# FIELD BODY TEMPERATURES OF BORNEAN FROGS: A STUDY OF THERMOREGULATORY STRATEGIES

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**Abstract:** Temperature has a great impact on ectothermic animals such as frogs, particularly on their physiological adaptation, habitat preferences, and ecological significance. This study is an attempt to understand the body temperature of Bornean frogs in their natural habitat. This knowledge is essential for us to have a better understanding of their thermoregulatory strategies and their ability to adapt to environmental changes. The primary objective of this study is to evaluate the body temperatures of Bornean frogs and their correlation with different habitat types. Therefore, we evaluated the body temperatures of 261 individuals from 40 different anuran species across five separate research sites located in Sarawak. The findings suggested that the body temperatures of frogs, which varied across different habitat types is intricately linked to their ecological niche. It was further indicated that frogs inhabiting lentic habitats (e.g., ponds) tend to exhibit a higher body temperature when compared with those residing in lotic (e.g., rivers) and terrestrial (including arboreal) habitats. Their temperature varied  between 19.9°C and 28.2°C. All the observed amphibians exhibited thermoconforming behaviours, whereby their body temperature closely corresponded to that of their surrounding substrate. Hence, it is clear that ponds and other water bodies act as temperature regulators for aquatic organism as they possess a high heat capacity and heat conductivity, effectively regulating temperature changes in the surrounding environments. However, further research on the link between body temperatures and various elevational zones is needed for a better understanding of the thermal regime of Bornean frog species.

Keywords: Bornean frog, substrate, habitat adaptation, temperature regulator, environmental changes.

## Introduction

Ectothermic animals have evolved unique mechanisms for regulating their body temperatures. This built in mechanisms enable them to make both behavioural and physiological adjustments in order to adapt to their environmental condition (Huey & Kingsolver, 1989). Temperature changes have been  shown to have major effects on anurans, including their metabolic rate regulation (Pough *et al*., 2007), control in activity and behaviour (Huey & Slatkin, 1976), growth and development (Angilletta, 2009), anuran reproduction (Shine, 2003), and physiological performance (Hochachka & Somero, 2002). Anurans exhibit varying degrees of temperature sensitivity in relation to their physiological activities (Martin & Huey, 2008). Throughout their life stages, anurans may encounter different microenvironments and experience fluctuations in body temperature, which can influence their physiological functions (Colinet *et al*., 2015; Levy *et al*., 2015). Additionally, continuous contact with specific thermal conditions can impact their temperature-related reactions of physiological activities, potentially resulting in illness, especially in elevated temperature conditions (Kingsolver & Woods, 2016).

Amphibians stand as one of the most imperilled animal species on a global scale, facing unparalleled rates of decline over the past

few decades (Stuart *et al*., 2004). The thermal physiology of amphibians is affected by global anthropogenic change (Katzenberger *et al*., 2014; Quiroga *et al*., 2019), as the greenhouse effect intensifies contributing to global warming. A swift increase in the overall global temperature has been well documented. Recent scholarly works have pointed to rising temperatures caused by deforestation and global warming in Borneo resulting in a rise in global temperatures (Dungey, 2021). Over 34% of Borneo's old-growth forests were lost between 1973 and 2015, with an average deforestation rate of approximately 0.25 million hectares per year, while Sarawak lost about 80% of its primary forest during this time (Gaveau *et al*., 2016; Gaveau *et al*., 2019; Keuffner, 2023; Mohd-Azlan *et al*., 2023). Temperature fluctuations can also be caused by a variety of factors, including geographic location, elevation, proximity to bodies of water, plant cover, and local weather patterns (Callendar, 1961).

Ectotherms, including Bornean frogs, are highly influenced by daily temperature fluctuations in their habitat (Paaijmans *et al*., 2013). While increased temperatures can accelerate growth rates, they may also cause thermal stress, especially during heat waves (Burraco *et al*., 2020). Conversely, cold conditions can lead to lethargy or torpor, significantly reducing their metabolic activities, potentially leading to fatal outcomes with prolonged exposure (Burraco *et al*., 2020). Despite these critical temperature effects, the body temperature of Bornean frogs across different habitats remains understudied. This research seeks to address the following questions: (1) How does the body temperature of Bornean frogs vary across their different habitat types? (e.g., lentic, lotic, and terrestrial) and (2) How does the ability to resist water loss correlate with their specific niches and physiological adaptations? We hypothesised that lotic habitats (flowing water) exhibit greater thermal stability compared with terrestrial and lentic (still water) habitats.

## Materials and Methods

### *Study Site*

Fieldwork was carried out in five different study locations in the state of Sarawak, located in East Malaysia (the north-western Borneo); Bung Jagoi, Bau (N 1°20'47.04"; E 110°2'37.32"), Matang Wildlife Centre, Lundu (N 1°36'33.84"; E 110°9'36.72"), West Campus, UNIMAS, Samarahan (N 1°28'3.72"; E 110°25'54.84"), Kampong Telok Melano, Sematan (N 2°0'25.2"; E 109°38'45.6"), and Mulu National Park, Long Lama Miri (N 4°5'31.56"; E 114°53'44.88") (Figure 1).

