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Phenotypic Diversity of Tree Shrews (*Tupaia belangeri*) with Implications for Biomedical Animal Research

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ABSTRACT

Background: *Tupaia belangeri* is increasingly recognized as an essential animal model in neuroscience, metabolic disorders and emerging infectious diseases due to its close phylogenetic relationship to primates and its small body size. Phenotypic traits are crucial for studying biological systems. Tree shrews are widely used in environmental adaptation research due to their genetic diversity and phenotypic polymorphism. The measurement of its physical indicators and skull provides a new perspective for exploring the adaptive characteristics of different tree shrew populations. Establishing population-specific morphometric reference values is therefore essential for standardizing veterinary dosing and ensuring translational reliability when tree shrews are used as models for metabolic, neurodegenerative, or emerging infectious diseases.

Methods: To elucidate the phenotypic diversity of the Tree shrew (*Tupaia belangeri*) and its relationship with environmental factors, the present study measured the body shape and skull indicators of 134 individuals across 12 regions.

Result: The results showed that there had significant phenotypic differences between different geographic populations, with inter population variation significantly greater than intra population variation, indicating that differentiation mainly occurs between populations. Especially Daxin population (*T. b. tonquinia*) and the Hainan population (*T. b. modesta*) had larger body mass and length, whereas the Kunming population (*T. b. chinensis*) was relatively smaller. Environmental factor analysis revealed significant correlations between latitude, altitude, annual average temperature, atmospheric pressure and precipitation with the morphological traits of tree shrews, with altitude had the most significant impact on phenotypic differences. The clustering and principal component analysis results also confirmed the geographical differentiation of the tree shrew in morphological studies. The research findings emphasized the role of environmental factors in shaping the phenotypic diversity of the tree shrew and provide important insights into the evolution and ecological adaptation of this species, which was of great significance for biodiversity conservation and ecosystem management.

Key words: Biodiversity conservation, Environmental factors, Geographical differentiation, Morphology, Phenotypic diversity, *Tupaia belangeri*.

INTRODUCTION

Tupaia belangeri is rapidly gaining prominence as an alternative non-rodent model in biomedical research. Compared to traditional rodents, tree shrews have a closer evolutionary relationship with primates, exhibit highly similar brain cytoarchitecture and display metabolic responses that closely mimic human pathologies. Consequently, they have been successfully employed in models of depression, myopia, hepatitis B virus infection and type 2 diabetes. Phenotypic traits are essential for studying the phylogeny and taxonomy of organisms (Cardini, 2016), influenced by both genetics and environment (Kawecka and West-Evans, 2019). Animals may differentiate in phenotypic traits to adapt to various environment. Physical indicators and skull morphology are key features of mammals (Larson, 2018). Traditional methods of mammalian taxonomy also use physical indicators and skull morphological characteristics as important basis. The distribution and morphological characteristics of *Tupaia belangeri* divide it into six subspecies: *T. b. chinese*, *T. b. modesta*, *T. b. yunali*, *T. b. gaoligongensis*, *T. b. tonia* and *T. b. yaoshanensis* (Wang 1987; Ren *et al*., 2020a, 2020b). Environmental factors, especially precipitation, significantly influence phenotypic

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variation in animals, promoting adaptive differentiation in mammalian body traits, particularly in tropical and subtropical species (Kang *et al*., 2024; Maestri *et al*., 2016).

The competition between species may also be a selection pressure that leads to variations in physical traits (Calcagno *et al*., 2017). A study of *Apodemus speciosus* and *Eothenomys smithii* skulls found that the interorbital skull's narrowest width and upper dentition length in *E. smithii* increased with lower environmental temperatures (Salewski *et al*., 2010). Research on *Tamiasciurus hudsonic* skulls showed a strong link between morphological differences and environmental factors (Larson, 2018; Ren *et al*., 2020a, 2020b; Wang *et al*., 2024).

Tupaia belangeri is widely distributed in Southeast Asia and north of the Karate Isthmus, including southern China. The Yunnan Guizhou Plateau is the northern boundary of its distribution and it is the only species of Scandenia in China (Gao *et al*., 2016; Ren *et al*., 2020a, 2020b). The diverse natural environment provides an ecological niche that promotes population differentiation and diffusion. Its high genetic diversity and phenotypic polymorphism make it significant for studying adaptation to different environments (Zhu *et al*., 2014; Wang *et al*., 2015). Moreover, morphological features such as skull, nasal bone and teeth also undergo differentiation (Yang *et al*., 2024). Our previous research found significant differences in skull characteristics among tree shrews in different regions, reflecting the adaptive variation of tree shrews to different ecological environments (Gao *et al*., 2017).

