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# Bergmann's Rule Examination based on the Morphology of the Long-tailed Dwarf Hamster (*Cricetulus longicaudatus*)

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## ABSTRACT

**Background:** To investigate whether the variation in phenotypic traits of the long-tailed dwarf hamster (*Cricetulus longicaudatus*) across different environments in Shanxi province conforms to Bergmann's rule. This study collected *C. longicaudatus* from 9 regions in Shanxi province, namely, Kelan county, Wutai county, Wuzhai county, Qin county, Shanyin county, Xi county, Lingchuan county, Loufan county and Zuoquan county.

**Methods:** We analyzed the differences in body and skull indicators of *C. longicaudatus* in different regions and combined environmental factors to explore whether these indicators conform to Bergmann's rule.

**Result:** Significant inter-population differences were found in multiple phenotypic traits. Hierarchical clustering divided the nine populations into two groups: Group I (Zuoquan, Qin, Wutai, Lingchuan, Shanyin) and Group II (Loufan, Kelan, Wuzhai, Xi). Correlation analysis with environmental factors confirmed that phenotypic variation conformed to Bergmann's rule, indicating geographic differentiation in *C. longicaudatus* across Shanxi.

**Key words:** Bergmann's rule, *Cricetulus longicaudatus*, Phenotypic variation.

## INTRODUCTION

Phenotypic differentiation is fundamental to speciation and adaptive evolution (West-Eberhard, 2003).In rodents, morphological variations reflect genetic and ecological adaptation (Pergams and Lawler, 2009; Jia *et al.*, 2024), with body and skull traits as key markers (Caumul *et al.*, 2005). Their correlation aids classification (Xiong and Zhang, 2007; Tai *et al.*, 2001; Ren *et al.*, 2023), as shown in *Eothenomys wardi* (Zeng *et al.*, 2013), penile morphology across eight species (Yang *et al.*, 1992) and *Apodemus sylvaticus* mandible and molar analyses (Renaud and Michaux, 2003), revealing species status, intergeneric and intrageneric differences and island-related patterns (Michaux *et al.*, 2007). Bergmann's rule (larger body size in cold) and Allen's rule (larger appendages in warm) (Bergmann, 1848; Allen, 1877) show variable conformity: Geomyidae follow Bergmann's (Ashton *et al.*, 2000), *E. miletus* only Allen's (Ren *et al.*, 2020) and some neither (Du *et al.*, 2017). Widespread *C. longicaudatus* (Cricetidae) was collected from nine Shanxi regions (Kelan, Wutai, Wuzhai, Qin, Shanyin, Xi, Lingchuan, Loufan, Zuoquan) based on evidence of prior divergence.

## MATERIALS AND METHODS

### Experimental animal processing

This study was conducted at the Agricultural and Pastoral Rodent Pest Laboratory, Plant Protection College, Shanxi Agricultural University, Shanxi, China. In 2025, 101 adult male *C. longicaudatus* were collected from nine Shanxi counties: Kelan (KL, 1939.1, 13), Wutai (WT, 1427, 15), Wuzhai (WZ, 1460, 20), Qin (QX, 986, 6), Shanyin (SY, 1163.3, 7), Xi (XX, 1222.5, 15), Lingchuan (LC, 1359.2, 10), Loufan (LF, 1301, 7), Zuoquan (ZQ, 1128, 8). Individuals were identified as adults by developmental traits and housed individually to minimize reproductive effects. Sampling locations are shown in Fig 1.

Environmental data (latitude, altitude, temperature) came from local sources and CMA (http://sx.cma.gov.cn/) based on 2025 records. All animal procedures complied with China's Ministry of Science and Technology regulations (Approval No. SXAU-EAW-2024M.JE.004022321).

### Morphological measurements

Captured samples were quarantined for flea control, weighed and transferred to the laboratory. After euthanasia, morphological indicators were measured immediately.

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Body weight was measured using an electronic balance (0.001 g precision). External traits (0.01 cm) included BL, TL, LFL/RFL, LHL/RHL, LEL/REL (Gao, 2017; Ren, 2022). Skull measurements included CL, CBL, PNL, ZW, LD, SKW, CH, EBL, UCL_L/LCL_L (Yang *et al.*, 2005; Xia *et al.*, 2006). All measurements were performed by a single experimenter. Traits were classified as body or cranial traits.

