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Habitat-linked morphological variation in the Asian water monitor lizard (*Varanus salvator*) across urban, agricultural, and forest landscapes in peninsular Malaysia

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The Asian water monitor lizard, *Varanus salvator* is a widespread carnivorous reptile in Malaysia, yet the effects of habitat disturbance on its morphology remain poorly understood. This study examined 168 individuals from urban, agricultural, and forest habitats using morphometric measurements of snout–vent length (SVL), weight, skull length, thigh width, and body condition. To assess shape-level differences independent of body size, size-corrected traits were calculated as residuals from log–log regressions against SVL. Principal Component Analysis (PCA), Linear Discriminant Analysis (LDA), and one-way MANOVA were used to evaluate morphological divergence among habitats. Results showed that morphological variation was structured primarily by habitat type rather than site-specific effects. SVL did not differ significantly across habitats, indicating similar growth potential across the disturbance gradient. However, urban lizards exhibited consistently larger relative traits, and better body condition than those from agricultural habitats, with forest individuals showing mixed patterns but closer to agricultural lizards. Lizards from agricultural habitats had the narrowest thighs and poorest condition, potentially a result of habitat specific stressors. These findings suggest that habitat type influences energy allocation to structural and performance-related traits, rather than limiting size. While *V. salvator* appears morphologically adaptable to anthropogenic environments, future studies incorporating sex, diet, and predator interactions are needed to clarify the drivers of trait variation and assess potential fitness consequences in disturbed landscapes.

Key words: Asian water monitor lizard; disturbance; habitat; morphology; varanids.

The Asian water monitor lizard (*Varanus salvator*) is the second largest Varanid lizard after the Komodo Dragon, *Varanus komodoensis* (Gaulke & Horn, 2004), and can reach lengths of more than three meters (Randow, 1958). This species

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is found in Southeast Asia (KOCH & BÖHME, 2010; QUAH *et al.*, 2021) where it is abundant at low elevations (KHADIEJAH *et al.*, 2019). *Varanus salvator* exhibits a strong preference for a semi-aquatic lifestyle (YOUNG *et al.*, 2016), often inhabiting areas near waterways such as rivers, lakes, and mangroves (COTA *et al.*, 2009). The species has also been documented on beaches and islands (RUSLI *et al.*, 2020), as well as displaying arboreal (STANNER, 2020) and burrowing behaviours (COTA, 2011; GIBBON *et al.*, 2024). This species is also heavily exploited in the skin trade (KHADIEJAH *et al.*, 2019) and is consumed in certain regions (UYEDA *et al.*, 2014).

Varanus salvator is a generalist carnivore that actively hunts and scavenges (KULABTONG & MAHAPROM, 2014; TEE *et al.*, 2018; GUERRERO-SANCHEZ *et al.*, 2023). This behaviour positions the species as an important contributor to top-down control of prey populations and carrion removal, providing critical ecosystem services, such as nutrient cycling and disease regulation (BEASLEY *et al.*, 2019). In Malaysian agricultural and urban habitats, where predator communities are less diverse and often replaced by generalist species (TWINING *et al.*, 2017; SEBASTIÁN-GONZÁLEZ *et al.*, 2019), the ecological importance of a large, disturbance-tolerant predator such as *V. salvator* is further emphasized. For example, their predation on disturbance-tolerant prey such as pest rat species (KULABTONG & MAHAPROM, 2014), which are both abundant and considered agricultural pests (PUAN *et al.*, 2011), helps reduce the need for ecologically damaging chemical control methods. This is critical in mitigating the risk of secondary poisoning of non-target species by anticoagulant rodenticides (RAVINDRAN *et al.*, 2022). Furthermore despite its ecological significance in disturbed habitats, little attention has been given to the role of *V. salvator* in urban habitats (LUNA & RAUSELL-MORENO, 2024), where it is often the largest and most abundant natural (Tee *et al.*, 2018). Given the ecological significance and abundance of this species, monitoring these populations is essential to ensure they do not suffer long-term negative consequences from occupying highly disturbed habitats.

Much of previous research on the effects of habitat disturbance on wildlife focused on population dynamics, using metrics like population size, extinction risk, or species richness (JOHNSON *et al.*, 2020; CORDIER *et al.*, 2021; MUNSTERMANN *et al.*, 2022). Though crucial, studies analysing broad scale patterns at the level of populations or species risk overlooking individual level morphological and behavioural responses that are important for understanding disturbance effects on population dynamics and ecosystem function (as reviewed in MACDONALD *et al.*, 2024). Morphological responses to disturbance vary by species, geography, and disturbance type (JESSOP *et al.*, 2012; FALVEY *et al.*, 2020), and can be influenced by additional factors such as climate and invasive predators (MACDONALD *et al.*, 2024). Furthermore, individual-level traits such as body condition, which serve as proxies for energy reserves, are particularly important because they are sensitive to habitat disturbance, with documented negative impacts on reptiles (MACDONALD *et al.*, 2024).