All five study locations were sampled for two to three hours starting from 18:30 onwards by traversing pathways that includes non-aquatic ecosystems that are distant from water sources, ponds, and streams. Frogs were found sporadically by listening for calling males or by using headlamps and their eyeshine to spot them on ground level, in lotic and lentic bodies of water, and perched in the foliage of plants up to a height of two metres above ground. Since no frogs had been collected from hiding locations, all measurements of frogs that were captured are those of active frogs (i.e., samples taken while active).

### *Sampling Method*

Given the varying average size of the species, body temperature taken from external skin temperature was calculated as it is the only way to get comparable and precise measurements (Navas *et al*., 2013). Using an infrared laser thermometer (Extech 42510A Wide Range Mini Infrared Thermometer), body temperatures (Tb) of 261 individuals and 40 different species were measured to the nearest 0.1°C at the dorsal part of the body. Once the body temperature was successfully taken, substrate temperatures (Ts), which are directly in contact with the frogs (e.g., soil surface, rocks, and leaves of plants) were taken with the infrared laser thermometer. The subject was not touched during the thermal recordings,

which were conducted at less than one metre between the subject and the substrate. At the site of capture of every individual, ambient temperature (Ta) and humidity (Th) were then measured using the 4-in-1 environmental meter (Extech 45170 4-in-1 Environmental Meter). We primarily concentrated on substrate temperature since it is more ecologically significant than ambient temperature and humidity. After the measurements, the individuals were taken to the base camp for further identifications. Their sex was recorded and the Weight (W), Tibia Length (TL), and Snout-Vent Length (SVL) of the adult specimens were measured.

This study evaluated the body temperatures of 261 individuals from 40 distinct frog species across five research sites in Sarawak. The samples represented various habitats: Terrestrial, arboreal, and semi-aquatic. Frogs were categorised into several habitat and substrate groups according to their observed location and conditions.

Based on the specific circumstances in which they were located, the frogs were divided into three types of habitat: Flowing water, non-flowing water, and non-aquatic. The frogs were classified under flowing water or non-flowing water if they were located in the water or within one metre of a water source. Frogs were placed in the non-aquatic region if they were found far from any water body, often more than 100 metres way.

Depending on the substrate that a frog was sitting on, two substrates were allocated to them, which are aquatic (directly in water) and non-aquatic (out of the water). Frogs in the non-aquatic habitat category were all counted in the non-aquatic substrate category, but frogs in the flowing water and non-flowing water habitat categories might be in either the aquatic or non-aquatic substrate categories.
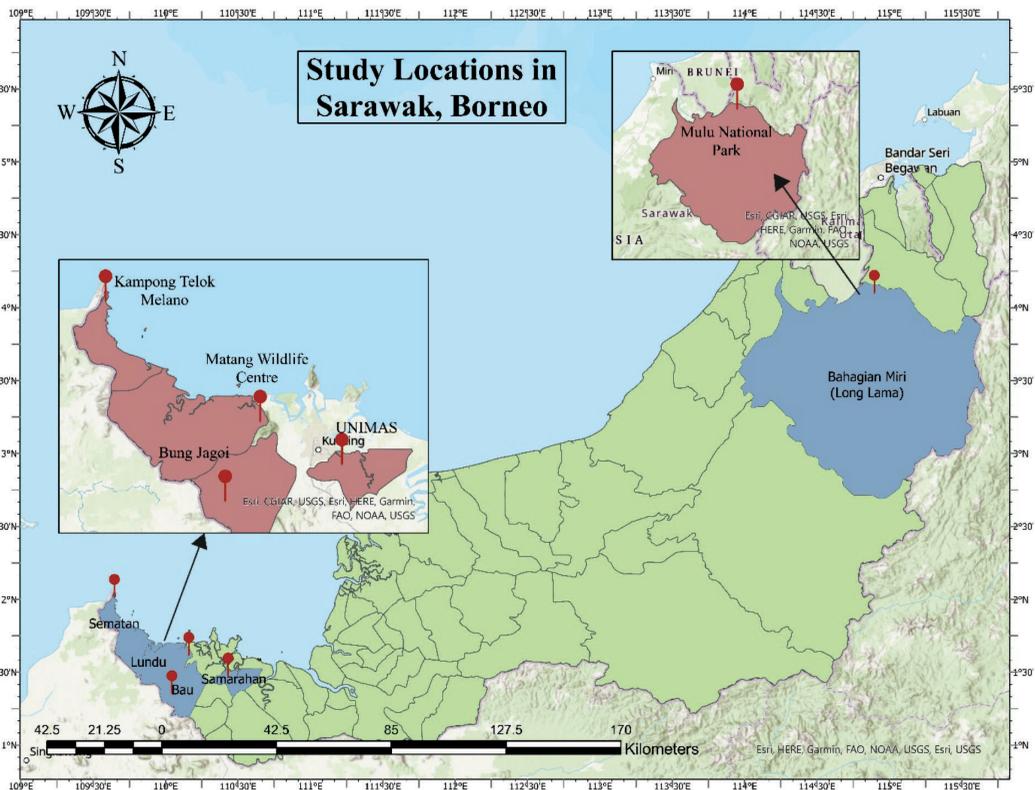