### Statistical methods

Data were analyzed using SPSS 27.0 and R 4.5.1. Normality tests confirmed all variables met normality assumptions. One-way ANOVA with Levene's test and Tukey's HSD compared phenotypic traits among populations. PCA and cluster analysis revealed differentiation patterns; morphological and geographical distance matrices were compared via Mantel test (Mantel, 1967; Legendre and Legendre, 2012). Phenotypic differentiation coefficient ($VST = \delta^2t/s / (\delta^2t/s + \delta^2t)$) was calculated, where $\delta^2t/s$ and $\delta^2t$ represent among- and within-population variance components (Pfrender and Lynch, 2000); this coefficient, analogous to genetic differentiation, is widely applied in population studies (Meng *et al.*, 2013; Ren *et al.*, 2025). Coefficient of variation (CV = S/X, S = standard deviation, X = trait mean) assessed trait dispersion. Spearman correlations examined trait–environment relationships (latitude, altitude, temperature) to test Bergmann's rule.

## RESULTS AND DISCUSSION

### Analysis of the differences in body and skull indices among populations

ANOVA revealed significant inter-population differences in multiple phenotypic traits (Table 1). Body weight showed no significant difference among regions ($P>0.05$). Body length varied significantly ($P<0.01$), with XX population the largest (significantly greater than WZ, LC, LF and ZQ) and ZQ/WZ the smallest. Tail length was greatest in QX and smallest in WT. Tail-to-body ratio differed highly significantly ($P<0.01$), with LF, QX and ZQ significantly higher than WT, which was the lowest. Forelimb lengths differed significantly ($P<0.01$), with WZ and KL significantly longer than SY and WT; hindlimb lengths also differed significantly ($P<0.01$), with QX and WZ significantly longer than WT. Ear length differed significantly ($P<0.01$), with KL and XX significantly longer than LC, WZ and ZQ (LC shortest). Ear width differed significantly ($P<0.01$), with LF (left) and QX (right) largest and WT smallest.

Most cranial traits showed no significant regional differences ($P>0.05$), except cranial height ($P<0.01$), which was highest in XX and significantly higher than in LC, QX and WT. Other traits (cranial length, condylobasal length, occipitonasal length, zygomatic width, interorbital width, skull width, ear bulla length and upper/lower tooth row length) showed no significant differences ($P>0.05$).

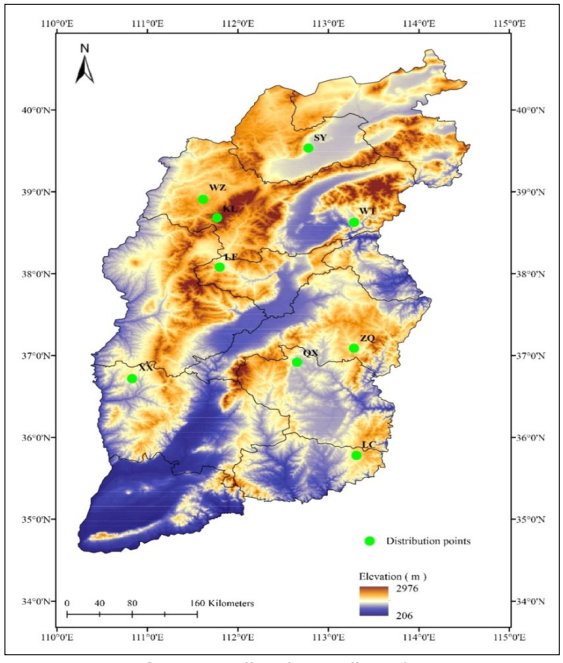



**Fig 1:** Details of sampling sites.

### Analysis of phenotypic trait variation within and between populations

Variance component analysis for 22 traits (Table 2) revealed significant variance distribution differences among populations. Random error: 46.64%-91.01% (mean 69.91%); within-population: 4.71%-9.12% (mean 6.92%); among-population: 0-48.75% (mean 23.17%). Among-population variance generally exceeded within-population variance for most traits.

Body weight showed the lowest VST (6.96%), with random error variance at 90.39%. Body surface traits showed high differentiation: VST values for body length, tail length and tail-to-body ratio were 75.64%, 88.68% and 91.11%, respectively. Limb length VST ranged from 86.78% (left forelimb) to 91.37% (right hindlimb); ear-related traits all exceeded 86% (right ear width at 88.73%). For skull traits, skull width (SKW) and cranial height (CH) showed moderately high VST (77.90% and 79.01%), indicating stable inter-population differentiation. However, cranial length (33.02%), condylobasal length (18.50%) and occipitonasal length (30.56%) showed lower VST. Zygomatic width, interorbital width and upper/lower tooth row length had zero among-population variance and VST = 0, indicating no detectable inter-population differentiation.

