver of reproductive isolation in this genus (Rowley et al., 2010; Chen et al., 2020).

3.5 *Leptobrachium ingeri*

Leptobrachium ingeri (Inger's Black-eyed Litter Frog) is a forest-dwelling species typically inhabiting lowland rainforests of coastal areas in Borneo. The advertisement call of this species consists of a series of 12 to 13 notes per calling bout (Figure 5), with each note composed of a single pulse. Calling activity is relatively low in repetition rate, averaging three to five call bouts per 60 seconds under natural conditions. Spectrographic analysis shows that *L. ingeri* produces a distinctly low-pitched call, with a dominant frequency centered around 1.9 kHz. The spectrogram also reveals the presence of visible harmonic bands, indicating energy concentration at integer multiples of the fundamental frequency.

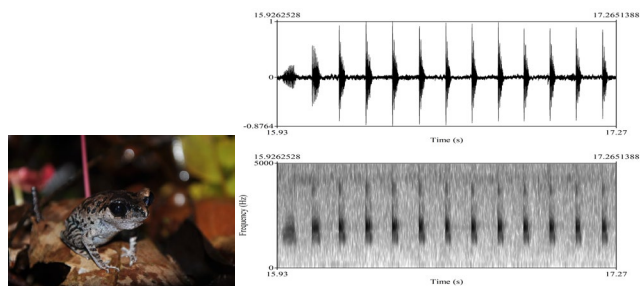


Figure 5: *Leptobrachium ingeri* photographed in situ, accompanied by the oscillogram and spectrogram of a representative advertisement call illustrating its vocal characteristics.

Low-frequency vocalizations in *Leptobrachium* species are believed to be advantageous for long-distance communication in densely vegetated rainforest environments, where lower frequencies experience less attenuation and scatter (Gerhardt & Huber, 2002; Wells, 2007; Zhao et al., 2021). Furthermore, the slow calling rate and deep tonal quality are characteristic of *Leptobrachium* species and may serve as effective mechanisms for species recognition and mate attraction, particularly in environments where multiple anuran species vocalize simultaneously (Legett & McGregor 2021).

3.6 *Leptobrachium montanum*

Leptobrachium montanum (Montane Large-eyed Litter Frog) is a species commonly found in primary montane forests of Borneo, typically inhabiting elevations above 800 meters. The advertisement call of this species consists of a short series of seven notes per calling bout, with each note composed of a single pulse (Figure 6). The calling activity is relatively slow, with approximately four call repetitions per 60-second period.

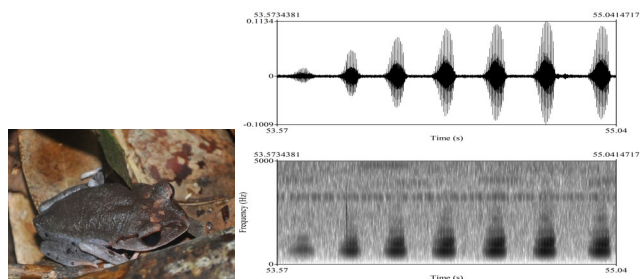


Figure 6: *Leptobrachium montanum* photographed in situ, accompanied by the oscillogram and spectrogram of a representative advertisement call illustrating its vocal characteristics.

Spectrographic analysis reveals that *L. montanum* produces a low-pitched call, with a dominant frequency centered around 848 Hz. Additionally, four harmonics are visible on the final note of each call sequence, suggesting increased vocal energy distribution across multiple frequency bands towards the end of the call. This harmonic enrichment may play a role in enhancing call detectability or conveying information about male quality (Foratto et al., 2021). Low-

frequency calls, typical for *Leptobrachium* species, are well-suited for transmission in dense montane environments, where low-frequency sounds experience less degradation and can travel longer distances (Zhao et al., 2021).

3.7 *Pelobatrachus nasutus*

The advertisement call of *Pelobatrachus nasutus* (Bornean Horned Frog), formerly known as *Megophrys nasuta*, is characterized by a loud, distinctive "honk" call, consisting of a single note per calling bout (Figure 7). In this study, the observed call repetition rate was approximately two notes per 60 seconds, although it is known that the repetition rate can increase significantly during the rainy season, likely in response to heightened breeding activity and environmental humidity (Malkmus et al., 2002; Bolitho et al., 2023).

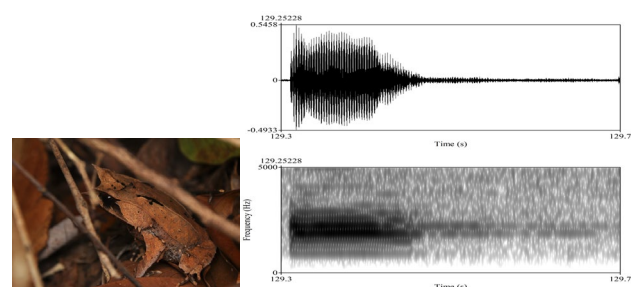


Figure 7: *Pelobatrachus nasutus* photographed in situ, accompanied by the oscillogram and spectrogram of a representative advertisement call illustrating its vocal characteristics.

Spectrographic analysis shows that *P. nasutus* produces a low-pitched call, with a dominant frequency centered around 2.1 kHz. Notably, around six harmonics are clearly visible in the spectrogram, with the third harmonic exhibiting the highest energy concentration, serving as the dominant frequency band.