The influence of habitat disturbance on body morphology of *V. salvator* in Malaysia, particularly body size and condition, needs exploring given inconsistent findings that suggest these variables are closely associated to the specific habitats being studied. For example, TWINING *et al.*, (2017) reported larger individuals with better body condition in disturbed habitats like logged areas and oil palm plantations, while KHADIEJAH *et al.*, (2019) observed the opposite, with larger individuals in natural habitats such as forests and mangroves, likely due to the removal of plantation-dwelling individuals before they can grow. Interestingly, KHADIEJAH *et al.*, (2019) found similar body conditions across disturbed and natural habitats. In contrast, GUERRERO-SANCHEZ *et al.*, (2021; 2023) detected no significant differences in size or condition between forest and oil palm habitats, attributing this to a trade-off between resource availability and competition. While existing studies have explored *V. salvator* in forests and agricultural or logged habitats, urban habitats remain underexplored, particularly in Malaysia (LUNA & RAUSELL-MORENO, 2024).

In urban habitats, *V. salvator* often achieves high population densities (WONGTIENCHAI *et al.*, 2021), supported by abundant but unevenly distributed resources such as food waste and small mammal prey (SHOCHAT *et al.*, 2006; PUAN *et al.*, 2011). This resource availability may contribute to larger body sizes and better body conditions, similar to other Varanid species (JESSOP *et al.*, 2012). However, in anthropogenic habitats without hunting pressure, a shift toward larger individuals can lead to negative outcomes such as increased aggression and cannibalism (SHINE *et al.*, 1996; UYEDA *et al.*, 2015; BHATTACHARYA & KOCH, 2018), potentially creating an ecological trap (FLETCHER *et al.*, 2012).

In addition to overall body size and condition, other morphological traits may offer insights into habitat-related adaptations. One such trait is head morphology, particularly skull length. Head dimensions can influence functional performance, including bite force, which is often associated with dietary niche (MEYERS *et al.*, 2018). Larger skulls can accommodate stronger jaw musculature, potentially which can offer advantages when processing harder or larger prey (FRENCH *et al.*, 2018; TAVERNE *et al.*, 2020). In lizards, variation in head size has been linked to differences in prey type and foraging ecology, reflecting local environmental demands (UROŠEVIĆ *et al.*, 2014), as well as dominance or intraspecific competition under high-density conditions, primarily through increased bite force (VERWAIJEN *et al.*, 2002). For *V. salvator*, prey availability likely differs substantially across forest, agricultural, and urban habitats: forested environments likely offer a broader range of natural prey, agricultural areas often harbour disturbance-tolerant pest species (PUAN *et al.*, 2011), while urban habitats provide a mix of anthropogenic refuse and disturbance-tolerant pest species (UYEDA, 2009; KULABTONG & MAHAPROM, 2014; UYEDA *et al.*, 2015). Given these contrasting foraging landscapes, skull length may vary across habitats as a morphological response to divergent dietary pressures.

Following this, limb morphology, specifically thigh width may similarly serve as an ecologically informative trait. Limb structure in lizards is closely tied to habitat use and locomotor strategies such as running, climbing, or burrowing (D'AMORE *et al.*, 2018; CORTÉS-PARRA *et al.*, 2022). Habitat disturbance, especially in anthropogenic landscapes, often leads to reduced substrate and structural complexity (ZEMP *et al.*, 2019), and increased presence of disturbance tolerant predators (AZHAR *et al.*, 2012), which can alter the patterns of movement and potentially shape limb morphology (DONIHUE, 2016). These ecological pressures may drive shifts in locomotor behaviour, with corresponding changes in thigh morphology reflecting adaptations to altered habitat structure and predator-mediated selection.

To better understand how *V. salvator* responds morphologically to different levels of anthropogenic habitat disturbance, this study investigates how body size, condition, skull length, and thigh width vary across urban, agricultural, and forest habitats in Peninsular Malaysia. Furthermore, to account for both absolute size and shape, we included analyses of raw traits and size-corrected values. Specifically, we tested the following hypotheses: (1) Lizards in urban and agricultural habitats will exhibit larger body size and higher condition than those in forests due to access to anthropogenic food sources; (2) Lizards in disturbed habitats will exhibit smaller thigh widths than those in forests, reflecting altered locomotor demands or increased escape behaviours; (3) Morphological differences will be shaped by habitat type rather than sampling location, indicating generalizable habitat-linked pressures.

MATERIALS AND METHODS

Sampling locations

This study conducted sampling in three habitat types: urban, agriculture, and forest. Location of urban habitats were Universiti Sains Malaysia on Penang Island (5.353, 100.299) (USM_Urban), and the second location was Universiti Malaysia Terengganu campus in Terengganu (5.413, 103.087) (UMT_Urban). The sampling for the agriculture habitat was conducted in two oil palm plantations: Kiara Jubli Estate Sdn. Bhd., in Southern Perak (3.726, 101.283) (KJ_Agriculture), and Sempadan Asasi Sdn. Bhd. (SA), Gopeng, Perak (4.460, 101.131) (SA_Agriculture). Finally, sampling in forest habitats was conducted in Chagar Hutang Turtle Sanctuary (CH) on Pulau Redang in Terengganu (5.812, 103.007) (CH_Forest).