CV for each trait varied significantly among populations (Table 3), with mean CV ranging from 2.17% to 19.08%. Body weight was highest (19.08%), followed by tail length (13.90%), tail-to-body ratio (13.77%) and body length (8.82%). Limb length mean CV: 8.14%-9.88%. Ear length: 10.56% (left) and 10.35% (right); ear width: 8.93% (left) and 9.31% (right). Skull traits showed low variation: cranial length (4.17%), condylobasal length (4.19%), occipitonasal length (3.84%), skull width (2.17%), cranial height (3.06%). Ear bulla length (6.54%) was relatively high among skull

**Table 1:** Analysis of variation in body metrics and skull metrics of long-tailed dwarf hamsters (*Cricetulus longicaudatus*) from different regions.

| Traits | KL | LC | LF | QX | SY | WT | WZ | XX | ZQ | *F*_value | *P*_value |
|---|---|---|---|---|---|---|---|---|---|---|---|
| BW | 23.14±1.46 | 21.19±1.37 | 23.48±1.62 | 20.91±1.00 | 23.05±2.36 | 25.44±1.75 | 22.05±1.07 | 25.14±1.18 | 21.50±1.35 | 1.06 | >0.05 |
| BL | 9.18±0.29bc | 9.09±0.21bc | 9.12±0.27bc | 9.26±0.25bc | 9.34±0.45bc | 9.94±0.22bc | 8.91±0.20c | 10.27±0.22a | 8.96±0.21c | 4.07 | <0.01 |
| TL | 3.67±0.19c | 3.88±0.17bc | 4.47±0.13ab | 4.55±0.23a | 3.96±0.30abc | 2.84±0.10d | 4.01±0.15abc | 4.02±0.17abc | 4.40±0.13ab | 8.57 | <0.01 |
| TL/BL | 0.40±0.02b | 0.43±0.02ab | 0.49±0.01a | 0.48±0.02a | 0.42±0.03ab | 0.29±0.01c | 0.46±0.02ab | 0.40±0.02b | 0.49±0.01a | 10.98 | <0.01 |
| LFL | 3.31±0.14a | 2.95±0.08bc | 3.23±0.09ab | 3.24±0.14ab | 2.65±0.12c | 2.69±0.08c | 3.33±0.07a | 3.03±0.11ab | 3.20±0.07ab | 6.75 | <0.01 |
| RFL | 3.32±0.13a | 2.96±0.08bc | 3.22±0.09ab | 3.23±0.13ab | 2.66±0.12d | 2.69±0.08cd | 3.34±0.06a | 3.04±0.11ab | 3.20±0.07ab | 7.26 | <0.01 |
| LHL | 4.62±0.11ab | 4.56±0.09ab | 4.43±0.15ab | 4.78±0.08a | 4.27±0.13b | 3.79±0.09c | 4.72±0.09a | 4.20±0.17b | 4.46±0.07ab | 7.43 | <0.01 |
| RHL | 4.62±0.10ab | 4.55±0.09ab | 4.42±0.15ab | 4.79±0.08a | 4.26±0.14b | 3.79±0.09c | 4.79±0.07a | 4.31±0.13b | 4.53±0.06ab | 10.15 | <0.01 |
| LEL | 1.68±0.08a | 1.31±0.03b | 1.44±0.08ab | 1.49±0.04ab | 1.51±0.05ab | 1.66±0.03a | 1.41±0.05b | 1.67±0.05a | 1.36±0.06b | 8.18 | <0.01 |
| REL | 1.69±0.08a | 1.33±0.03d | 1.45±0.07cd | 1.50±0.04bcd | 1.54±0.06abc | 1.65±0.03ab | 1.42±0.05cd | 1.69±0.05a | 1.37±0.06cd | 7.40 | <0.01 |
| LEW | 1.26±0.01a | 1.24±0.01a | 1.34±0.06a | 1.34±0.07a | 1.26±0.03a | 1.11±0.02b | 1.33±0.03a | 1.30±0.03a | 1.24±0.02a | 6.87 | <0.01 |
| REW | 1.26±0.01b | 1.25±0.02b | 1.34±0.06ab | 1.40±0.07a | 1.29±0.03b | 1.11±0.02c | 1.33±0.03ab | 1.30±0.03ab | 1.26±0.02b | 7.57 | <0.01 |
| CRL | 25.76±0.41 | 24.86±0.46 | 25.87±0.32 | 25.02±0.53 | 24.81±0.50 | 25.38±0.25 | 24.65±0.50 | 26.08±0.19 | 25.37±0.63 | 1.28 | >0.05 |
| CBL | 22.90±0.39 | 21.91±0.43 | 23.00±0.12 | 22.59±0.45 | 22.51±0.34 | 22.88±0.21 | 21.87±0.52 | 23.00±0.24 | 22.57±0.64 | 1.13 | >0.05 |
| PNL | 19.17±0.22 | 18.49±0.23 | 19.02±0.25 | 18.69±0.44 | 18.49±0.24 | 18.77±0.19 | 18.18±0.42 | 19.23±0.15 | 18.88±0.44 | 1.25 | >0.05 |
| ZW | 13.30±0.26 | 12.98±0.19 | 12.93±0.20 | 13.45±0.11 | 13.17±0.22 | 12.99±0.15 | 12.98±0.29 | 13.19±0.13 | 13.24±0.20 | 0.66 | >0.05 |
| LD | 4.32±0.06 | 4.31±0.04 | 4.23±0.02 | 4.06±0.08a | 4.17±0.07 | 4.20±0.05 | 4.17±0.09 | 4.18±0.07 | 4.22±0.12 | 0.96 | >0.05 |
| SKW | 11.71±0.13a | 11.22±0.16b | 11.51±0.11ab | 11.49±0.07ab | 11.34±0.07b | 11.18±0.10b | 11.23±0.08b | 11.50±0.08ab | 11.21±0.09b | 3.04 | <0.01 |
| CH | 8.95±0.11bc | 8.74±0.13c | 9.23±0.09ab | 8.81±0.11c | 8.99±0.07abc | 8.78±0.07c | 9.09±0.12abc | 9.35±0.10a | 8.97±0.19abc | 3.15 | <0.01 |
| EBL | 2.93±0.05abc | 2.94±0.08abc | 2.71±0.07c | 2.98±0.08ab | 2.82±0.04abc | 2.89±0.06abc | 2.77±0.05bc | 3.02±0.10a | 2.92±0.09abc | 1.71 | >0.05 |
| UCL_L | 10.70±0.17 | 10.84±0.16 | 10.75±0.14 | 10.75±0.16 | 10.84±0.22 | 10.52±0.11 | 10.37±0.27 | 10.72±0.13 | 10.64±0.21 | 0.73 | >0.05 |
| LCL_L | 10.49±0.10 | 10.20±0.09 | 10.37±0.16 | 10.32±0.13 | 10.47±0.22 | 9.96±0.42 | 10.04±0.25 | 10.44±0.09 | 10.28±0.18 | 0.57 | >0.05 |

