

MORPHOLOGICAL VARIATION OF *Pelobatrachus nasutus* (SCHLEGEL, 1858) (ORDER: ANURA, FAMILY: MEGOPHRYIDAE) FROM DIFFERENT LOCALITIES IN SARAWAK

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Abstract: *Pelobatrachus nasutus* is a habitat generalist as it can dispersed across fragmented landscapes. Assessing the variation in morphological traits across populations is necessary to understand the potential impact of environmental changes on the species. This study investigates morphological variation within the species from various localities across Sarawak, East Malaysia. A total of 26 morphometric characteristics were measured on 58 specimens deposited in the UniMAS Zoological Museum and IBEC Laboratory. Statistical analyses were employed using Discriminant Function Analysis and the Post hoc Tukey test, revealing significant results in head length, forearm, and eye sizes, as well as snout to nare length and dorsal dermal fold length. The finding indicates that these external morphologies are useful characters for survivorship (feeding habit, escape mechanism, body immune defence) in their different habitat types. In addition, conspicuous tubercles were observed more abundantly on the dorsal skin of the frog found in non-protected forests, suggesting the frog's adaptation strategy to the environment. Overall, this study emphasised that *P. nasutus* can adapt to varying habitat conditions across fragmented landscapes in Sarawak through the optimal use of physical characteristics to suit their ecological needs in various habitat types.

Keywords: *Pelobatrachus nasutus*, morphology, habitats, Sarawak, adaptation strategy.

Introduction

Frogs are the most diverse and largest group of living amphibians on earth, possessing a wide range of shapes, colours, and sizes (Bradford, 2015). At least 40% of amphibians are listed as threatened, based on the International Union for Conservation of Nature (IUCN, 2022). Frogs are susceptible to environmental changes. They are an excellent indication of the ecosystem's health (Kriger, 2017) in which human contributions play a crucial role in conserving and protecting frog populations. Humans have destroyed the ecological needs of amphibians due to activities such as urbanisation, land clearing, and the constant usage of chemicals on the land for agricultural purposes.

Environmental changes due to anthropogenic activities will threaten frogs, eventually affecting their behaviour. Dealing with disruptions is important for survival in these ecosystems because if the species is unable

to utilise artificial resources; they are likely to go extinct (Ducatez *et al.*, 2018). According to Decena *et al.* (2020), habitat alteration has impacted the amphibian species not only on their diversity but also on their morphological structure. Li *et al.* (2018) added that animals with phenotypic plasticity have a high potential for facing anthropogenic impact. Predatory also influences the modification of the morphological structure of a species (Nunes *et al.*, 2014).

After 50 years of inhabiting fragmented habitats resulting from the construction of the hydroelectric dam, female species of *Odorrana schmackeri*'s exhibit dwarfism due to limited food resources availability and immigration (Wu *et al.*, 2020). Since frogs are extremely sensitive to habitat changes, it is important to consider species' responses to their adaptation to new habitats and climate change as a conservative measure (Luo, 2021). Anthropogenic activities

are harmful and detrimental to frogs (Eterovick, 2016). Therefore, designing more protected forests would help preserve wildlife habitats.

Morphological variation plays a crucial role in understanding the evolutionary process and adaptation to the ecology of organisms. Frogs demonstrate conservative morphological evolution (Stuart *et al.*, 2006). *Pelobatrachus nasutus* is a habitat generalist because it can disperse through fragmented areas (Deka *et al.*, 2019). Burger (2017) added that this species is difficult to breed in captivity, which is why understanding the differences between species from different localities is crucial for further conservation acts. This species is listed as the least concern in the IUCN Red List and somehow the population was threatened by loss of habitat in the wild (Mexico, 2000). This study embarks on a research question as a habitat generalist: Do the morphological characters differ among individuals of *P. nasutus* from different localities? This study is crucial as morphological variation among populations can indicate adaptation to local environmental conditions. Understanding these differences can give insights into the species' ecological requirements, which are essential for effective conservation management and for

predicting how populations might respond to environmental changes. The null hypothesis is that there is no morphological variation among individuals of *P. nasutus* from different localities in Sarawak. Hence, this study aims to determine the morphological variation among individuals of *P. nasutus* across various localities in Sarawak.

Materials and Methods

Study Area

Voucher specimens measured in this study were collected from eight distinct locations situated in three geographically different regions of Sarawak (Figure 1). Two sites were in the Northeast (WILMAR Oil Palm Plantation and Gunung Mulu National Park), one site was in the Central (Pelagus in Kapit Division), and five sites were in the Western (Jagoi, Borneo Highland, Tanjung Datu National Park, Gunung Gading National Park, and Kubah National Park). These locations comprise different habitat types: Protected forests (Tanjung Datu National Park, Gunung Gading National Park, Jagoi, and Kubah National Park) and non-protected forests (Borneo Highland, Pelagus, and WILMAR Oil Palm Plantation).