Figure 1: Study locations in Sarawak, Borneo generated by ArcGIS Pro 3.0.1

### Data Analysis

The relationship between Tb, Ts, Ta, and Th were analysed, including their mean temperature, standard deviation, and variances with IBM SPSS version 26. The changes of these variables were used to examined how it affects body temperatures of frogs that were recorded during sampling. Pearson's correlation coefficient analysis, in IBM SPSS version 26 was used to test the autocorrelation of dependent variables (e.g., Tb) with independent variables (e.g., Ts, Ta, and Th) of different habitat types. Pearson's correlation coefficient was used because the indicators selected in this study follows a Gaussian or normal distribution. Variables with correlation below the suggested threshold of 0.7 were eliminated while variables with correlation that are significant were included in statistical analysis (Fielding & Haworth, 1995; Chin, 1998).

When subjected to modelling, the degree of thermoregulation is determined by the gradient of the linear correlation between the operative environmental temperature and body temperature ($0 \leq k \leq 1$). A value of $k = 0$ signifies an ideal thermoregulator, whereas a value of $k = 1$ indicates an ideal thermoconformer (Huey & Slatkin, 1976; Angilletta, 2009).

### Results

#### Number of Individuals Found

A total of 261 frog individuals from 40 different species of six families were found and recorded during the sampling in 2022/2023 (Figure 2; Table 1). About 27.20% (n = 71) of the total species were primarily represented by family Dicroglossidae, with family Ranidae accounting for 21.84% (n = 57), family Bufonidae for 21.07% (n = 55), family Rhacophoridae for 19.92% (n = 52), family Megophryidae for 5.36% (n = 14), and family Microhylidae for 4.60% (n = 12). *Fejervarya limnocharis* (Grass Frog) from family Dicroglossidae was found to be the most abundant in five locations (11.49%; n = 30), followed by *Polypedates*

*leucomystax* (Four-lined Tree Frog) from family Rhacophoridae (10.3%; n = 27), and *Duttaphrynus melanostictus* (Common Sunda Toad) from family Bufonidae (9.96%; n = 26).

A total of 20 species discovered during the sampling period are endemic to the Borneo region, including *Ansonia spinulifer*, *Ingerophrynus divergens*, *Phrynoidis juxtasper*, *Fejervarya cancrivora*, *Limnonectes ibanorum*, *Limnonectes ingeri*, *Limnonectes leporinus*, *Occidozyga baluensis*, *Leptobrachium abbotti*, *Leptolalax fritinniens*, *Leptolalax gracilis*, *Kalophrynus meizon*, *Microhyla borneensis*, *Huia cavitympanum*, *Chalcorana megalonesa*, *CHalcorana raniceps*, *Meristogenys jerboa*, *Staurois guttatus*, *Staurois latopalmatus*, and *Philautus tectus* (Inger *et al*., 2017).

All frog species in Sarawak, Borneo except for one were categorised as Least Concern (LC) in the IUCN Red List Category, 2023. *Meristogenys jerboa* stands out as the only species classified as vulnerable (VU) from 2004 to 2023. Nine species, including *Ansonia spinulifer*, *Limnonectes ibanorum*, *Limnonectes ingeri*, *Limnonectes malesianus*, *Limnonectes paramacrodon*, *Occidozyga baluensis*, *Leptolalax gracilis*, *Nyctixalus pictus*, and *Philautus tectus* held the classification of Near Threatened (NT) between 2018 and 2022. Subsequently, their conservation status evolved, with updated assessments reflecting changes in their threat levels or vulnerability in later years.