Research on ecological differentiation has shown that the genetic level of tree shrew populations in different regions has differentiated, but environmental differences plays a major driving role in phenotypic differentiation (Pal *et al*., 2021; Ren *et al*., 2023). This study investigates the relationship between phenotypic diversity and environmental factors in the *T. belangeri* population from Belangor by measuring body and cranial characteristics. The aimed is to elucidate the correlation between adaptive differentiation and environmental factors and to verify whether phenotypic differentiation occurs to adapt to environmental changes and ensure survival. Beyond its ecological implications, the pronounced phenotypic differentiation we document here has direct biomedical and veterinary relevance. Body mass and cranial dimensions are key covariates in dosing calculations and surgical planning for tree-shrew models of Alzheimer's disease, depression and metabolic syndrome. Regional differences in molar length and zygomatic breadth correlate with dietary specialization and gut microbiome composition-factors known to influence susceptibility to diet-induced obesity and Type 2 diabetes in this species. Establishing population-specific reference intervals for these morphometric traits will therefore improve veterinary diagnostics, refine humane endpoints and enhance translational fidelity across laboratories endpoints and enhance translational fidelity across laboratories, ultimately providing basic data for the animal models process of *T. belangeri*.

MATERIALS AND METHODS

Sampling of experimental animals

This study collected a total of 134 healthy, non-breeding adult tree shrews from 12 regions, considering the impact of seasonal changes on animal body size, sampling was conducted in the same season. However, due to the varying capture rates of animals in different locations, the sample size was not consistent across regions. According to Wang's study (1987), these populations represent the following subspecies: *T. b. chinensis*, including Yunnan: Kunming (KM, *n*=16); Luqun (LQ, *n*=10); Mengla (ML, *n*=8); Dali (DL, *n*=12); Xichang (XC, *n*=11), *T. b. modersta*: Hainan (HN, *n*=7), *T. b. yunalis*: Xingyi (XY, *n*=11); Hekou (HK, *n*=13), *T. b. gaoligongensis*: Pianma (PM, *n*=13); Tengchong (TC, *n*=12), *T. b. tonia*: Daxin (DX, *n*=7), *T. b. yaoshanensis*: Leye (LY, *n*=14). Data collection occurred from September 2018 to May 2019, with sampling details, including longitude, latitude and altitude, in Table 1. The geographical distance between sampling points was measured using a topographic map. Environmental data from the China Meteorological Administration, including atmospheric pressure, temperature and precipitation, were utilized in this study. These data can be accessed through the National Meteorological Information Center-China Meteorological Data Network (http://data.cma.cn/).

Morphological measurement and skull preparation method

The body mass (BM) of the tree shrew was measured using an electronic balance (0.01 g, SB10001) and its body indicators were measured using the method proposed by Gao *et al.* (2017). Measure the body length (BL), tail length (TL), ratio of tail length/body length (T/B), forelimb length (FLL) and hindlimb length (HLL) in their natural state and record them to the nearest 0.01 cm. The measurement of skull indicators in the tree shrew follows the methods of Yang *et al.* (2005) and Xia *et al.* (2007), including cranial length (CL), cranial basal length (CBL), cranial height (CH), zygomatic breadth (ZB), upper tooth row length (UTRL) and lower tooth row length (LTRL) and other indicators are recorded (0.01 cm). Moreover, preparation of skull based on the methods of Jia *et al*. (2009) and Wang *et al*. (2022).

Data analysis

We analyzed phenotypic diversity in 12 traits of the tree shrew using SPSS 26.0, applying one-way ANOVA, principal component analysis and cluster analysis. The phenotypic differentiation coefficient (VST) reflects the differentiation status between populations (Meng *et al*., 2013; Ren *et al*., 2020a), corresponding to the gene differentiation coefficient. The VST formula is:

$$VST = \frac{(\delta^2 t/s)}{(\delta^2 t/s + \delta^2 t)}$$

The coefficient of variation (CV) for phenotypic traits, calculated as

$$CV = \frac{S}{X}$$

Where
S = Standard deviation.
X = Mean.

Reflects dispersion (Ren *et al*., 2020a). Pearson correlation analysis was used to examine the relationships between environmental factors and phenotypic traits, while General Linear Models (GLM) assessed the impact of these factors on morphological indicators (Ren *et al*., 2020b). Canonical correlation analysis evaluated the contributions of environmental factors to phenotypic shape. Results are presented as means±SE, with $P<0.05$ deemed statistically significant.