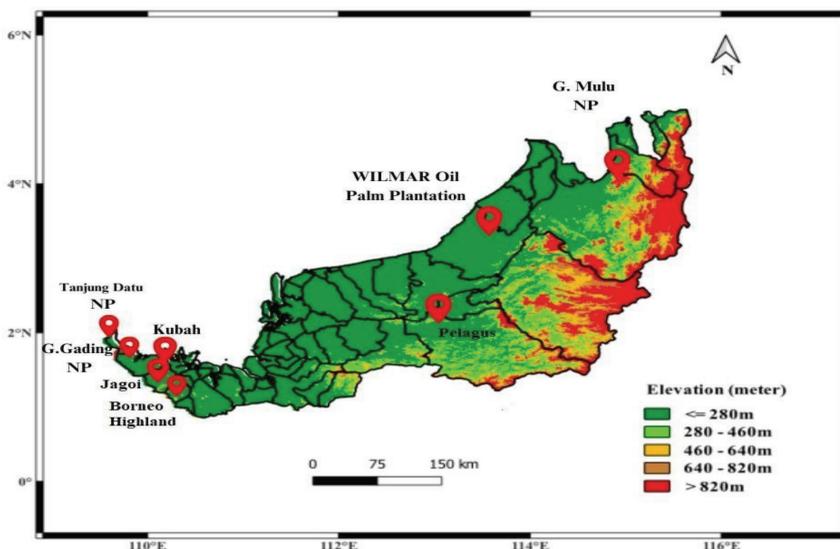


Figure 1: Localities of *Pelobatrachus nasutus* consist of Tanjung Datu NP, Gunung Gading NP, Kubah NP, Jagoi, Borneo Highland, Pelagus, WILMAR Oil Palm Plantation, and Gunung Mulu NP
Source: Generated using QGIS, 2023

Laboratory Work

Morphometric Measurement

A total of 58 individuals from the UniMAS Zoological Museum and IBEC Laboratory were measured in this study. A total of 26 morphometric characteristics [Figure 2 (A) and

Figure 2 (B)] of *Pelobatrachus nasutus* were taken in millimetres (mm) according to Table 1 description. The measurement taken was based on Matsui (1984) description.

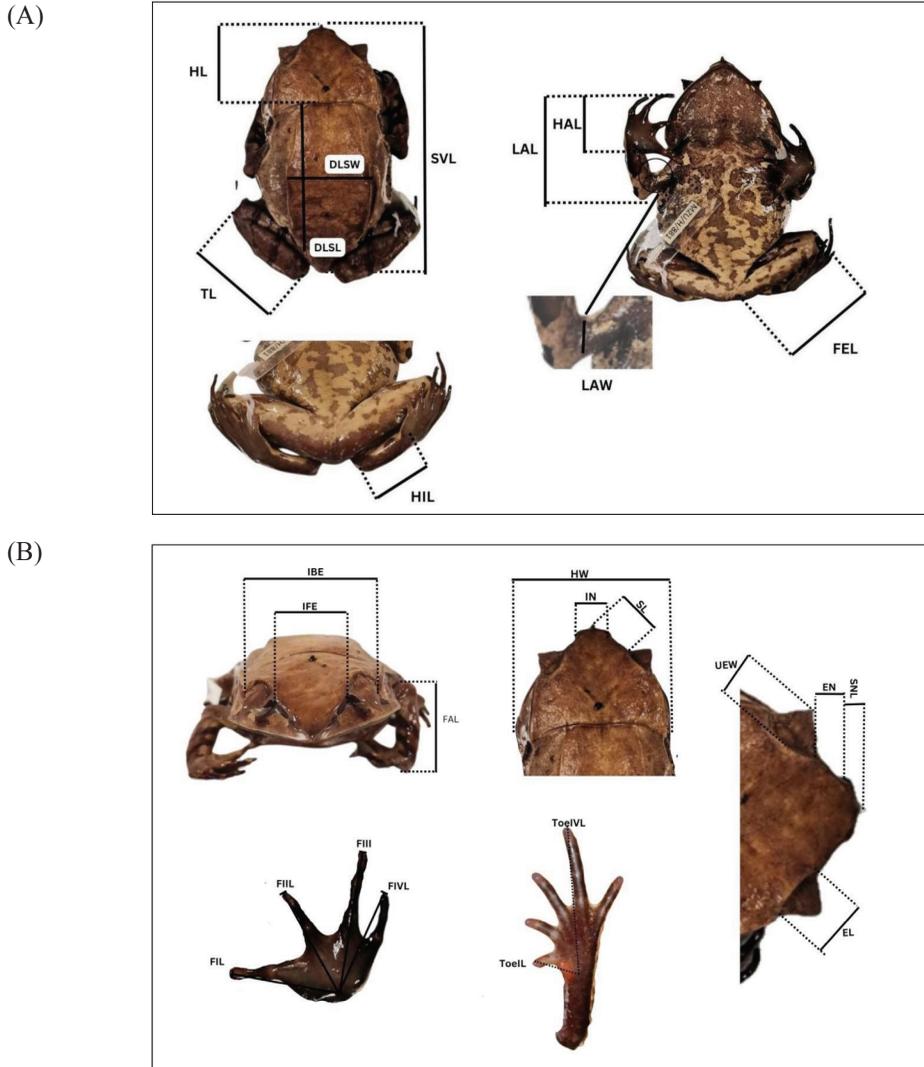


Figure 2: Body part measurements image of *Pelobatrachus nasutus*. (A) SVL = Snout-Vent Length, HL = Head Length, DLSL = Dorsal Lateral Stripe Length, DLSW = Dorsal Lateral Stripe Width, HAL = Hand Length, LAL = Longest Arm Length, LAW = Lower Arm Width, TL = Tibia Length, HIL = Hindlimb Length, FeL = Femur Length. (B) TOEIL = first toe length, TOEIVL = Fourth Toe Length, FIL = First Finger Length, FIIL = Second Finger Length, FIII = Third Finger Length, FIVL = Fourth Finger Length, IFE = Internal Front Eye, IBE = Internal Back Eye, IN = Internal Nare Distance, HW = Head Width, SL = Snout Length, UEW = Upper Eye Width, EN = Eye-Nare, SNL = Snout-Nare Length, EL = Eye Length, and FAL = Forearm Length