### Temperature Ranges of Bornean Frogs and Their Habitat Types

The body temperatures of the frogs examined varied between 19.9°C and 28.2°C, with a mean ± standard deviation body temperature of 23.7 ± 1.7°C in five study locations (Figure 3). The lowest body temperature recorded was 19.9°C as it was located in non-aquatic (forested) after heavy rains, whereas the highest body temperature recorded was 28.2°C as it was found in a non-flowing water habitat (temporary pond).
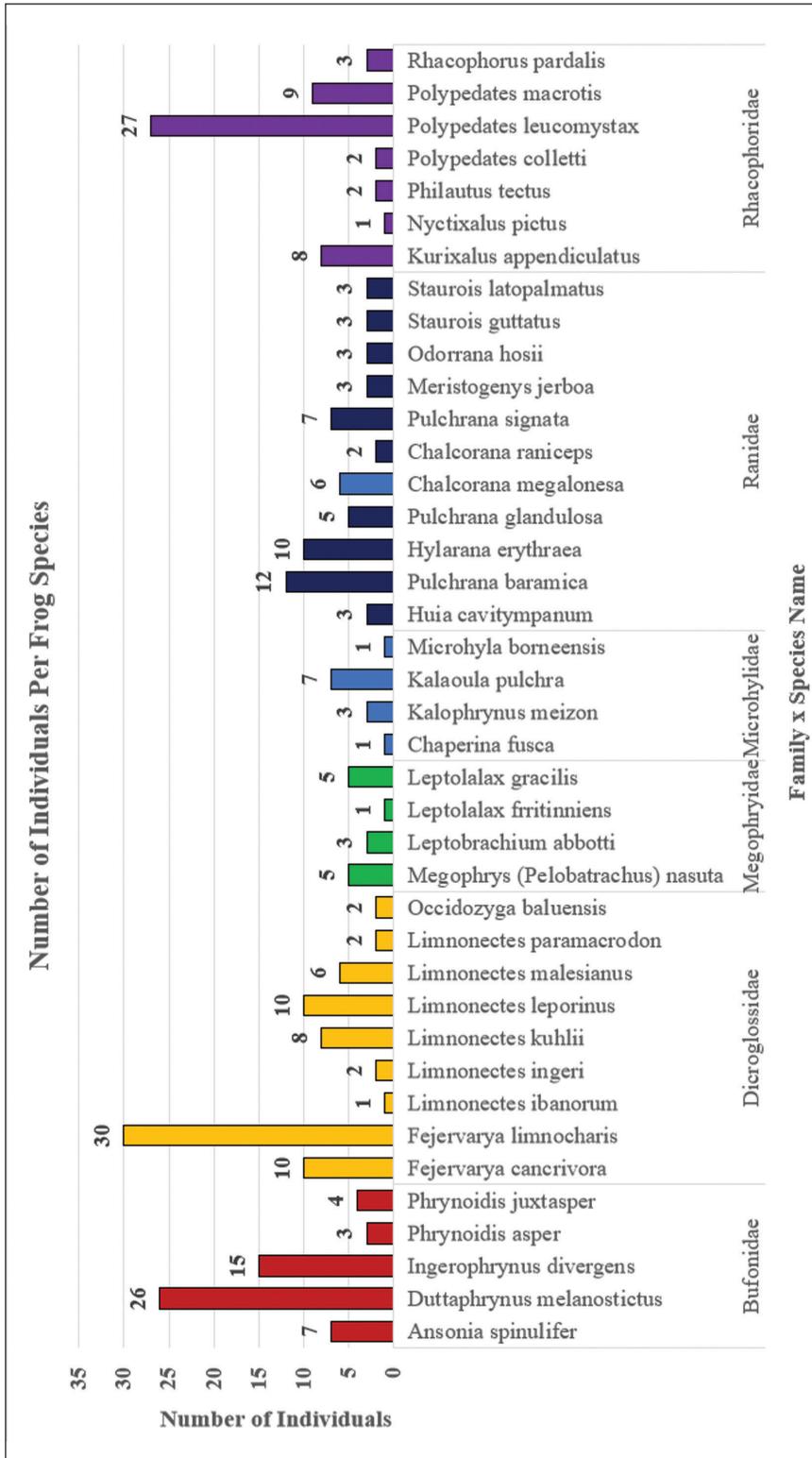
Figure 2: Number of individual frog species found during sampling in Sarawak, Borneo (2022/2023)

Table 1: Number of individual frog species found sampled in Sarawak, Borneo

| Family | Species Name | No. of Individuals | IUCN Status | IUCN Status 2023 | Species Distribution |
|---|---|---|---|---|---|
| Bufonidae | Ansonia spinulifer * | 7 | Near Threatened (2018) | Least Concern | Endemic |
| | Duttaphrynus melanostictus | 26 | Least Concern (2004) | Least Concern | Widely distributed |
| | Ingerophrynus divergens* | 15 | Least Concern (2004) | Least Concern | Endemic |
| | Phrynoidis asper | 3 | Least Concern (2004) | Least Concern | Widely distributed |
| | Phrynoidis juxtasper* | 4 | Least Concern (2004) | Least Concern | Endemic |
| Dicroglossidae | Fejervarya cancrivora* | 10 | Least Concern (2004) | Least Concern | Endemic |
| | Fejervarya limnocharis | 30 | Least Concern (2004) | Least Concern | Widely distributed |
| | Limnonectes ibanorum* | 1 | Near Threatened (2018) | Least Concern | Endemic |
| | Limnonectes ingeri* | 2 | Near Threatened (2018) | Least Concern | Endemic |
| | Limnonectes kuhlii | 8 | Least Concern (2004) | Least Concern | Widely distributed |
| | Limnonectes leporinus* | 10 | Least Concern (2004) | Least Concern | Endemic |
| | Limnonectes malesianus | 6 | Near Threatened (2022) | Least Concern | Widely distributed |
| | Limnonectes paramacrodon | 2 | Near Threatened (2022) | Least Concern | Widely distributed |
| | Occidozyga baluensis* | 2 | Near Threatened (2019) | Least Concern | Endemic |
| Megophryidae | Megophrys nasuta | 5 | Least Concern (2004) | Least Concern | Widely distributed |
| | Leptobrachium abbotti* | 3 | Least Concern (2004) | Least Concern | Endemic |
| | Leptolalax frritinniens* | 1 | Data Deficient (2019) | Data Deficient | Endemic |
| | Leptolalax gracilis* | 5 | Near Threatened (2019) | Least Concern | Endemic |
| Microhylidae | Chaperina fusca | 1 | Least Concern (2004) | Least Concern | Widely distributed |
| | Kalophrynus meizon* | 3 | Least Concern (2022) | Least Concern | Endemic |
| | Kalaoula pulchra | 7 | Least Concern (2004) | Least Concern | Widely distributed |
| | Microhyla borneensis* | 1 | Least Concern (2004) | Least Concern | Endemic |