RESULTS AND DISCUSSION

Phenotypic traits

It showed that there were significant differences in BM ($F_{11,122}=91.42$; $P<0.01$), BL ($F_{11,122}=74.02$; $P<0.01$), TL ($F_{11,122}=82.91$; $P<0.01$), T/B ($F_{11,122}=108.00$; $P<0.01$), FLL ($F_{11,122}=16.14$; $P<0.01$) and HLL ($F_{11,122}=31.46$; $P<0.01$) among different populations of the tree shrew (Fig 1). The DX population had the largest BM and BL, a smaller T/B and greater FLL and HLL. The HN population also had larger BM and BL, smaller TL and T/B and longer HLL. The KM population had the smallest BM and BL, but larger TL and T/B. The LY and KM populations showed similar trends. The populations with T/B greater than 1 include KM population, XC population, XY population, PM population, TC population and Leye population, where the TL is greater than the BL, while BL of other populations were smaller than TL. There were significant differences in skull indicators, including CL ($F_{11,122}=38.77$; $P<0.01$), CBL ($F_{11,122}=80.74$; $P<0.01$), CH ($F_{11,122}=86.68$; $P<0.01$), ZB ($F_{11,122}=169.10$; $P<0.01$), UTRL ($F_{11,122}=62.98$; $P<0.01$) and LTRL ($F_{11,122}=36.89$; $P<0.01$). Among them, the CBL, ZB, especially the length of UTRL and LTRL, DX and HN populations were significantly longer than those of other populations. The KM population had a smaller CL, CBL and CH (Fig 2).

Analysis of phenotypic trait variations

There was no effect on physical traits within the population ($P>0.05$), but inter-population grouping significantly impacted them ($P<0.05$), with no interaction between the two. When inter-subspecies grouping is random and intra-subspecies grouping is fixed, both significantly affect phenotypic traits ($P<0.05$), indicating phenotypic differentiation among populations of the same subspecies. The variance components of phenotypic traits within and between populations (Table 2) showed that the average variance percentage for the 12 traits was 8.43% within

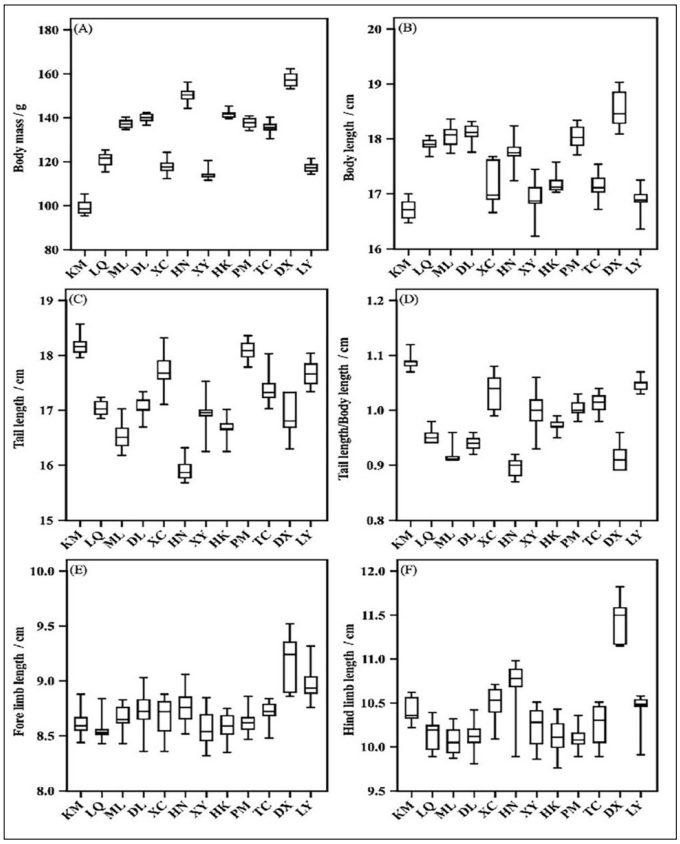


Fig 1: Box diagram of body indicators of different populations of *T. belangeri.*

populations, 72.11% between populations and 17.46% due to random error, indicating greater variation between populations. The VST between populations was 91.19%, with 81.27% from between populations and 9.24% from within populations, making inter-population variation the main source of phenotypic variation. The average coefficient of variation for the 12 traits among individuals was 1.44%, ranging from 0.50% to 3.39% (Table 3). The coefficients for BM, T/B, FLL, HLL and CH exceeded the average, while skull traits were more stable than physical indicators.