A permit to conduct research on this species was secured from the Department of Wildlife and National Parks Peninsular Malaysia (PERHILITAN), license number P-00003-15-19; and animal ethics approval was obtained from Universiti Sains Malaysia, animal ethics approval number USM/IACUC/2020/(123)(1064).

Sampling and measurement

Lizards were captured using baited traps measuring 50 x 50 x 120 cm. The following morphometric measurements were recorded: thigh width (cm), skull length (cm), snout-vent length (SVL) (cm), and weight (kg) (SHINE *et al.*, 1996; SHINE *et al.*, 1998; KOCH *et al.*, 2007; SMITH *et al.*, 2007; TWINING *et al.*, 2017; KHADIEJAH *et al.*, 2019; GUERRERO-SANCHEZ *et al.*, 2021). To obtain size corrected morphological variables, a log-log linear regression was performed, consisting of each allometric trait (thigh width, skull length, and weight) against SVL, following established approaches to control for body size scaling (Green, 2001). The residuals from these regressions were extracted and interpreted as indices of relative trait size (e.g. relative thigh width, body condition), representing shape variation independent of body size (Sion *et al*., 2021). A list of variables considered for analysis is provided in Table 1.

It is important to note that this study did not perform sex identification and, consequently, did not estimate sex ratios. While hemipenes eversion was attempted during sampling following the approach of Twining *et al*. (2017), the method proved impractical due to its time-consuming nature and limited reliability, particularly as partially everted hemipenes could be mistaken for hemiclitori. In the absence of DNA-based validation, the study opted to avoid subjecting the lizards to unnecessary handling for measurements that could not be confidently verified.

Data analysis

Principal Component Analysis. Principal Component Analysis (PCA) was applied to both raw measurements (e.g., SVL, skull length, weight) and size-corrected residuals (e.g., relative thigh width, body condition) to reduce dimensionality and mitigate multicollinearity prior to Linear Discriminant Analysis (LDA; Elhaik, 2022). The PCA was conducted using a correlation matrix and components with eigenvalues >1 were retained. These compo-

Table 1: The definition of the eight variables and the references in which the variables were used to predict lizard habitats. no. 1 to 7 were the predictor variables (independent), no. 8 was the target variable (dependent).

No.	Variable	Definition and Unit	Type	References
1.	Thigh width	Circumference of thigh at middle of thigh (cm)	Continuous	Similar to Smith *et al*., (2007)
2.	Skull length	Length from the tip of the snout to the base of the skull (cm)	Continuous	Shine *et al*., (1996); Shine *et al*., (1998); Twining *et al*., (2017)
3.	Snout-vent length (SVL)	Length from tip of snout to vent (cloaca) (cm)	Continuous	Shine *et al*., (1996); Shine *et al*., (1998); Koch *et al*., (2007); Twining *et al*., (2017); Khadiejah *et al*., (2019); Guerrero-Sanchez *et al*., (2021)
4.	Weight	Weight of animal (kg)	Continuous	Twining *et al*., (2017); Khadiejah *et al*., (2019); Guerrero-Sanchez *et al*., (2021)
5.	Relative thigh width	Residual from log-log regression between thigh width and SVL	Continuous	As above
6.	Relative skull length	Residual from log-log regression between skull length and SVL	Continuous	As above
7.	Body condition	Residual from log-log regression between weight and SVL	Continuous	As above
8.	Location	USM_Urban, UMT_Urban, KJ_Agriculture, SA_Agriculture, CH_Forest	Categorical	-

PC	Eigenvalue	Percentage of Variance	Cumulative Percentage
1	3.786	54.08	54.08
2	1.515	21.64	75.72
3	1.074	15.34	91.06
4	0.625	8.93	100.00
5	<0.0001	<0.0001	100.00
6	<0.0001	<0.0001	100.00
7	<0.0001	<0.0001	100.00

Table 2: Eigenvalue and Percentage of Variance from the PCA of raw and size -corrected variables.

nents were interpreted based on trait loadings and served as input variables for the subsequent LDA.

Linear Discriminant Analysis. A Linear Discriminant Analysis (LDA) was conducted to evaluate whether individuals could be morphologically discriminated based on habitat type, while also assessing the extent to which sampling location contributed to the observed separation. This multivariate classification technique identifies linear combinations of input variables that maximize separation among predefined groups (XANTHOPOULOS *et al.*, 2013). As LDA is sensitive to multicollinearity, the analysis was performed using the principal components derived from the prior PCA that met the eigenvalue cut off criterion, thus reducing noise from correlated or redundant traits (NÆS & MEVIK 2001).

Location (five levels: USM_Urban, UMT_Urban, KJ_Agriculture, SA_Agriculture, CH_Forest) was used as the grouping variable. The analysis produced canonical discriminant functions, which were evaluated based on the proportion of between-group variance explained and their statistical significance using Wilks' Lambda. Model performance was assessed through classification accuracy and leave-one-out cross-validation to estimate robustness. Discriminant scores were plotted along the first two canonical axes to visualize group separation, with 95% confidence ellipses superimposed to illustrate variation and overlap among sites.