Table 1: Description of morphometric abbreviation following Matsui (1984)

Code	Parameter	Description
SVL	Snout-Vent Length	Distance from tip of snout to posterior margin of vent
HW	Head Width	The widest angle at the jaws
HL	Head Length	Distance from the tip of the snout to the neck
SL	Snout Length	Distance from the tip of the snout to the anterior corner
SNL	Snout-Nare Length	Distance from the tip of the snout to the external nares
EN	Front Eye-Nare	Distance from the anterior corner of the eye to the posterior
IN	Internal	Nare distance
UEW	Upper Eyelid Width	Maximum width measured perpendicular to the anterior-posterior axis
EL	Eye Length	Distance from the back of the eye to the front of the eye
IFE	Internal Front Eye	Distance from the right front of the eye to the left front of the eye
IBE	Internal Back of the Eye	Distance from the right back of the eye to the left back of the eye
FAL	Forearm Length	Distance from elbow to base of outer palmar tubercle
LAL	Longest Arm Length	Distance from elbow to the tip of finger 4
HAL	Hand Length	Distance from the base of the outer palmar tubercle to the tip of Finger IV
LAW	Lower Arm Width Forearm	Diameter of the lower arm
FIL	First Finger Length	Distance from the middle metacarpal tubercle to the tip of first finger
FIIL	Second Finger Length	Distance from the middle metacarpal tubercle to the tip of second finger
FIIL	Third Finger Length	Distance from the middle metacarpal tubercle to the tip of third finger
FIVL	Fourth Finger Length	Distance from middle metacarpal tubercle
TL	Tibia Length	Distance from knee to heel
HIL	Hindlimb Length	Distance from heel to metacarpal tubercle
FEL	Femur Length	Distance from anus to knee
TOEIL	First Toe Length	From the metatarsal tubercle to the tip of the toe I
TOEIVL	Fourth Toe Length	From metatarsal tubercle to tip of toe IV
DLSL	Dorsal Lateral Stripe Length	The greatest length of dorsal stripe from the neck
DLSW	Dorsal Lateral Stripe Width	Greatest distance from left to right of two dorsal stripe

Sex Identification

Pelobatrachus nasutus displays sexual size dimorphism, which allows us to distinguish between males and females. Body dimorphism in this species includes body size, where the female's snout-vent length is larger than the

male's [Figure 3 (a)]. The other way to tell males from females is by observing the throat colour [Figure 3 (b)]. The darker throat is male and the lighter throat is female. This occurs during the breeding season (Rowley, 2015).

(A)



(B)



Figure 3: (A) Dorsal view of *Pelobatrachus nasutus* and (B) ventral view of *Pelobatrachus nasutus*

Statistical Analyses

The Shapiro-Wilk test was computed to assess the normality of the data and the results indicated that the data were not normally distributed for both males and females. Consequently, the raw morphometric data were standardised using a log₁₀-transformation in SPSS. After applying log₁₀-transformation, another Shapiro-Wilk test was run, which confirmed that the transformed data were normally distributed: Male ($P = 0.864$) and Female ($P = 0.856$), both greater than 0.05.

Subsequently, stepwise methods in Discriminant Function Analysis (DFA) were used to determine if there are significant

differences in morphology between populations. Males and females were analysed separately because when combined, the analysis showed there were no significant morphological differences. However, when they were pooled together, the study revealed morphological differences. Then, the log-transformed morphological characteristic was then analysed using the Post hoc Tukey test in IBM SPSS software to compare the mean of each morphological characteristic between populations. The mean value and standard deviation of 26 morphometric measurements belonging to 58 individuals, consisting of 29

females and 29 males, collected from different locations are shown in Appendix 2.

Results and Discussion

Morphometric of Male *Pelobatrachus nasutus*

Figure 4 shows the results of the Canonical Discriminant Function Analysis for the male *Pelobatrachus nasutus*. The first axis separates Central individuals from the two other regions

and the second axis shows less significant differences between individuals from Western and Northeastern regions.

Table 2 shows the value of Standardised Canonical Discriminant Function Coefficients using the stepwise method. The Eigenvalues and Wilks' Lambda values are shown in Tables 3 and 4, respectively. The comparison of the mean between regions using the Post hoc Tukey test is shown in Table 5.