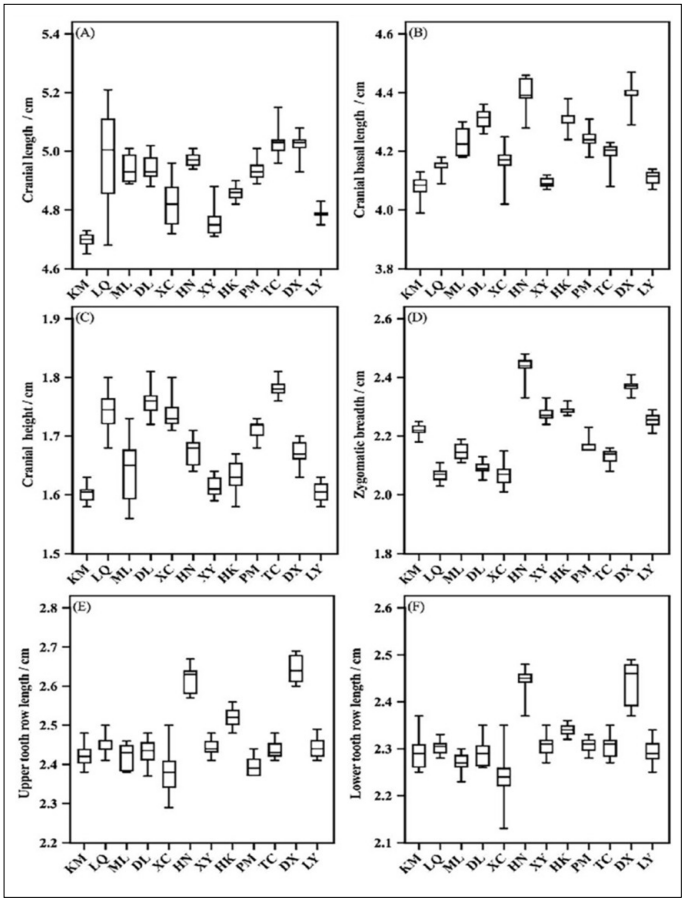


Fig 2: Box diagram of skull indicators of different populations of *T. belanger.*

Table 1: The information of sample site.

Subspecies	Population	Longitude	Latitude	Altitude (m)	Annual precipitation (mm)	Average annual temperature (°C)	Atmospheric pressure	Sample size
T. b. chinensis	(KM)	24.23	102.10	2000	1600	16.00	802.02	16
	(LQ)	25.25	102.14	1675	968	15.10	811.46	10
	(ML)	21.09	101.05	899	1500	20.80	943.538	8
	(DL)	24.41	98.52	2100	1100	15.80	812.81	12
	(XC)	27.32	101.46	1700	1800	17.30	837.44	11
T. b. modesta	(HN)	18.23	109.21	120	2000	5.20	1009.73	7
T. b. yunali	(XY)	23.38	104.51	1125	1600	16.80	869.60	11
	(HK)	22.30	103.23	1400	1800	25.58	911.62	13
T. b. gaoligongensis	(PM)	25.33	98.34	2900	1400	20.20	843.54	13
	(TC)	24.38	98.05	2050	1700	15.08	833.90	12
T. b. tonquinia	(DX)	22.29	106.39	375	1500	21.75	987.80	7
T. b. yaoshanensis	(LY)	24.30	106.10	1200	1800	17.08	899.60	14

Principal component and cluster analysis of physical and skull traits

Based on morphological traits, a tree diagram was created with similar results (Fig 3). The clustering analysis results showed that the HN population (*T. b. modesta*) and DX population (*T. b. tonquinia*) were clustered together, while the other populations are clustered into one branch. The other branch is further divided into TC population, PM population branch (*T. b. gaoligongensis*), DL population, ML population and LQ population branch (*T. b. chinensis*). The second branch is the HK and XY populations (*T. b. yunalis*), KM populations (*T. b. chinensis*), XC populations (*T. b. chinensis*) and LY populations (*T. b. yaoshanensis*) (Fig 4). Principal component analysis (PCA) was conducted on the morphological traits of the tree shrew (Fig 5) and the results showed that PCA1 was 99.74%, PCA2 was 0.07% and PCA3 was 0.11%. DX and HN populations were separated from the other populations, while the KM population lived in the lower right corner and all other populations had a mixture.

Analysis of the correlation between morphological indicators and environmental factors

This study investigated the correlation between environmental factors and morphological traits, such as latitude, longitude, altitude, average annual temperature, atmospheric pressure and precipitation (Fig 6). The results showed that latitude was significantly correlated with all morphological traits (P<0.05), with a positive correlation with TL, T/B and CH, as well as a negative correlation with residual morphological indicators. Longitude is not correlated with BM, T/B and CBL, but has a significant correlation with other traits (P<0.05). Among them, it is positively correlated with FLL, HLL, ZB, UTRL and LTRL and negatively correlated with BL, TL, CL and CH. There had no correlation between altitude and BL and CL, but there is a significant correlation with other traits (P<0.05). Among them, there is a positive correlation with TL, T/B and CH and a negative correlation with BM, FLL, HLL, CBL, ZB, UTRL and LTRL. There was no correlation between precipitation and BM, TL and CBL, but there is a significant

Table 2: Variation components and phenotypic differentiation coefficients among *T. belangeri* population.