P. nasutus inhabits lowland and hill dipterocarp forests, often near slow-moving streams or swampy areas, where the low-frequency, high-amplitude calls are well adapted for long-distance communication through dense vegetation (Zhao et al., 2021). Seasonal variation in calling rate is a common reproductive strategy in tropical amphibians, allowing males to maximize reproductive opportunities during peak breeding conditions (Cossio & Medina-Barcenas, 2020).

4. DISCUSSIONS

This study presents the first comparative analysis of advertisement calls among selected Megophryidae species from various habitats in Sarawak, Malaysian Borneo. The findings demonstrate clear interspecific variation in call characteristics, specifically in note repetition rate, dominant frequency, and the number of pulsed notes. Unique acoustic signatures allow researchers to identify species non-invasively, even in cryptic or nocturnal taxa, a method

increasingly used in acoustic monitoring and machine learning-based species recognition (Mitchell et al., 2020). Changes in call structure or calling effort may signal habitat degradation, noise pollution, or climate stress, especially in sensitive taxa like acid frogs whose chorusing behavior reflects environmental pressures (Mitchell et al., 2020). For example, frogs near urban streams may shift to higher frequencies to avoid masking by anthropogenic noise, a behavioral adaptation that flags ecological disturbance and reflects acoustic plasticity in response to human-modified habitats (Brodie et al., 2022).

The note repetition rate was the most distinctive parameter, significantly varying among species. *Leptobrachella gracilis* exhibited the highest repetition rate (364 notes/minute), contrasting sharply with the extremely low rates observed in *Pelobatrachus nasutus* (2 notes/minute) and *Leptobrachium montanum* (4 notes/minute). This finding aligns with previous studies suggesting that faster note repetition rates are typical among smaller, fast-calling species (Amram et al., 2018; Köhler et al., 2017), while larger-bodied frogs tend to produce fewer, slower notes (Dasi & Shahriza, 2022; Deka & Zainudin, 2025). For instance, *Leptobrachium smithi*, a large-bodied species from Langkawi, was reported to produce short, single-note calls at a rate of 4–6 calls per minute (Dasi & Shahriza, 2022), further supporting the relationship between body size and slower call rates. Spectral or fine-scale temporal features, such as note repetition rate (Amram et al., 2018), are important for species recognition.

Dominant frequency further reflected species-specific differentiation, with smaller species such as *Leptobrachella mjobergi* and *L. juliandringi* producing higher frequency calls (9.8 kHz and 8.1 kHz, respectively), while larger-bodied species like *Leptobrachium montanum* produced much lower frequency calls (~0.8 kHz). This inverse relationship between dominant frequency and body size is well-established in anuran bioacoustics literature (Gerhardt & Huber, 2002; Deka & Zainudin, 2025) and is primarily attributable to morphological constraints of the vocal apparatus, such as the size and mass of the laryngeal cartilages and vocal cords (Deka et al., 2015). Larger frogs typically possess more massive vocal folds and longer vocal tracts, which favor the production of lower-frequency sounds. Conversely, smaller frogs are limited to producing higher frequencies due to their reduced vocal structures. This trend has been demonstrated across diverse anuran lineages, including ranids, hylids, and megophryids, supporting the notion that dominant frequency serves as an honest signal of body size in many species (Feng et al., 2006; Köhler et al., 2017). Moreover, high-frequency calls may offer advantages in cluttered forest environments by reducing sound attenuation over short distances, a potential adaptive function

in small stream-breeding species inhabiting noisy or densely vegetated habitats (Dasi & Shahriza, 2022). High-frequency signals can enhance signal clarity in close-range communication, which is typical for small, stream-breeding frogs with low encounter rates (Zhao et al., 2021).

Interestingly, *Leptobrachium ingeri* and *L. montanum* produced the highest number of pulsed notes per call (13 and 7, respectively), whereas most *Leptobrachella* species produced only 1–3 pulsed notes. This difference may reflect phylogenetic divergence between *Leptobrachium* and *Leptobrachella* species, where *Leptobrachium* tend to have more complex calls with longer durations, possibly linked to their habitat use and behavioral ecology (Goutte et al., 2013). Call complexity, including pulse number and duration, is also thought to be associated with female mate choice and may function as an honest indicator of male fitness or energy reserves (Webster et al., 2023) in some megophryid lineages. Additionally, phylogenetic analyses have suggested that call traits such as pulse number and call duration can be evolutionarily conserved within genera, further supporting their taxonomic and behavioral relevance (James et al., 2024).

The variability in call parameters among species suggests that acoustic signals play a pivotal role in reproductive isolation and species recognition within the Megophryidae family. These results corroborate earlier findings where call characteristics were shown to effectively distinguish closely related species in Sarawak's Ranidae (Marly et al., 2017; Zainudin et al., 2010) and Bufonidae (Amram et al., 2018).

From a conservation perspective, acoustic surveys provide a non-invasive and efficient method for monitoring cryptic anuran species, particularly in dense tropical habitats where visual identification is challenging. Given the ongoing habitat disturbances in Borneo, particularly due to logging and agricultural expansion, documenting acoustic diversity offers valuable insights for future taxonomic studies and habitat management strategies.

5. CONCLUSIONS

This study highlights the significant variation in advertisement call characteristics among Sarawak Megophryidae species, with note repetition rate and dominant frequency serving as key distinguishing features. These bioacoustic differences likely reflect both phylogenetic relationships and ecological adaptations within the family. Our findings underline the importance of integrating acoustic analysis into species identification, biodiversity monitoring, and conservation planning, especially for morphologically cryptic groups such as Megophryidae. Future studies should aim to expand sampling to other regions of Borneo, include

more individuals per species, and explore seasonal and environmental influences on call characteristics to further elucidate the bioacoustics diversity of Bornean anurans.

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