Multivariate Analysis of Variance (MANOVA). A one-way MANOVA was conducted to assess whether seven morphological traits SVL, weight, skull length, thigh width, and three size-corrected residuals (thigh width, skull length, body condition) differed significantly across five sampling locations (treated as a fixed factor). The reason for a comparative MANOVA test is to confirm the result of LDA in the classification of a group of multiple traits. Wilks' Lambda was used to assess the overall effect; significant results were followed by univariate ANOVAs with effect sizes reported as partial η^2. Levene's Test evaluated variance homogeneity. When violated, Games–Howell post hoc tests were used; otherwise, Tukey's HSD was applied. This analysis identified location-based morphological variation and the traits driving these differences. All statistical analysis were conducted using the Statistical Package for the Social Sciences (SPSS) (IBM CORP, 2019) for Windows version 26 and by using R programming with R version 4.3.0.

RESULTS

PCA

This study sampled a total of 168 *V. salvator* from three habitat types: urban (n= 68), agriculture (n= 60), and forest (n= 40). PCA was conducted on raw and size-corrected morphological variables. Three components with eigenvalues >1 were retained, accounting for 91.06% of the total variance (PC1 = 54.08%, PC2 = 21.64%, PC3 = 15.34%) (Table 2). PC1 was strongly associated with raw size-related traits: thigh width (0.962), weight (0.934), skull length (0.932), and SVL (0.895), and is interpreted as a general body size axis. PC2 loaded most heavily on size-corrected variables, including relative thigh width (0.781), body condition (0.597), and relative skull length (0.564), capturing body proportion (shape) related variation. Finally, PC3 was strongly associated with skull size and shape: skull length (0.304) and relative skull length (0.687) (Table 3). These three components were used in the subsequent Linear Discriminant Analysis.

LDA

LDA was conducted using PC1, PC2, and PC3 to analyse morphological separation across locations. The overall model was significant (Wilks' $\lambda = 0.765$, $\chi^2 = 43.70$, df = 8, $p < 0.001$), indicating meaningful group-level separation. Function 1 explained 68.6% of the between-group variance, Function 2 explained the remaining 29.7%, and Function 3 explained the remaining 1.7% (Table 4). Given the insignificant contribution of Function 3 to the between-group variance, only Functions 1 and 2 were used in further analysis. Group centroids along Function 1 showed separation between sampling locations, with USM_Urban (1.208) and UMT_Urban (0.882) occupying positive values, SA_Agriculture (–1.118) and KJ_Agriculture (–0.323) positioned on the negative end, and CH_Forest (-0.655) overlapping with the agricultural

Table 3: Component matrix of PC1, PC2, and PC3.

Component	PC1	PC2	PC3
Thigh width	0.962	0.004	-0.003
Skull length	0.932	-0.143	0.304
SVL	0.895	-0.444	-0.006
Weight	0.934	-0.118	-0.304
Relative thigh width	0.372	0.781	0.004
Relative skull length	0.303	0.597	-0.646
Body condition	0.295	0.564	0.687

Table 4: Summary of Canonical Discriminant Functions.

Function	Eigenvalue	Percentage of variance	Cumulative percentage	Canonical correlation
1	0.800	68.6	68.6	0.667
2	0.346	29.7	98.3	0.507
3	0.020	1.7	100.0	0.139

Table 5: Group centroids of Location along function 1 Score.

Location	Function 1 score
USM_Urban	0.882
UMT_Urban	1.208
SA_Agriculture	-1.118
KJ_Agriculture	-0.323
CH_Forest	-0.655

habitats (Table 5). Discriminant scores are plotted in Figure 1, with individuals distributed along the first two canonical functions and 95% confidence ellipses.

To assess the stability of the classification model, cross-validation was performed using the leave-one-out method. Overall, 51.2% of cross validated grouped cases were correctly classified. The highest cross-validated classification accuracy was observed for CH_Forest (62.5%), followed by USM_Urban (55.2%), SA_Agriculture (50.0%), UMT_Urban (41.0%) and KJ_Agriculture (40.0%) (Table 6). Significant misclassifications (>20%) primarily occurred between sites of the same habitat type: UMT_Urban individuals and USM_Urban individuals were most often misclassified as each other, while SA_Agriculture and KJ_Agriculture individuals were most frequently misclassified as one another. Forest individuals (CH_Forest) were misclassified as KJ_Agriculture individuals 25% of the time, but forest individuals also had the lowest proportion of misclassification (Table 6).

MANOVA

A one-way MANOVA was conducted to assess whether morphological traits differed significantly across the five sampling locations. The analysis included seven dependent variables: thigh width, skull length, snout–vent length (SVL), weight, relative thigh width, relative skull length, and body condition. Location level variation across the 7 variables was significant (Wilks' $\lambda = 0.357$, $F(16, 489.446) = 12.257$, $p < 0.001$). Follow-up univariate ANOVAs showed significant effects of location on six of the seven morphological traits: thigh width, skull length, weight, relative thigh width, relative skull length, and body condition. SVL did not differ significantly across locations (Table 7).