Triats	Variance components			Proportion of variance components/%			Phenotype
	Within population	Among population	Random error	Within population	Among population	Random error	differentiation coefficient/ %
BM	0.000	258.702	6.893	0.00	97.40	2.60	100.00
BL	0.000	0.340	0.054	0.00	86.29	13.71	100.00
TL	0.009	0.424	0.500	0.96	45.44	53.59	98.00
T/B	0.000	0.003	0.000	2.93	97.07	0.00	97.07
FLL	0.015	0.033	0.007	27.27	60.00	12.73	68.75
HLL	0.000	0.134	0.037	0.00	78.36	21.64	100.00
CL	0.000	0.011	0.040	0.00	21.57	78.43	100.00
CBL	0.012	0.020	0.000	37.44	62.40	0.15	63.00
CH	0.000	0.004	0.001	0.00	80.00	20.00	100.00
ZB	0.000	0.014	0.001	0.00	93.33	6.67	100.00
UTPL	0.001	0.007	0.000	12.50	87.50	0.01	87.50
LRTL	0.001	0.004	0.000	20.00	80.00	0.01	80.00
Mean				8.43	74.11	17.46	91.19

Table 3: Variation coefficients of phenotypic traits in *T. belangeri* populations.

Traits	KM	LQ	ML	DL	XC	HN	XY	HK	PM	TC	DX	LY	Mean
BM	3.20	2.63	1.47	1.34	2.82	2.45	2.18	1.18	1.80	2.03	2.09	2.04	2.10
BL	1.07	0.59	1.08	0.89	2.09	1.66	1.88	0.90	1.62	1.29	1.77	1.25	1.34
TL	0.91	0.82	1.58	1.09	1.84	1.31	1.86	1.12	1.19	1.54	2.29	1.24	1.40
T/B	1.22	1.31	1.91	1.20	2.84	1.90	3.45	1.04	1.39	1.97	2.74	1.25	1.85
FLL	1.26	1.27	1.42	1.96	1.98	1.99	1.89	1.33	1.22	1.14	2.68	1.63	1.65
HLL	1.32	1.59	1.53	1.66	1.91	3.39	2.13	1.96	1.62	2.05	2.10	1.81	1.92
CL	0.51	3.32	0.97	0.92	1.60	0.50	0.98	0.49	0.70	0.92	0.91	0.41	1.02
CBL	0.83	0.63	1.12	0.74	1.56	1.35	0.43	0.81	0.73	1.11	1.21	0.54	0.92
CH	0.91	1.93	3.33	1.36	1.48	1.42	0.96	1.58	1.25	0.77	1.36	0.91	1.44
ZB	0.99	1.09	1.31	1.10	2.07	1.98	1.10	0.59	1.21	1.28	1.02	1.07	1.23
UTPL	1.03	0.98	1.39	1.39	2.37	1.32	0.90	0.99	1.00	0.92	1.30	1.01	1.22
LRTL	1.47	0.68	0.94	1.39	2.28	1.43	0.94	0.52	0.66	1.01	1.85	1.08	1.19
Mean	1.23	1.40	1.50	1.25	2.07	1.72	1.56	1.04	1.20	1.34	1.78	1.19	1.44

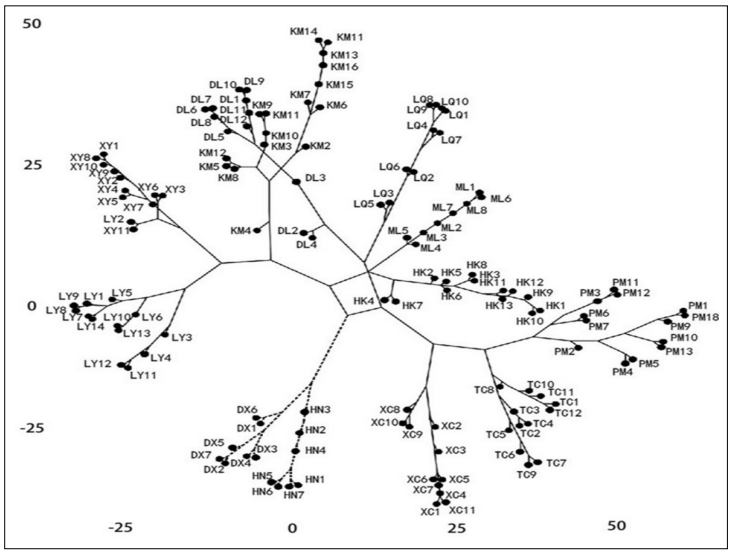


Fig 3: Tree plot of morphological traits of different populations of *T. belangeri.*