| Family | Species | Individuals | IUCN status (year) | IUCN status | Distribution |
|---|---|---|---|---|---|
| Ranidae | Huia cavitympanum* | 3 | Least Concern (2019) | Least Concern | Endemic |
| | Pulchrana baramica | 12 | Least Concern (2004) | Least Concern | Widely distributed |
| | Hylarana erythraea | 10 | Least Concern (2004) | Least Concern | Widely distributed |
| | Pulchrana glandulosa | 5 | Least Concern (2004) | Least Concern | Widely distributed |
| | Chalcorana megalonesa* | 6 | Least Concern (2018) | Least Concern | Endemic |
| | Chalcorana raniceps* | 2 | Least Concern (2004) | Least Concern | Endemic |
| | Pulchrana signata | 7 | Least Concern (2004) | Least Concern | Widely distributed |
| | Meristogenys jerboa* | 3 | Vulnerable (2004) | Vulnerable | Endemic |
| | Odorrana hosii | 3 | Least Concern (2004) | Least Concern | Widely distributed |
| | Staurois guttatus* | 3 | Least Concern (2018) | Least Concern | Endemic |
| | Staurois latopalmatus* | 3 | Least Concern (2004) | Least Concern | Endemic |
| Rhacophoridae | Kurixalus appendiculatus | 8 | Least Concern (2004) | Least Concern | Widely distributed |
| | Nyctixalus pictus | 1 | Near Threatened (2022) | Least Concern | Widely distributed |
| | Philautus tectus* | 2 | Near Threatened (2018) | Least Concern | Endemic |
| | Polypedates colletti | 2 | Least Concern (2004) | Least Concern | Widely distributed |
| | Polypedates leucomystax | 27 | Least Concern (2004) | Least Concern | Widely distributed |
| | Polypedates macrotis | 9 | Least Concern (2004) | Least Concern | Widely distributed |
| | Rhacophorus pardalis | 3 | Least Concern (2004) | Least Concern | Widely distributed |
| Total species | 40 | | | | |
| Total individuals | | 261 | | | |

*Species endemic to Borneo based on Inger *et al.* (2017).

The correlation between body temperature and substrate temperature exhibits a strong positive relationship across three habitat types, with correlation coefficients (*r*-value) for; flowing water = 0.992, non-flowing water = 0.903, and non-aquatic = 0.940 (Table 2).

The *k*-value for; flowing water = 1.01, non-flowing water = 0.86, and non-aquatic = 0.91. The overall variance of Tb was 3.0°C, highest in non-flowing water habitats (3.7°C), and similar in flowing water and non-aquatic habitats (2.8°C) (Table 3). All habitat categories have a *p*-value < 0.01.

The temperature of the substrate was 23.7 ± 1.8°C throughout all three environments, with a 0.1°C different as mean ± standard deviation of body temperature of the frogs examined. The lowest substrate temperature (18.1°C) recorded was in a non-flowing water habitat and the highest substrate temperature (28.8°C) recorded was non-aquatic habitat, as shown in Table 3. The overall variance of Ts was 3.3°C, highest in non-flowing water habitat (4.2°C), and lowest in flowing water habitats (2.7°C).

## Discussion

Sarawak is renowned for its vast and different type of forests, each possessing distinctive ecosystem attributes and abundant biodiversity (Choy, 2014). They are tropical rainforests, peat swamp forests, mangrove forests, hill dipterocarp forests, kerangas forests, montane forests, limestone forests, freshwater swamp forests, and secondary forests (Forest Department Sarawak, 2020). The current study sampled the lowland mixed dipterocarp forests

Table 2: The autocorrelation between dependent variable (body temperature, Tb) and independent variables (substrate temperature, Ts; ambient temperature, Ta; humidity, Th) with Pearson's correlation coefficient, *r*

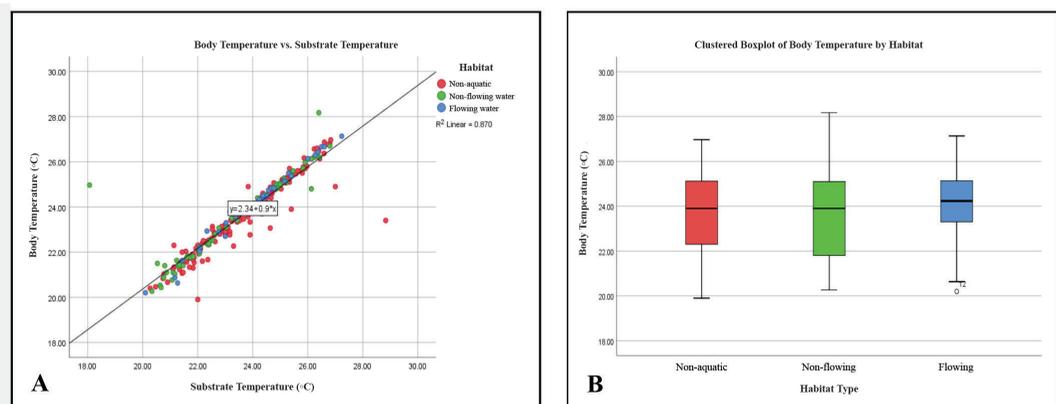| Habitat Types | Pearson's Correlation Coefficient (*r*) | | |
| --- | --- | --- | --- |
| | Tb & Ts | Tb & Ta | Tb & Th |
| Flowing water | 0.992* | -0.189 | 0.523 |
| Non-flowing water | 0.903* | -0.143 | -0.143 |
| Non-aquatic | 0.940* | 0.102 | 0.348 |

*Variables with strong positive correlation.