Table 6: Cross-Validated Classification Accuracy of Sampling Location. High misclassification rates between sites within the same habitat reinforce that morphological structure is habitat-linked rather than site-specific. Bold values indicate the percentage of accurate true positive predictions and asterisks (*) indicate the percentage of false positive predictions.

Location	Accuracy of Cross-Validated Group Membership (Percentage)					
	UMT_ Urban	USM_ Urban	SA_ Agriculture	KJ_ Agriculture	CH_ Forest	Total
UMT_Urban	**41.0**	35.9*	0.0	12.8	10.3	100.0
USM_Urban	24.1*	**55.2**	3.4	3.4	13.8	100.0
SA_Agriculture	3.3	0.0	**50.0**	26.7*	20.0	100.0
KJ_Agriculture	10.0	13.3	26.7*	**40.0**	10.0	100.0
CH_Forest	0.0	5.0	25.0*	7.5	**62.5**	100.0

Table 7: ANOVA and Levene's test results are provided for each trait at sampling locations. (Games–Howell post hoc test was used for traits with unequal variances (Levene's p < 0.05); Tukey's HSD was used otherwise.)

Trait	F-value	ANOVA p-value	Levene's p-value	Location	Mean	SE	N
Thigh Width	3.804	0.006	0.020	UMT_Urban	20.728	4.215	39
				USM_Urban	22.193	3.405	29
				SA_Agriculture	18.817	4.037	30
				KJ_Agriculture	18.557	4.153	30
				CH_Forest	21.133	5.534	40
Skull Length	4.630	0.001	0.085	UMT_Urban	12.092	1.836	39
				USM_Urban	13.014	1.388	29
				SA_Agriculture	11.520	1.616	30
				KJ_Agriculture	11.633	1.645	30
				CH_Forest	11.305	2.113	40
SVL	0.811	0.520	0.001	UMT_Urban	69.718	12.735	39
				USM_Urban	74.731	8.627	29
				SA_Agriculture	73.561	12.926	30
				KJ_Agriculture	70.300	13.100	30
				CH_Forest	72.578	17.308	40
Weight	2.798	0.028	<0.001	UMT_Urban	7.501	4.642	39
				USM_Urban	9.666	3.595	29
				SA_Agriculture	7.351	3.694	30
				KJ_Agriculture	6.550	3.500	30
				CH_Forest	9.330	6.166	40
Relative Thigh Width	17.518	<0.001	0.252	UMT_Urban	1.064	1.418	39
				USM_Urban	1.061	1.270	29
				SA_Agriculture	-1.973	1.864	30
				KJ_Agriculture	-1.278	1.828	30
				CH_Forest	0.631	2.689	40
Relative Skull Length	35.494	<0.001	0.818	UMT_Urban	0.498	0.601	39
				USM_Urban	0.807	0.656	29
				SA_Agriculture	-0.544	0.548	30
				KJ_Agriculture	-0.032	0.554	30
				CH_Forest	-0.639	0.685	40
Body Condition	8.678	<0.001	0.224	UMT_Urban	0.106	2.215	39
				USM_Urban	0.729	2.535	29
				SA_Agriculture	-1.226	1.643	30
				KJ_Agriculture	-1.024	1.472	30
				CH_Forest	1.056	1.866	40

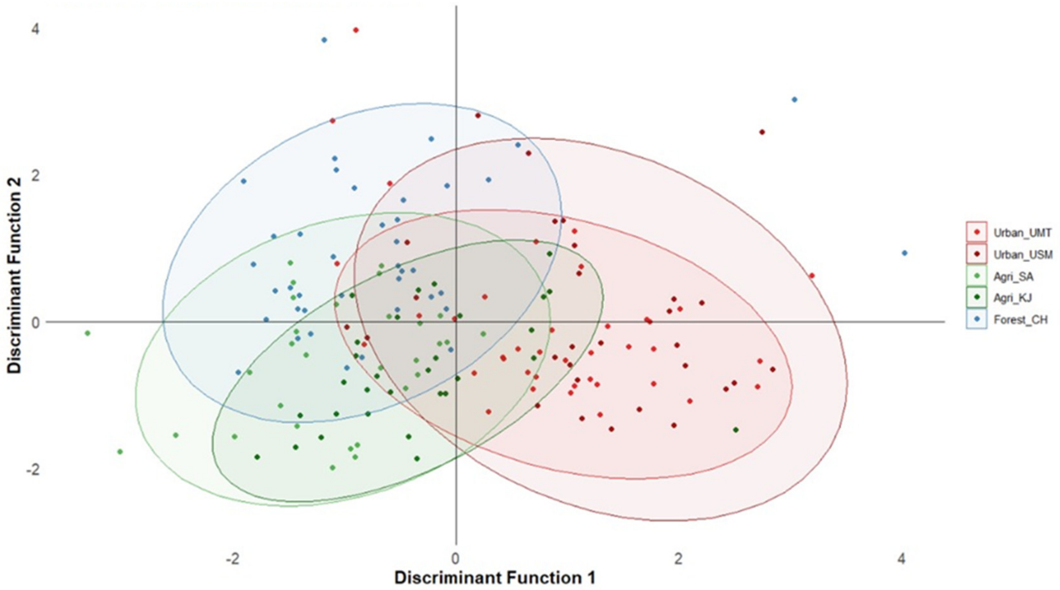

Figure 1: Scatterplot of discriminant scores along Function 1 and Function 2 with 95% confidence ellipses for each sampling location.