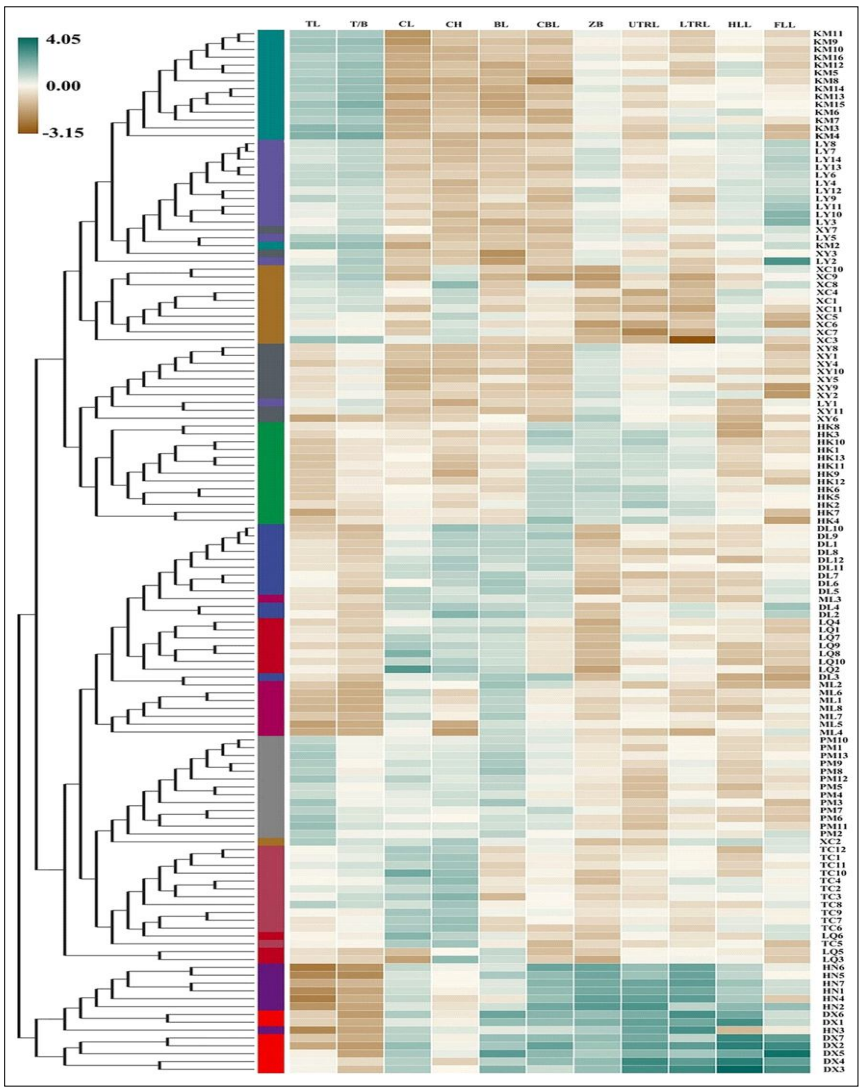


Fig 4: Cluster analysis heat map of body indicators.

correlation with other traits (P<0.05). Among them, there was a positive correlation with T/B, FLL, HLL, ZB, UTRL and LTRL and a negative correlation with BL, CL and CH. The annual average temperature is only positively correlated with BM and negatively correlated with CH (P<0.05). Atmospheric pressure was correlated with all traits (P<0.05), with a positive correlation with BM, BL, FLL, HLL, CL, CBL, ZB, UTRL and LTRL and a negative correlation with TL, T/B and CH.

Canonical correlation analysis between morphological indicators and environmental factors

The results revealed six highly significant canonical correlation relationships (P<0.01), with coefficients of 0.964, 0.958, 0.875, 0.690, 0.561 and 0.536. Longitude, latitude, atmospheric pressure and altitude significantly affect the morphological traits of the tree shrew, while precipitation has a lesser impact and annual average temperature has the smallest effect (Fig 7, 8).

Physical indicators and skull morphology are essential for studying interspecies and intraspecific relationships (Tai *et al*., 2001; Ren *et al*., 2020a, 2020b). Adaptations to altitude, vegetation, latitude and climate lead to variations in body and skull structures, which are linked to dietary habits, habitat and living conditions. The study found significant phenotypic differentiation in *T. belangeri* among populations, with greater variation between populations than within them. This indicates that phenotypic variation primarily distinguishes populations, while some variation also occurs within subspecies. The results of this study highlighted that the DX population has a larger BM and BL, a smaller TL and T/B and longer FLL and HLL, which may be related to its rocky habitat, but further research is needed to verify this. The clustering analysis results showed that the HN population (*T. b. modesta*) and the DX population (*T. b. tonquinia*) were clustered together, while the other populations were clustered into one branch and further divided into TC population and PM population (*T. b. gaoligongensis*),