Figure 3: The interplay of Bornean frog body temperatures and substrate temperatures is depicted graphically (°C). (A) A regression line suggesting a strong, positive relationship between body and substrate temperatures in three distinct environments is shown; flowing water (blue), non-flowing water (green), and non-aquatic (red). (B) Bornean frog body temperatures in three distinct habitat types are colour-coded in A

Table 3: Body temperature (Tb) and substrate temperature (Ts) values were acquired from a varied collection of frogs in Borneo, Sarawak, in three habitat types. The correlations between Tb and Ts are shown by ranges with means ± standard deviations, variances, and Pearson's correlation coefficient (*r*). *p*-value < 0.01 was the significance level for each comparison

| Habitat | *n* | Mean ± SD Tb (°C) | Mean ± SD Tsubs (°C) | Var Tb | Var Tsubs | Min-Max Tb (°C) | Range (°C) | Min-Max Tsubs (°C) | *r* | *p*-value (0.01) |
|---|---|---|---|---|---|---|---|---|---|---|
| Flowing water | 37 | 24.1 ± 1.7 | 24.1 ± 1.7 | 2.8 | 2.7 | 20.2 - 27.1 | 6.9 | 20.1 - 27.2 | 0.992 | 0.000 < 0.01 |
| Non-flowing water | 69 | 23.6 ± 1.9 | 23.4 ± 2.0 | 3.7 | 4.2 | 20.3 - 28.2 | 7.9 | 18.1 - 26.8 | 0.903 | 0.000 < 0.01 |
| Non-aquatic | 155 | 23.7 ± 1.7 | 23.8 ± 1.7 | 2.8 | 3.0 | 19.9 - 27.0 | 7.1 | 20.3 - 28.8 | 0.940 | 0.000 < 0.01 |

of Mount Bung Jagoi, Matang Wildlife Centre, and Mulu National Park, as well as an open field in West Campus, UniMAS, and Kampong Telok Melano. The researchers identified and recorded 261 frogs from 40 different species of six families. As most of the sampling sites were conducted in urban settings, certain frog species have the potential to display commensal behaviour with humans, adapting well to this lifestyle to enhance their survival chances (Zainudin *et al*., 2017; Marques *et al.*, 2018). As forest areas become more accessible, frog species that exhibit commensal behaviour with humans have the chance to encroach upon forested areas, potentially displacing indigenous species in the process (Grafe & Das, 2014). The authors found the three most prevalent species recorded demonstrated the capability to thrive and adjust to challenging environments.

Inger *et al*. (2017) reported that Grass Frog or Kampung Frog (i.e., *Fejervarya limnocharis*) is restricted to disturbed and even unproductive, habitats that are associated with human activities (e.g., agriculture, roadside borders, lawns, and football fields), and it is a prevalent species in rural and urban areas due to its adaptability and notable mating calls. The Four-lined Tree Frog (i.e., *Polypedates leucomystax*) have similar behaviours and they can be found in various disturbed habitats everywhere and are closely associated with humans in both urban and rural area. Inger *et al*. (2017) also mentioned that Common Sunda Toad or Asian Common Toad (i.e., *Duttaphrynus melanostictus*) is the only Bornean toad that does not inhabit a forest and it is more capable of adapting to environments impacted by human activities compared with other frogs (Licata *et al*., 2020).

The measurement of frog body temperatures contributes to our understanding of their ecology, guides conservation efforts, and provides useful data for researching the influence of environmental changes on these anurans (Kozak & Wiens, 2010; Lowe, 2012). In this study, the mean body temperature of 23.7 ± 1.7°C of the specimens was analysed across five study locations. These results are

consistent with the body temperatures of other anuran species that have been recorded in tropical areas between 2013 and 2022 (Navas *et al*., 2013; Rasolonjatovo *et al*., 2020; Ruthsatz *et al*., 2022). We concluded that Bornean frogs exhibit varying body temperatures across different habitats and these variations are closely tied to their ecological preferences. Our finding indicates that frogs residing in non-flowing habitats such as ponds, exhibit higher body temperatures compared with those in stream habitat with flowing water and terrestrial habitats that are non-aquatic. These results align with the findings of Ruthsatz *et al*. (2022).