Post hoc comparisons were performed on the 6 traits that varied significantly between locations (Appendix 1). For thigh width, USM_Urban lizards had significantly greater values than both SA_Agriculture ($p = 0.030$) and KJ_Agriculture ($p = 0.016$). No significant differences were detected between the two urban sites (UMT_Urban and USM_Urban), between the two agricultural sites (SA and KJ), or between any urban and forest locations. With respect to relative thigh width, UMT_Urban and USM_Urban both had significantly larger values than SA_Agriculture and KJ_Agriculture (all $p < 0.001$), while CH_Forest also exceeded both agricultural sites (both $p \leq 0.001$). No differences were observed between the two urban locations, or between CH_Forest and either urban site.

Table 8: Summary of significant post hoc differences between locations for raw and size corrected variables.

Trait	Significant differences	Summary pattern
Thigh width	USM > SA, KJ	Urban > Agriculture
Relative thigh width	UMT, USM, CH > SA, KJ	Urban and Forest > Agriculture
Skull length	USM > SA, KJ, CH	Urban > Agriculture and Forest
Relative skull length	UMT, USM > SA, KJ, CH	Urban > Agriculture and Forest
Weight	USM > KJ	Urban > Agriculture
Body condition	USM, CH > SA, KJ	Urban and Forest > Agriculture

Next, the skull lengths of USM_Urban lizards were significantly longer than SA_Agriculture ($p = 0.012$), KJ_Agriculture ($p = 0.026$), and CH_Forest ($p = 0.001$). No significant differences were found between UMT_Urban and USM_Urban, or between the two agricultural sites. The relative skull length of UMT_Urban lizards had significantly greater values than SA_Agriculture ($p < 0.001$), KJ_Agriculture ($p = 0.005$) and CH_Forest ($p < 0.001$). Similarly, USM_Urban lizards showed significantly higher values than SA_Agriculture ($p < 0.001$), KJ_Agriculture ($p < 0.001$), and CH_Forest ($p < 0.001$). SA_Agriculture relative skull lengths were significantly smaller than KJ_Agriculture ($p = 0.013$), and CH_Forest relative skull lengths were significantly smaller than all habitats except SA_Agriculture (all $p \leq 0.001$). No differences were found between UMT_Urban and USM_Urban.

The weights of lizards from USM_Urban lizards were significantly heavier than KJ_Agriculture ($p = 0.011$). No other pairwise differences were significant, and weights did not differ within habitat types. Finally, USM_Urban lizards had significantly better condition than SA_Agriculture ($p = 0.002$) and KJ_Agriculture ($p = 0.008$) and UMT_Urban lizards had significantly better body condition than SA_Agriculture (0.05). CH_Forest individuals also exhibited significantly higher body condition than both agricultural sites (both $p \leq 0.001$). No differences were detected within the urban or agricultural locations, or between the urban and forest location. Overall, the post hoc results consistently indicate that urban lizards exhibit the largest raw and size corrected morphological traits between habitat types (Table 7). Forest lizards showed a mixed pattern across traits, and agricultural habitats exhibited generally smaller raw and corrected traits (Table 8). Mean values with 95% confidence intervals for each trait across locations and habitats are provided in Appendix 2, illustrating the patterns summarized in Table 7.

DISCUSSION

This study investigated the influences of habitat type on morphological variation in *V. salvator* across urban, agriculture, and forest habitats. Urban lizards consistently exhibited larger trait values than those from agricultural locations, regardless of whether raw or size-corrected variables were analysed. In contrast, forest lizards showed a mixed pattern: they were sometimes indistinguishable from both other habitats (e.g., raw thigh width, weight), sometimes smaller than urban lizards and similar to agriculture (e.g., raw and relative skull length), and sometimes similar to urban lizards and larger than agriculture (e.g., relative thigh width, body condition). Interestingly, snout–vent length (SVL) did not differ significantly between habitats.

Though it should be noted that the sample size for the forest population was smaller than those in urban and agricultural habitats, which could be a possible reason for the inconsistent differences. It is also notable that forest individuals consistently clustered more closely with agricultural lizards in both trait values and discriminant space, while no significant differences were detected across all traits between sites within the same habitat category, i.e., between the two urban (UMT and USM) or two agricultural (SA and KJ) locations. These patterns are supported by the results of the LDA and MANOVA, which showed that variation in morphology was structured primarily by habitat type, rather than by location, indicating that observed morphological differences reflect broader habitat linked pressures rather than location specific variation.