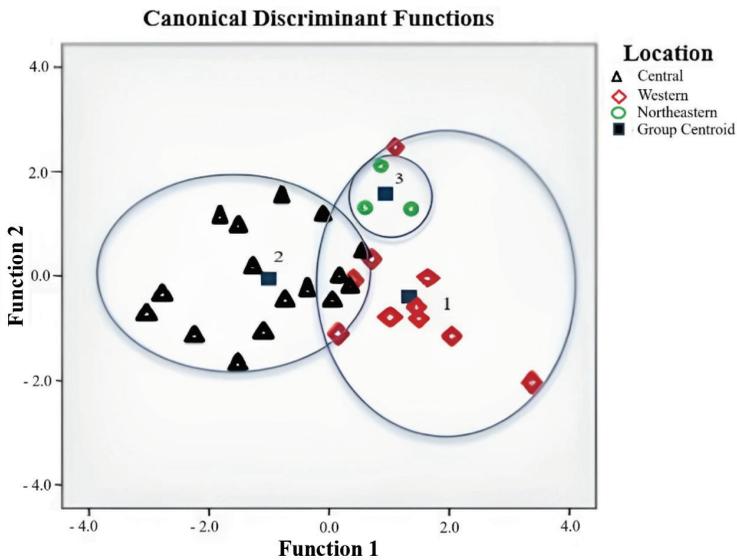


Figure 4: Plots of individual males of *Pelobatrachus nasutus* belonging to three a priori groups (Western, Central, and Northeastern)

Table 2: Standardised Canonical Discriminant Function Coefficients of males *Pelobatrachus nasutus* using stepwise method in discriminant analysis function

	F1	F2
Head length	1.792	-0.588
Lower arm length	-1.485	-0.726
Eye length	-0.034	1.647

Table 3: Eigenvalues of Canonical Discriminant Function of males *Pelobatrachus nasutus*

Function	Eigenvalue	Percentage of Variance	Cumulative (%)	Canonical Correlation
1	1.408	80.2	80.2	0.765
2	0.349	19.8	100.0	0.508

Table 4: Wilks' Lambda Canonical Discriminant Function of males *Pelobatrachus nasutus*

Test of Functions	Wilks' Lambda	Chi-square	df.	Sig.
1 through 2	0.308	29.448	6	0.000
2	0.742	7.477	2	0.024

Table 5: Multiple comparisons between regions of each morphometric measurement of male *P. nasutus* using Post hoc Tukey test result showed two morphological structures with a significant difference

Morphological Characteristic	Mean Difference between Region	Standard Error	Significant ($p < 0.05$)
Head length	Central-Western	0.03	0.01
	Central-Northeastern	0.04	0.99
	Western-Northeastern	0.04	0.19
Upper eyelid width	Central-Western	0.03	0.01
	Central-Northeastern	0.05	0.95
	Western-Northeastern	0.04	0.23

Morphometric of Female *Pelobatrachus nasutus*

Figure 5 shows the results of the Canonical Discriminant Function Analysis for the female *Pelobatrachus nasutus*. The first axis and the second axis show significant differences between individuals from Central, Western, and Northeastern. Table 6 shows the value of

Standardised Canonical Discriminant Function Coefficients using the stepwise method. The Eigenvalues and Wilks' Lambda values are shown in Tables 7 and 8, respectively. The comparison of the mean between regions using the Post hoc Tukey test is shown in Table 9.

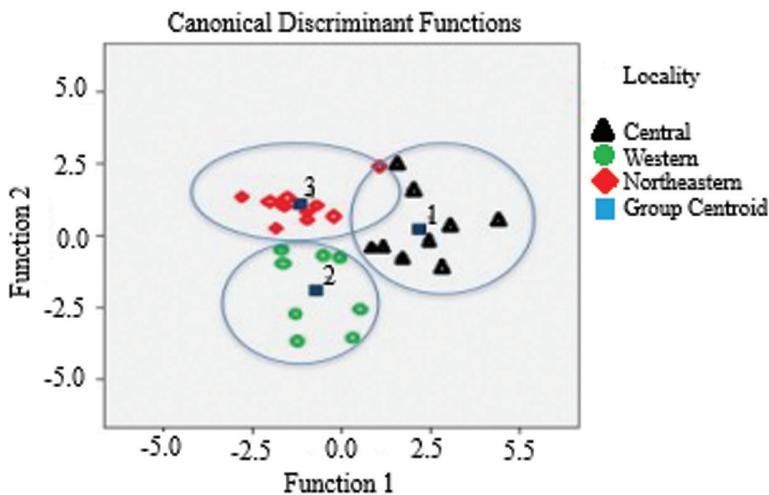


Figure 5: Plots of individual females of *Pelobatrachus nasutus* belonging to three priori groups. 1 is population located at Central, 2 is population located at Western, and 3 is population located at Northeastern Sarawak

Table 6: Standardised Canonical Discriminant Function Coefficients of females, *Pelobatrachus nasutus* using stepwise method in discriminant analysis function

Characteristic	Function 1	Function 2
Hand length	-3.346	-2.063
Lower arm length	3.452	2.783
Front eye to nare	5.081	-2.566
Snout to nare length	-5.037	2.072

Table 7: Eigenvalues of Canonical Discriminant Function of females *Pelobatrachus nasutus*

Function	Eigenvalue	Percentage of Variance (%)	Cumulative (%)	Canonical Correlation
1	2.420	59.0	59.0	0.841
2	1.681	41.0	100.0	0.792

Table 8: Wilks' Lambda Canonical Discriminant Functions of females *Pelobatrachus nasutus*

Test of Functions	Wilks' Lambda	Chi-square	df.	Sig.
1 through 2	0.109	54.283	8	0.000
2	0.373	24.160	3	0.000