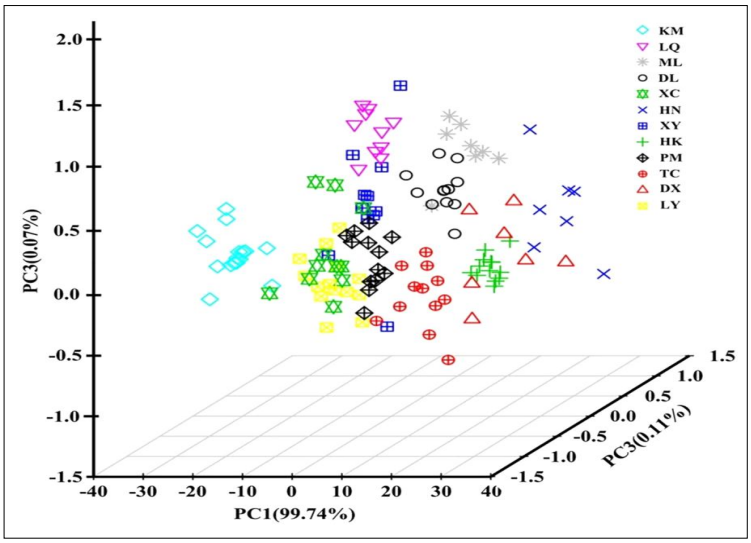


Fig 5: PCA 3D plot of body indicators of different populations of *T. belangeri.*

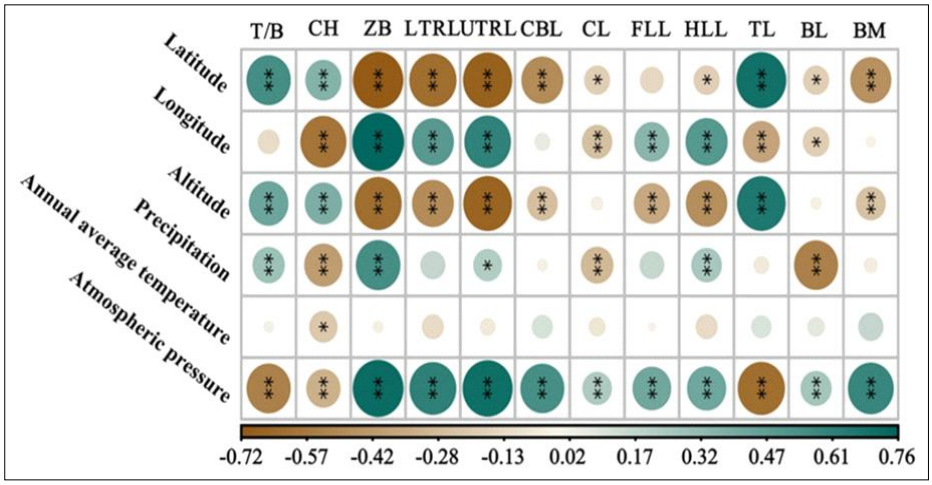


Fig 6: Correlation between environmental factors and morphological characters of *T. belangeri*, * as P<0.05 and ** as P<0.01.

DL population, ML population and LQ population (*T. b. chinensis*) branches; HK population, XY population (*T. b. chinensis*), KM population (*T.b.chinensis*), XC population (*T. b. chinensis*) and LY population (*T. b. yaoshanensis*) branches. Based on morphological data, *T. b. chenensis*, *T. b. yunalis* and *T. b. yaoshanensis* from KM and XC were clustered together, indicating that these three subspecies had similar phenotypes, which was consistent with the results of our research group on the genetic differentiation of tree shrews (Ren *et al*., 2023).

Changes in animal body size related to environmental factors like latitude, altitude and temperature can improve our understanding of their life histories (Lou *et al*., 2012). Two explanations address how temperature affects body size and skull morphology. Bergmann's law indicates that animals in warmer climates have smaller body sizes and larger surface areas for heat dissipation, while those in colder climates have larger body sizes and smaller surface areas for heat retention (Ren *et al*., 2020a, 2020b; He *et al*., 2023; Huang *et al*., 2012). Low and high-temperature treatments were applied to newborn piglets. Results showed that those raised in cold environments have a reduced surface area-to-body weight ratio, supporting Allen's rule, which states that limb length decreases in cold climates (Zhu *et al*., 2024). Most evidence for Bergmann's law comes from the New and Old Arctic regions, mainly in temperate climates, where heat conservation mechanisms are effective (He *et al*., 2023). However, tropical species do not often conform to Bergmann's law as temperate species do (Rodríguez *et al*., 2008). The results of this study indicated that most of the morphological traits of *T. belangeri* were significantly correlated with latitude, longitude, altitude and atmospheric pressure, while only CH was positively correlated with annual average temperature, which contradicts Bergmann's law. *T. belangeri* is a species that diffuses from the tropics and is mainly distributed in tropical