Size correction (residuals from log-log regression against SVL) improved the resolution of habitat linked differences. This is supported by clearer and more extensive post hoc contrasts in the size-corrected traits compared to their raw counterparts. For instance, raw thigh width distinguished only USM from agricultural sites, whereas the relative measure revealed that UMT and CH also differed significantly from agriculture. Similar improvements were seen in skull length, where relative values distinguished both urban sites from agricultural and forest locations, in contrast to the raw variable which only separated USM. Body condition also provided clearer ecological separation than raw weight, highlighting significant differences between urban and forest lizards relative to agriculture. These patterns indicate that size corrected traits allowed biologically meaningful variation in shape and condition to emerge more clearly, reinforcing the role of habitat in driving morphological divergence and not sampling location.

The improved resolution in size-corrected traits likely reflects their ability to isolate shape-level differences from overall body size (SION *et al.*, 2021). These size-corrected variables provide a clearer view of how organisms allocate structural investment in traits such as limbs or skulls under different ecological conditions (HUTTON & MCGRAW, 2016). While raw traits may reflect broad growth patterns or disturbance responses (PUTMAN & TIPPIE, 2020), size-corrected traits are more sensitive to localised pressures such as locomotor demands, resource structure, and predation pressure (BUTLER & LOSOS, 2002; KLECKA & BOUKAL, 2013; D'AMORE *et al.*, 2018; MACDONALD *et al.*, 2024).

Across all three habitat types, *V. salvator* individuals exhibited similar snout–vent lengths (SVL), despite marked differences in other traits. This finding directly contradicts our initial hypothesis that lizards in urban and agricultural habitats would be larger than those in forests, due to increased access to anthropogenic food waste (UYEDA, 2009; UYEDA *et al.*, 2015) or pest prey (PUAN *et al.*, 2011). Instead, the lack of SVL divergence suggests that all habitats provide sufficient resources for lizards to reach comparable adult body sizes. These results align with those of GUERRERO-SANCHEZ *et al.*, (2021, 2023), who found no significant size differences between *V. salvator* in forest and oil palm habitats, attributing this to a balance between resource availability and density-dependent competition. However, they contrast with studies reporting larger individuals in disturbed habitats due to greater food availability (TWINING *et al.*, 2017), or in undisturbed habitats, where lower harvesting pressure allows lizards to attain larger sizes (KHADIEJAH *et al.*, 2019). The consistency of SVL across habitats in this study suggests that habitat-related pressures do not limit overall growth potential, but instead influence how energy is allocated beyond structural size. These findings underscore the value of finer-resolution analyses of individual morphological components such as skull and limb dimensions, rather than relying solely on broad proxies like SVL or weight, which, although widely used to represent body size, may obscure ecologically meaningful variation in shape and function (SHINE *et al*., 1996; SHINE *et al*., 1998; KOCH *et al*., 2007; TWINING *et al*., 2017; KHADIEJAH *et al*., 2019; GUERRERO-SANCHEZ *et al*., 2021).

Body condition differed significantly, with individuals from urban and forest habitats exhibiting higher condition than those in agricultural areas. This outcome only partially supports our initial hypothesis, which predicted improved condition in both urban and agricultural lizards due to their proximity to anthropogenic food resources. While urban lizards may indeed benefit from high-calorie, spatially clustered food sources such as waste and pests as prey (SHOCHAT *et al*., 2006; PUAN *et al*., 2011; ORO *et al*., 2013; KULABTONG & MAHAPROM, 2014), the poorer condition observed in agricultural habitats suggests that food availability alone does not determine condition. Agricultural landscapes may present energetic trade-offs due to higher disturbance, or increased physiological stress (AZHAR *et al*., 2012; HOLZNER *et al*., 2021; GUERRERO-SANCHEZ *et al*., 2023). This is consistent with findings in other vertebrate taxa, where chronic environmental disturbance elevates stress responses and may reduce condition (MACDONALD *et al*., 2024).

This pattern contrasts with TWINING *et al*. (2017), who reported higher body condition in lizards from logged and plantation habitats but aligns more closely with GUERRERO-SANCHEZ *et al*., (2021, 2023), who found no significant differences in size or condition between forest and oil palm sites. It also broadly reflects the findings of KHADIEJAH *et al*. (2019), who found lower condition in plantation-dwelling individuals. However, it is important to note that none of these previous studies included urban habitats in their comparisons. The present findings therefore extend existing work by demonstrating that despite the anthropogenic pressures in urban environments, these habitats potentially offer sufficient resources, supporting lizards with comparable conditions to those in forest habitats and better condition than those in agricultural habitats. Notably, this study did not assess prey abundance, diet diversity, or levels of predation and human conflict, which may further explain differences in condition across habitats. The inclusion of such ecological data would improve the interpretation of morphological variation and should be a priority for future research.