Table 9: Multiple comparisons between regions of each morphometric measurement of female *Pelobatrachus nasutus* using Post hoc Tukey test result showed two morphological structures with significant difference

Morphological Characteristic	Mean Difference between Region	Standard Deviation	Significant ($p < 0.05$)
Snout-vent-length	Central-Western	0.03	0.00
	Central-Northeastern	0.03	0.00
	Western-Northeastern	0.29	0.72
Dorsal stripe length	Central-Western	0.06	0.11
	Central-Northeastern	0.06	0.04
	Western-Northeastern	0.05	0.91
Lower arm length	Central-Western	0.05	0.04
	Central-Northeastern	0.04	0.90
	Western-Northeastern	0.04	0.06

Skin Observation

Based on Table 10, in Gunung Gading NP, one individual possessed light brown body color while the other possessed dark gray. Borneo Highland also possessed one light brown individual and one dark grey individual. The body colour of individuals from Gunung Mulu NP and Pelagus possessed all different colours.

In Gunung Mulu NP, two individuals were light brown, three individuals were dark brown, four individuals were light grey, and three individuals were dark grey. Meanwhile, the highest number of tubercles observed on frog skin originated from Pelagus of Central Sarawak.

Table 10: Observation of males and females *Pelobatrachus nasutus* specimens' skin colour and the number of tubercles present in each individual

Habitat Types	Locality	Number of Individuals (n)	Skin Colour				Number of Tubercles (Min-Max)
			Light Brown	Dark Brown	Light Grey	Dark Grey	
Protected forest	Gunung Gading NP	5	1			4	4-10
	Gunung Mulu NP	12	2	3	4	3	1-9
	Kubah NP	5	3	2			0-3
	Tanjung Datu NP	10		7	1	2	4-16
	Jagoi NP	2			1	1	5-7
Non-protected	Pelagus	19	7	3	2	5	1-20
	WILMAR Oil Palm Plantation	3	1	1	1		1-5
	Borneo Highland	2	1			1	6-9

The results showed significant morphological variation in *Pelobatrachus nasutus* between males and females from different localities. The Post hoc Tukey test revealed a significant difference in the Snout-Vent Length (SVL) of *P. nasutus* from the Central, Western, and Northeastern regions. Male frogs from the Northeastern region, particularly from Gunung Mulu NP exhibit larger body size (mean \pm standard deviation = 81.35 ± 9.85), compared to other locations. The mean comparison of the population in Northeastern showed that the body size of the population in Gunung Mulu NP is larger than WILMAR Oil Palm Plantation. This study contradicts Hsu's (2014), which suggested that the population at higher altitudes possess smaller body sizes than those at lower altitudes. The current results supported Richter-Boix (2011), suggesting that the availability of food resources and activity patterns contribute to the differences in body size regardless of different altitudes. The result reflects that the Gunung Mulu NP as a protected area provides sufficient food resources for the growth of *P. nasutus* while the population in the oil palm plantation area potentially has limited food resources due to fragmented forest remnants, resulting in slower growth. However, in the populations of Gunung Gading NP and Tanjung Datu NP, female frogs possessed smaller SVL than males. This is contrary to the findings of Ibragimova

et al. (2018) on *Rana arvalis*, where females in unprotected habitats possess smaller body sizes than females in protected areas. In other regions, females' SVL is larger than males, illustrating sexual dimorphism in body size in *P. nasutus*.

Morphometric data analysis revealed significant differences in the upper eyelid of male *Pelobatrachus nasutus*. In general, frogs use their eyelid for blinking and to maintain moisture in their eyes. This species exhibits a pointy eyelid due to the presence of an appendage like the horn, that aids in camouflage amongst leaf litter on the forest floor (Zainudin et al., 2018). Observation of this species showed that the eyelids had the same pattern as the snout, suggesting that these features primarily serve the purpose of camouflage, which mimics the end tip of leaf litter on the forest floor. The mean comparison result showed that the population from Gunung Mulu NP had the highest mean value of upper eyelid width while the lowest mean value was from Gunung Gading NP. This indicates that this species' camouflaging behaviour is extreme at Gunung Mulu NP, likely due to predatory pressure.

Another measurement taken was the Internal distance of the Front Eye (IFE) (Appendix 2), which had the highest mean value in the Central region, Pelagus. The eyes' structure is very crucial for spotting predators and prey.

In this current study, based on the result of the stepwise method and mean comparison between the region of the Post hoc Tukey test the upper eye width and the eye length were significant in male *Pelobatrachus nasutus*. Frogs that have burrowing behaviour possess smaller eye sizes due to adaptation to dark environments (Thomas *et al.*, 2020). The mean value of eye size showed that the population from Kubah NP possesses the smallest eye size (mean \pm SD; female: 7.11 ± 0.21 , male: 10.00 ± 2.40). This result corresponds with *P. nasutus* as a terrestrial species. This finding also indicates that Kubah NP maintains its forest structure, which is comprised of dense canopy cover that reflects the darker surrounding environment on Kubah NP's forest floor.

The measurement of Head Length (HL) (Appendix 2) is proportionate with the size of the snout length. This is proved by the highest mean value of head length observed within individuals from Gunung Mulu NP (mean \pm SD; female: 31.81 ± 4.23 , male: 27.78 ± 5.30) while the lowest from Gunung Gading NP (mean \pm SD; female: 23.67 ± 0.81 , male: 23.67 ± 0.81). The head length of this species was linked to their feeding behaviour, as a longer head length allows a larger gap during feeding. A larger gap indicates high competition for food resources and predation in the habitat of Gunung Mulu NP for *P. nasutus* because of the extreme mimicry behaviour.