Anurans regulate their body temperatures by relocating within their environment and seeking microhabitats with different temperatures such as basking in the sun to warm up or seeking shade and burrows to cool down (Schulte, 2015; Sinclair *et al*., 2016; González-del-Pliego *et al*., 2020). Their body temperature is influenced by environmental factors such as ambient temperature, humidity, and atmospheric pressure (Gonzalez & Briggs-Gonzalez, 2022), as well as internal changes and behavioural adaptations, including life cycle stage, genetic adaptation, and orientation (Centeno *et al*., 2015; Farallo *et al*., 2018). Regardless of whether the frog is in freshwater or dry land, its skin is essential for maintaining fluid balance (Larsen, 2021). Their skin is highly transparent and consists of stratified squamous epithelium in the epidermis, with the Stratum Corneum (SC) made up of a very thin layer of keratinised cells (Llewelyn *et al*., 2019; Varga *et al*., 2019). The hydration state and skin morphology of amphibians significantly influence their ability to engage in behavioural thermoregulation, as dehydration restricts their mobility and thermoregulatory choices (Navas *et al*., 2008; Rozen-Rechels *et al*., 2019; Ortega *et al*., 2023). Our study revealed that frogs inhabiting various ecological niches demonstrate distinctive temperature preferences and behaviours to regulate their body temperatures and the ability to resist water loss is closely associated with their specific niches and adaptations.

Aquatic or semi-aquatic frogs exhibit increased resistance to evaporative water loss in high temperatures compared with terrestrial or arboreal frogs (Mokhatla *et al*., 2019; Acosta-L *et al*., 2023), resulting in the retention of moisture on the skin. This leads to the maintenance of higher body temperatures which are vital for improving muscle function, locomotion, and overall performances (Akat Çömden *et al*., 2023). Aquatic and semi-aquatic frogs possess adaptations that allow them to prevent water loss by residing in or near water. The epidermis of aquatic or semi-aquatic frogs has larger intercellular spaces in surface layers compared to basal layers, facilitating easier water penetration without requiring impermeability (Toledo & Jared, 1993). Relying on thinner skin for respiration and gas exchange (Seymour & Bradford, 1992; Clarke, 1997), they can potentially reduce water loss by maintaining a lower body temperature for thermoregulation.

Our findings have confirmed that both stream-dwelling frogs and pond-dwelling frogs possess the attribute of being thermoconformers. This indicates that their body temperatures depend solely on substrate temperatures, as shown by the *k*-values (Table 3) for flowing water (1.01), non-flowing water (0.86), and non-aquatic environments (0.91). Relying significantly on environmental temperature, their thermal limits remain constant and do not vary in response to seasonal changes in climatic parameters (de Oliveira Anderson *et al*., 2018). It is noteworthy that the variability of body temperature (Tb) in frogs residing in streams is relatively lower (2.7) (Table 3), indicating a decreased level of intrapopulation variation compared to pond-dwelling frogs (3.7) (Table 3), which demonstrates the highest Tb variance. Duellman and Trueb (1994) has stated that frogs that reside in streams primarily occupy their time in water, which offers a thermally consistent habitat. The consistent water temperature may benefit species by acting as a buffer against environmental temperature fluctuations and preventing thermal stress (von Tschirnhaus & Correa, 2021). Research conducted by Hussain

*et al*. (2021) suggested that global warming and human activities had a substantial impact on small bodies of freshwater supply (e.g., ponds, reservoirs, and lakes) and temperature as a result of increased in greenhouse gas levels in the troposphere. Greenhouse gases effectively trap heat in the atmosphere, creating a phenomenon called the greenhouse effect (Rajak, 2021). Elevated air temperatures in these scenarios are likely to heighten the demand for evapotranspiration (Islam *et al*., 2012a) as high evapotranspiration demand can potentially contribute to an increase in water temperature.

The correlation between ambient temperature and the body temperatures of amphibians is typically significant (Mokhatla *et al*., 2019). Utilising modifications between Tb and Ts is a traditional method for assessing the degree of thermoregulation in ectotherms, as proposed by Huey and Slatkin (1976). All groups in this research display nocturnal behaviour and the Tb was significantly impacted by Ts, indicating thigmothermic tendency as the frogs absorb heat passively through conduction from the surfaces they are in contact with (Lazcano *et al*., 2022). The Pearson product correlation coefficient indicates a strong positive association ($r > 0.7$) between frog body temperature (Tb) and substrate temperatures (Ts), showing changes in substrate temperature are closely related to corresponding changes in frog body temperatures across all three habitats. This correlation was statistically significant, just as Khatiwada *et al*. (2020) concluded that alterations in substrate temperature coincide with variations in frog body temperature. This study shows flowing water ($r = .992$, $p < .01$), non-flowing water ($r = .903$, $p < .01$), and non-aquatic habitat ($r = .940$, $p < .01$) (Table 2), indicating a rise in substrate temperature would result in an elevated body temperature in frogs.