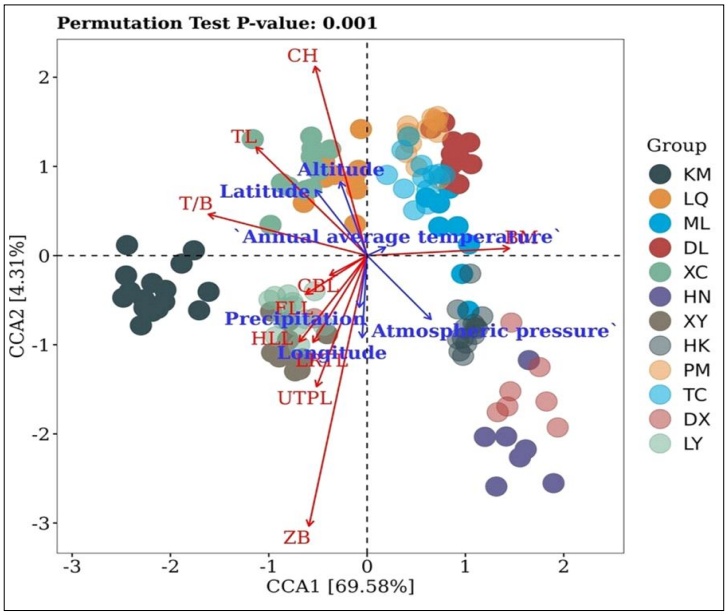


Fig 7: Canonical correlation analysis of *T. belangeri* morphological traits and environmental factors.

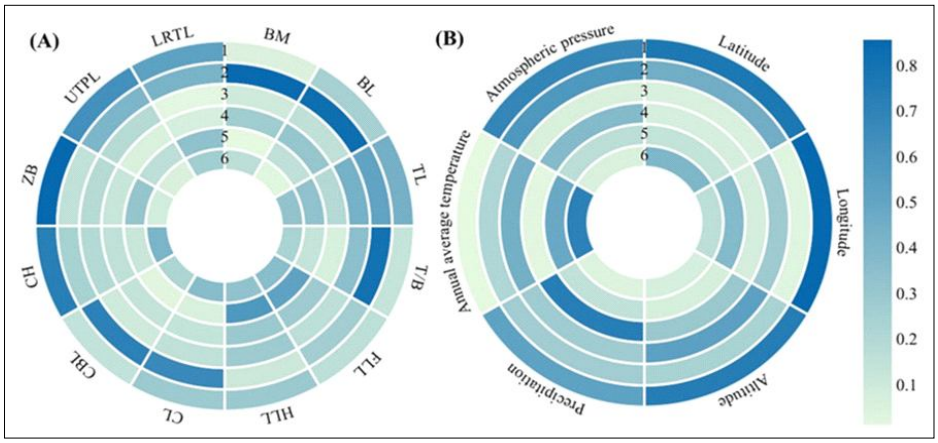


Fig 8: Canonical correlation analysis of the set of *T. belangeri* morphological traits and environmental factors.

and subtropical regions. Temperature cannot explain the phenotypic differentiation of *T. belangeri* (Correll *et al*., 2016; Hendges *et al*., 2020). Canonical correlation analysis also showed that the annual average temperature had the smallest contribution to the phenotypic variation of *T. belangeri*, supporting the previous result. Precipitation can affect the resources of habitats, which may affect body shape changes (Maestri *et al*., 2016; Hendges *et al*., 2020). Several omnivorous mammals (Yomtov and Geffen, 2006), including primate populations (Kang *et al*., 2024; Meloro *et al*., 2014), had shown a similar relationship between body size and precipitation. Most mammals feed on plants and the abundance and availability of these foods are directly related to precipitation in tropical forests (Meloro *et al*., 2014; Portillo-Quintero *et al*., 2015). In this study, some physical indicators of *T. belangeri* were significantly correlated with precipitation and the results of canonical correlation analysis showed that precipitation had a significant contribution to phenotypic traits, suggesting that precipitation may have affected the food resources of habitat environment in *T. belangeri* (Correll *et al*., 2016; Maestri *et al*., 2016), which further affects its body size. The study also highlights altitude as a key factor in the phenotypic variation of *T. belangeri*.

CONCLUSION

In conclusion, it had been conducted on the morphological and cranial traits of various subpopulations of *T. belangeri* and the results showed that the phenotype of *T. belangeri* had significant differentiation, with interspecific variation being greater than intraspecific variation and interspecific variation being the main factor in phenotype variation. Skull traits were more stable than physical traits. The clustering analysis results clustered the *T. b. modesta* and *T. b. tonia* together and the *T. b. chenensis*, *T. b. yunalis*, *T.b. aoshanensis* together, which was consistent with the genetic data results in the previous study. Altitude, longitude, latitude and atmospheric pressure may be environmental factors that affect *T. belangeri*. All of the above results indicated that it exhibited significant phenotypic differentiation when adapting to different environmental changes, suggesting that the morphological changes of *T. belangeri* can also serve as an important indicator for its animal modeling as a reference.

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Ethical approval

All animal procedures were within the rules of Animals Care and Use Committee of School of Life Sciences, Yunnan Normal University. This study was approved by the committee (13-0901-011).

Conflict of interest

All authors declare that they have no conflicts of interest.

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