The forearm (LAL) (Appendix 2), which includes lower arm length and hand length measurements showed significant differences between the individuals. The mean comparison showed that *Pelobatrachus nasutus* from the Central region, Pelagus (mean \pm SD; female = 22.45 ± 6.52 , male = 19.14 ± 3.41) possessed the highest value of hand length while the lowest mean value was from Kubah NP (mean \pm SD; female = 11.95 ± 0.22 , male = 15.38 ± 4.81). The variation of forearm lengths observed from these localities suggests that the mode of locomotion varies for individuals in Pelagus and Kubah NP. This might be due to the frogs' activities such as jumping away from predators or the frogs moving to find cooler areas. This

finding can be a good indicator that Pelagus and Kubah NP retain a high number of predators.

In this study, Dorsal Lateral Stripe Length (DLSL) was also measured. The dorsal skin stripes have a similar function to tubercles, which are composed of serous glands, which are important for the species' defence against microorganisms (Zainudin *et al.*, 2018). Post hoc Tukey test of DLSL between populations in Central and Northeastern regions ($p = 0.04$ significant at p -value < 0.05) showed that there are significant differences in DLSL but less significant differences between Western-Northeastern ($p = 0.91$) and Central-Western ($p = 0.11$). The length of the dorsal lateral stripe was longer in the Central region, indicating that *Pelobatrachus nasutus* in the Pelagus is exposed to the polluted areas. Meanwhile, frogs found in non-protected forests possessed the highest number of tubercles on the dorsal skin (Table 10). The abundance of tubercles indicates a high level of predatory and pollution in Pelagus, the species adapts to the environment. The presence of the tubercles aligns with the presence of a mucous gland that regulates water absorption and provides moisture for the frog skin (Zainudin *et al.*, 2018). An increase in the number of tubercles indicates the area is less humid and exposed to sunlight (Zainuddin *et al.*, 2018), thus, indicating that the frogs are experiencing desiccation in that area. This reflects that the habitat in Pelagus, which is considered a dry environment causes the species to be exposed to more sunlight due to the loss of forest canopy in that area.

In terms of body colouration, *Pelobatrachus nasutus* samples exhibited varying colours from light grey, dark grey, light brown, and dark brown colours. This species is known for its expertise in camouflage amongst leaf litter on forest floors. Body colouration is one important strategy for success to become less visible and hide from predators and while foraging for prey (Rojas, 2017). The population from Pelagus and Gunung Mulu NP exhibit all body colours: Light brown, dark brown, light grey, and dark grey. The darker body colouration of this species indicates the environment was relatively dark

and hiding spots were available. Plus, the lighter body colouration could be due to the species inhabiting brighter areas, which could be due to land clearing.

Conclusions

In conclusion, this study revealed significant morphological characteristics among the *Pelobatrachus nasutus* population from different locations. Based on the result, several morphological characters showed significant differences amongst the population. The head length, lower arm length, eye size, upper eye width, hand length, front eye to nares and snout to nares length, dorsal dermal fold length, and number of tubercles. The morphometric data showed that the population differs from each other mostly in terms of features that relate to locomotion, camouflaging, and feeding behaviour. The finding highlights the influence of factors such as food availability, activity patterns, predatory pressure, and environmental conditions on the morphological characteristics of *P. nasutus*.

The result showed that the population from the protected areas possessed larger body size, lesser number of tubercles, and larger upper eyelids. Thus, non-protected areas (Pelagus, WILMAR Oil Palm Plantation, and Borneo Highland) showed that there is a highly significant difference in the morphological characters when compared to protected areas (Gunung Gading NP, Tanjung Datu NP, Gunung Mulu NP, Kubah NP, and Jagoi NP) using mean values. Hence, the finding of this study suggests that natural habitats of *P. nasutus* in non-protected areas require conservation efforts because any changes in its environment potentially affect the species morphologies character function for adaptation.

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Conflict of Interest Statement

The authors declare that they have no conflict of interest.

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Appendices

Appendix 1: Abbreviations

Snout-Vent Length	SVL
Head Width	HW
Head Length	HL
Snout Length	SL
Snout-Nare Length	SNL
Front Eye-Nare	EN
Internal Nare Distance	IN
Maximum Upper Eyelid Width	UEW
Eye Length	EL
Internal Front Eye	IFE
Internal Back of Eye	IBE
Forearm Length	LAL
Lower Arm Length	LAL
Hand Length	HAL
Lower Arm Width Forearm	LAW
First Finger Length	FIL
Second Finger Length	FIIL
Third Finger Length	FIILL
Fourth Finger Length	FIVL
Tibia Length	TL
Hindlimb	HIL
First Toe Length	TOEIL
Fourth Toe Length	TOEIVL
Dorsal Lateral Stripe Length	DLSL
Dorsal Lateral Stripe Width	DLSW
National Park	NP
<i>Pelobatrachus nasutus</i>	<i>P. nasutus</i>
Millimeter	mm

Appendix 2: Average of morphometric female individuals (Mean ± Sd)