Differences in both raw and relative thigh width exhibited strong signals of habitat linked morphological variation. Urban lizards consistently exhibited wider thighs than agricultural individuals, with forest lizards also exceeding agricultural sites in the size corrected analysis. For the size corrected thigh widths, urban and forest lizards exhibited similar thigh widths. This pattern goes against our hypotheses that both anthropogenic habitats would have smaller thigh widths compared to the forest habitat. Despite that, the pattern could still be attributed to habitat driven trade-offs in locomotive demands. Forest habitats and potentially urban habitats possibly require greater limb robustness to support increased movement through structurally complex terrain and larger home ranges (Zemp *et al.*, 2019; Guerrero-Sanchez *et al.*, 2022).

In contrast, narrower thighs in agricultural habitats could reflect morphological adjustments under different selective pressures. One plausible explanation is predator avoidance. Feral dogs were frequently observed in the agricultural habitats sampled in this study and are reported in other agricultural habitats in Malaysia (Azhar *et al.*, 2012), although no direct predation events were recorded in this study. However, feral dogs have been documented preying on other varanid species, such as *V. bengalensis* (Bhatt & Mori, 2022), suggesting that they may pose a similar threat to *V. salvator*. Their presence could potentially influence lizard morphology through behavioural or performance-related selection pressures. Literature on lizard biomechanics indicates that smaller thigh muscles may permit faster limb cycling during escape responses, enhancing sprint speed (Marsh & Bennett, 1985; 1986; Higham *et al.*, 2011; Albuquerque *et al.*, 2023). While this study did not measure predator abundance or locomotor performance, the observed reduction in thigh width may be consistent with a strategy favouring rapid escape over muscular robustness. Further research quantifying predator presence, interaction, and locomotor performance is needed to determine whether predator-driven selection explains reduced limb robustness in agriculture-dwelling lizards.

Both raw and size-corrected skull length were significantly larger in urban lizards compared to those from agricultural and forest habitats. This pattern could reflect one of two possible mechanisms: (1) urban environments may favour individuals with larger skulls due to ecological or behavioural advantages, or (2) urban populations may be male-biased, resulting in a greater proportion of individuals with inherently larger skulls being sampled. Longer skulls may enhance prey handling, scavenging efficiency, dominance, or intraspecific competition under high-density conditions (Urošević *et al.*, 2014; French *et al.*, 2018) through increased bite force (Verwaijen *et al.*, 2002).

However, the observed variation in skull length is unlikely to reflect dietary specialization alone, given *V. salvator*'s generalist feeding habits (Kulabtong & Mahaprom, 2014; Guerrero-Sanchez *et al.*, 2023). One possible explanation for larger skulls in urban individuals is increased energy availability from anthropogenic food sources, potentially permitting greater investment in traits linked to foraging or competition. However, this interpretation remains tentative. Agricultural individuals did not exhibit longer skulls than those in forests, suggesting that increased food access or reduced movement in disturbed landscapes (Guerrero-Sanchez *et al.*, 2022, 2023) does not consistently translate to cranial development. Similar spatial constraints are common in urban environments and have been associated with reduced home range sizes in reptiles and other terrestrial vertebrates (Šálek *et al.*, 2015; O'Donnell & delBarco-Trillo, 2020), but whether such constraints drive morphological change remains uncertain.

Furthermore, the reduced thigh width observed in agriculture habitat lizards may indicate competing energetic demands or performance trade-offs that complicate any simple energy allocation model. Since this study did not directly examine diet composition, energy budgets, or behaviour, further research is needed to clarify the ecological mechanisms underlying skull variation.

A different plausible explanation for the observed differences might be sexual dimorphism. Skull size is known to be sexually dimorphic in *V. salvator*, with males typically possessing larger skulls (KOCH *et al*., 2007; SMITH *et al*., 2007). Although sexing was attempted, reliable field identification was not feasible (see Methods), and no validated non-invasive or morphometric methods currently exist for this species. As such, variation in sex ratios across habitats represents a key variable that may influence skull length (KOCH *et al*., 2007; SMITH *et al*., 2007). Future studies incorporating accurate sex identification will be essential to disentangle sex-based from ecological drivers of skull variation and to fully evaluate the adaptive significance of this trait. It is also notable that the importance of raw and corrected skull traits is further underscored by the PCA, where skull length and relative skull length together formed an independent component (PC3), suggesting that skull morphology is not merely a reflection of overall size or shape, but a distinct axis of morphological variation in *V. salvator*. Together, these results suggest that *V. salvator* maintains a consistent growth trajectory across habitats, while allocating energy differently depending on local conditions. Urban habitats appear to support greater investment in structural and condition-related traits, whereas agricultural environments may impose constraints or shift priorities toward performance-based traits such as limb morphology.

CONCLUSION

This study shows that *V. salvator* maintains consistent body size across urban, agricultural, and forest habitats, while diverging in condition, and thigh width. These findings suggest that habitat type influences how energy is allocated to functional traits rather than limiting growth. The decoupling of size and shape highlights the species' morphological plasticity and emphasizes the value of trait-specific, size-corrected analyses. Urban lizards may benefit from resource abundance, whereas agricultural individuals appear to face trade-offs linked to disturbance or predator pressure. Future research incorporating sex identification, dietary data, and potential predator interactions will be critical to better understand the ecological drivers of these patterns and how large generalist reptiles adapt to human-modified environments.

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