The highest body temperature observed in our study (28.2°C) (Table 3) was typically seen in non-flowing aquatic habitats, similar to Ruthsatz *et al*. (2022), which illustrates the thermal stability these environments provide, unlike fast-flowing streams or rivers. Non-

flowing water bodies (e.g., ponds and lakes) have stable temperatures due to their depth and minimal water movement that allows accumulation of heat (Longhini *et al*., 2021). According to González-del-Pliego *et al*. (2020), the stable thermal environment is crucial for ectothermic frogs, allowing them to maintain the ideal body temperatures required for metabolic processes, reproduction, and movement. Recent research by Evans *et al*. (2020) emphasises the role of habitat use and basking behaviour under climate change adaptation. These adaptations are crucial for frogs' survival and reproductive success amidst environmental fluctuations. Additionally, pond habitat quality, including the availability of basking spots and vegetation has a substantial impact on frog population diversity and health (Jansen & Healey, 2003).

The lower substrate temperature recorded (18.1°C) (Table 3) was documented in non-flowing aquatic habitats such as ponds and lakes, reflects their relatively stable temperature conditions. The lack of turbulence in these habitats enables for temperature layering, allowing the substrate to stay cooler and minimising the mixing of warm and cold water, which results in more consistent temperatures over time (Dodds *et al*., 2013; Bergey, 2024). Non-flowing water bodies such as ponds and lakes have stable thermal environments due to restricted water movement and depth, allowing heat to accumulate and warmer surface temperatures (Bergey, 2024). Direct sunlight warms surface layers, creating constant thermal environments. Vegetation along the banks helps to keep substrate temperatures cooler by providing shade (Brettschneider *et al*., 2023). Despite seasonal and climatic variations, substrate temperatures, which are correlated with water temperatures remain colder due to thermal inertia and the insulating qualities of sediment (Brettschneider *et al*., 2023; Bergey, 2024). Non-aquatic habitats encounter heightened substrate temperature (28.8°C) (Table 3) due to the intense solar radiation and the limited moisture in the substrate. Longhini *et al*. (2021) examined how temperature acclimatisation

impacts amphibian physiological performance, noting that high substrate temperatures, especially in areas with minimal vegetation cover can influence their metabolic rates and general health. Increased solar exposure can cause substrate temperatures to exceed ambient air temperatures, especially during midday when solar radiation is at its highest. The moisture content of substrate is critical for temperature regulation, as dry substrates heat up faster and retain heat longer than moist substrates, allowing water to evaporate and mitigate temperature increases (Inforsato *et al*., 2020). According to Ovenden *et al*. (2021), drier conditions result in higher substrate temperatures due to the lack of evaporative cooling. Dubiner *et al*. (2024) found that locations with little vegetation and moisture can have elevated substrate temperatures, frequently around or above 28°C, due to increased solar exposure.

The temperature exhibited by Bornean frogs in their natural habitat were observed to vary between 19.9°C and 28.2°C, which correspond to the temperatures that are deemed most favourable for facilitating the optimal growth and reproductive capacity of Batrachochytrium dendrobatidis (Bd) (17°C to 23°C) (Stevenson *et al*., 2013; Sonn *et al*., 2017). The results indicate that the likelihood of Bd infection varies depending on the habitat of the frog, as pond-dwelling frogs have a greater ability to avoid the infection by choosing to inhabit warm temperatures of pond water.

The chytrid fungus, specifically named *Batrachochytrium dendrobatidis* (Bd) is a recently discovered pathogen responsible for a fungal disease in amphibians known as chytridiomycosis (Ruggeri *et al*., 2018). It has been observed that infections caused by Bd become more severe when the amphibian host's body temperature matches the optimal growth temperature of the former, consequently leading to a significant decline in amphibian population worldwide (Stevenson *et al*., 2013; Stevenson *et al*., 2020). In order to reduce their risk of infection, tropical amphibians may engage in behavioural thermoregulation by frequently inhabiting microhabitats that are not conducive to the pathogen's optimal developmental temperature (Rowley & Alford, 2013; Stevenson *et al*., 2013). This indicates that even minor environment or behavioural adjustments can have a significant impact on an individual's susceptibility to infection (Richards-Zawacki, 2010). However, the ability of an individual to intentionally induce behavioural fever while infected relies on habitat temperature variability and the ability to locate favourable microclimates (Beukema *et al*., 2021). Therefore, evaluating the association between ecological determinants and body temperatures of frogs can aid in an initial evaluation of the risk of diseases (Sauer *et al*., 2018; von May *et al*., 2018; Rasolonjatovo *et al*., 2020).

## Conclusions

In conclusion, Bornean frogs, like other amphibians, employ various strategies to regulate their body temperature in accordance with variations in ambient and substrate temperature, as these adaptations aid in sustaining their physiological functions and behaviours, which ultimately enhance their survival in the multifaceted ecosystems of Borneo. Our study demonstrates a correlation between the ecology of Bornean frogs and their body temperatures, with frogs from non-flowing habitats exhibiting higher body temperatures in contrast to those from stream and terrestrial habitats. The thermophysiological data pertaining to frogs in Borneo has the potential to assess the susceptibility of not only these specific amphibians but also other amphibian species in relation to changes in their surrounding environment. Further research is necessary to correlate body temperatures across different elevation zones and diel variance in order to comprehend the thermal patterns of Bornean frog species. The analysis of body temperatures of different anuran species that inhabit varied habitats can also potentially assist in the assessment of disease risk in the amphibian community.

**Conflict of Interest Statement**

The authors declare that they have no conflicts of interest.

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