	Pelagus	Gunung Gading NP	Borneo Highland	Tanjung Datu NP	WILMAR		Gunung Mulu NP	Kubah NP	Jagoi NP
					Oil Palm Plantation				
SVL	97.44±21.76	60.10 ±15.87	64.79±1.07	53.56±22.27	82.80±0.61	92.89±11.53	51.57±28.31	N/A	
HL	31.29±5.62	20.00±5.82	21.48±0.92	21.57±16.29	28.20±2.40	31.81±4.23	16.52±0.05	N/A	
DLSL	52.83±14.16	31.65±9.80	33.85±2.70	30.98±16.40	44.90±0.66	50.18±7.54	25.99±0.49	N/A	
DLSW	25.14±7.21	15.10±4.19	16.46±0.35	18.21±17.64	23.57±0.37	25.81±4.00	11.85±0.05	N/A	
LAL	23.26±3.51	15.69±4.75	17.96±1.58	18.88±17.68	20.93±0.70	23.86±2.79	13.51±0.37	N/A	
HAL	22.45±6.52	14.32±4.90	14.90±0.29	17.65±18.25	19.41±0.86	22.19±2.90	11.95±0.22	N/A	
LAL	45.48±9.91	29.50±8.96	31.19±0.51	29.78±17.58	32.23±0.64	43.91±5.25	25.09±0.22	N/A	
LAW	6.42±1.74	3.89±2.27	3.86±0.76	9.57±20.73	6.06±1.37	6.92±1.12	2.42±0.11	N/A	
TL	37.34±7.82	23.00±7.26	25.43±1.78	25.28±18.55	30.09±0.19	34.69±4.20	19.42±0.12	N/A	
FeL	38.51±8.20	24.36±10.21	24.21±0.83	26.24±18.79	31.92±0.70	36.73±4.71	20.73±0.93	N/A	
HIL	20.46±4.24	12.95±3.33	15.51±0.07	17.38±20.41	15.79±1.41	20.32±2.96	11.42±0.53	N/A	
TOEIL	12.38±4.04	7.31±3.55	7.96±0.40	12.60±21.75	11.14±1.98	11.19±2.56	5.89±0.38	N/A	
TOEIVL	32.84±8.59	19.63±7.47	21.56±1.84	23.56±20.13	22.43±5.66	29.76±4.46	15.12±0.64	N/A	
FIL	17.03±4.64	9.69±2.23	11.45±0.25	15.12±21.79	12.67±0.05	15.02±2.98	8.02±0.36	N/A	
FIIIL	17.03±4.91	10.05±2.98	10.98±0.99	15.26±22.01	13.90±0.53	15.93±2.27	8.13±0.12	N/A	
FIIIL	22.57±6.28	13.73±4.36	15.00±0.89	18.21±21.64	19.19±1.19	21.59±2.68	12.07±0.15	N/A	
FIVL	17.43±5.26	9.99±3.93	10.97±0.84	15.28±22.60	14.12±1.39	16.31±2.49	8.43±0.14	N/A	
IFE	16.56±3.73	10.28±2.44	10.37±0.17	15.33±22.93	13.39±0.17	15.47±2.55	9.49±0.16	N/A	
IBE	32.44±7.31	20.38±4.26	21.97±0.82	23.75±21.63	28.57±0.91	30.12±6.73	19.12±0.20	N/A	
IN	8.72±1.91	5.62±1.46	6.01±0.18	11.95±24.42	8.01±0.06	8.71±1.00	4.45±0.16	N/A	
HW	42.11±10.31	29.46±8.72	31.03±0.54	30.73±21.42	38.93±0.79	45.20±6.74	25.10±0.15	N/A	
SL	13.37±3.93	8.80±2.75	9.29±0.12	14.54±24.34	14.13±0.24	14.95±2.48	7.64±0.15	N/A	
UEW	14.56±2.75	9.83±0.05	10.83±0.66	15.28±24.83	15.49±0.22	16.26±3.39	10.14±0.33	N/A	
EN	6.64±1.24	4.23±0.74	3.86±0.13	11.12±26.52	5.28±0.02	5.98±1.18	3.97±0.30	N/A	
SNL	7.16±1.63	4.79±1.45	5.20±0.08	11.75±26.65	8.64±0.37	8.53±1.46	3.64±0.15	N/A	
EL	12.42±2.91	8.26±1.89	7.57±0.32	14.36±26.55	12.32±1.59	11.81±1.09	7.11±0.21	N/A	

Appendix 3: Average of morphometric male individuals (Mean \pm Sd)

	Pelagus	Gunung Gading NP	Borneo Highland	Tanjung Datu NP	WILMAR Oil Palm Plantation	Gunung Mulu NP	Kubah NP	Jagoi
SVL	77.57 \pm 13.35	67.72 \pm 5.71	N/A	68.48 \pm 4.28	80.12 \pm 0.40	81.35 \pm 9.85	66.42 \pm 20.13	79.86 \pm 0.14
HL	28.03 \pm 3.70	23.67 \pm 0.81	N/A	22.03 \pm 1.24	27.15 \pm 0.39	27.78 \pm 5.30	22.62 \pm 6.39	26.90 \pm 1.01
DLSL	41.69 \pm 7.65	35.88 \pm 1.26	N/A	35.05 \pm 4.16	39.87 \pm 0.38	43.96 \pm 2.81	37.32 \pm 12.16	41.84 \pm 2.74
DLSW	27.25 \pm 22.01	18.77 \pm 1.98	N/A	18.88 \pm 1.73	19.95 \pm 0.54	22.50 \pm 1.49	18.17 \pm 5.92	21.28 \pm 2.24
LAL	20.43 \pm 3.86	18.26 \pm 0.99	N/A	17.79 \pm 1.29	20.36 \pm 0.41	20.93 \pm 1.33	101.73 \pm 162.85	20.23 \pm 0.86
HAL	19.14 \pm 3.41	16.46 \pm 1.68	N/A	16.33 \pm 1.22	18.75 \pm 0.29	19.34 \pm 0.80	15.38 \pm 4.81	18.49 \pm 0.33
LAL	38.69 \pm 6.74	33.96 \pm 2.05	N/A	32.69 \pm 2.42	38.75 \pm 0.47	39.68 \pm 2.58	31.37 \pm 9.56	38.11 \pm 2.60
LAW	5.04 \pm 1.39	5.34 \pm 1.22	N/A	5.18 \pm 0.83	4.94 \pm 0.16	5.28 \pm 1.95	4.72 \pm 2.18	5.85 \pm 0.37
TL	30.85 \pm 5.47	27.13 \pm 1.75	N/A	25.54 \pm 1.40	29.44 \pm 0.57	30.35 \pm 2.05	24.55 \pm 7.16	29.90 \pm 0.16
FeL	31.51 \pm 6.36	29.64 \pm 1.98	N/A	28.17 \pm 1.45	30.87 \pm 0.08	31.58 \pm 4.62	25.94 \pm 7.43	30.55 \pm 0.66
HIL	17.16 \pm 3.01	15.16 \pm 0.97	N/A	18.98 \pm 13.36	16.60 \pm 0.26	17.06 \pm 1.11	14.12 \pm 4.75	18.02 \pm 0.90
TOEIL	9.34 \pm 1.95	8.34 \pm 1.57	N/A	8.08 \pm 0.83	9.99 \pm 0.65	9.95 \pm 0.58	9.89 \pm 5.68	8.58 \pm 0.14
TOEIVL	26.01 \pm 5.23	22.21 \pm 1.34	N/A	21.05 \pm 1.70	26.05 \pm 0.47	27.29 \pm 2.15	20.48 \pm 6.74	25.36 \pm 0.98
FIL	13.39 \pm 2.31	12.05 \pm 1.01	N/A	11.82 \pm 0.90	12.67 \pm 0.05	14.34 \pm 0.41	11.06 \pm 3.53	13.07 \pm 1.03
FIIIL	13.92 \pm 2.74	12.28 \pm 1.17	N/A	11.94 \pm 0.67	13.87 \pm 0.37	14.12 \pm 0.38	11.27 \pm 4.03	13.30 \pm 0.47
FIIIL	18.76 \pm 3.78	16.51 \pm 1.77	N/A	15.92 \pm 0.70	19.84 \pm 0.41	18.87 \pm 0.63	14.75 \pm 5.12	18.24 \pm 0.14
FIVL	13.91 \pm 3.04	12.04 \pm 1.43	N/A	11.86 \pm 0.73	14.84 \pm 0.77	13.74 \pm 0.55	10.84 \pm 3.63	14.43 \pm 0.59
IFE	13.61 \pm 2.33	12.15 \pm 0.91	N/A	11.50 \pm 0.63	13.02 \pm 0.24	13.44 \pm 0.66	11.35 \pm 2.98	13.56 \pm 0.90
IBE	27.59 \pm 3.97	24.59 \pm 4.08	N/A	23.05 \pm 1.73	26.77 \pm 0.22	28.55 \pm 3.32	23.18 \pm 5.94	27.65 \pm 1.86
IN	7.50 \pm 1.26	6.55 \pm 0.26	N/A	6.24 \pm 0.23	8.43 \pm 0.21	7.66 \pm 0.84	6.50 \pm 1.64	7.73 \pm 0.04
HW	37.96 \pm 5.75	32.95 \pm 1.84	N/A	31.86 \pm 1.51	36.37 \pm 0.34	39.08 \pm 2.90	31.17 \pm 8.96	38.92 \pm 1.15
SL	11.90 \pm 3.23	10.45 \pm 0.78	N/A	9.82 \pm 0.46	13.83 \pm 0.41	12.49 \pm 2.56	13.98 \pm 9.62	12.05 \pm 0.49
UEW	13.73 \pm 1.70	10.78 \pm 1.43	N/A	10.77 \pm 0.89	11.43 \pm 0.24	14.31 \pm 2.44	11.85 \pm 3.30	12.66 \pm 2.04
EN	5.39 \pm 0.99	4.88 \pm 0.77	N/A	4.57 \pm 0.48	5.65 \pm 0.18	5.60 \pm 0.11	4.47 \pm 0.97	5.30 \pm 1.27
SNL	6.65 \pm 1.48	5.85 \pm 0.65	N/A	5.05 \pm 0.43	7.21 \pm 0.11	6.89 \pm 2.36	5.33 \pm 1.67	6.37 \pm 0.25
EL	9.94 \pm 2.18	8.89 \pm 0.18	N/A	9.17 \pm 1.10	12.62 \pm 0.51	11.89 \pm 1.92	10.00 \pm 2.40	10.22 \pm 0.67