Note: BW: Body weight; BL: Body length; TL: Tail length; TL/BL: Tail-to-Body Ratio; LFL: Length of left forelimb; RFL: Length of right forelimb; LHL: Length of left hindlimb; RHL: Length of right hindlimb; LEL: Length of left ear; REL: Length of right ear; LEW: Width of left ear; REW: Width of right ear; CRL: Cranial length; CBL: Cranial base length; PNL: Occipitonasal length; ZW: Zygomatic width; LD: Interorbital width; SKW: Cranial width; CH: Cranial height; EBL: Ear bulla length; UCL_L: Upper tooth row length (Left); LCL_L: Lower tooth row length (left).

The measurement data of each trait are presented as mean ± standard error (mean ± SE) and different lowercase letters indicate that the difference of the same trait among different geographical populations reaches a statistically significant level (P<0.05).

**Table 2:** Variance components and inter-population phenotypic differentiation coefficients VST of phenotypic traits.

| Traits | Variance components | | | Proportion of variance components% | | | Phenotype differentiation coefficient% |
|---|---|---|---|---|---|---|---|
| | Within population | Among population | Random error | Within population | Among population | Random error | |
| BL | 0.0667 | 0.2071 | 0.6744 | 7.03 | 21.84 | 71.12 | 75.64% |
| TL | 0.0313 | 0.2452 | 0.3165 | 5.28 | 41.35 | 53.37 | 88.68% |
| TL/BL | 0.0004 | 0.0041 | 0.004 | 4.71 | 48.24 | 47.06 | 91.11% |
| LFL | 0.0089 | 0.0584 | 0.09 | 5.66 | 37.13 | 57.22 | 86.78% |
| RFL | 0.0084 | 0.0599 | 0.0846 | 5.49 | 39.18 | 55.33 | 87.70% |
| LHL | 0.0138 | 0.1027 | 0.1399 | 5.38 | 40.05 | 54.56 | 88.15% |
| RHL | 0.0105 | 0.1111 | 0.1063 | 4.61 | 48.75 | 46.64 | 91.37% |
| LEL | 0.0024 | 0.0198 | 0.0238 | 5.22 | 43.04 | 51.74 | 89.19% |
| REL | 0.0024 | 0.0185 | 0.0246 | 5.27 | 40.66 | 54.07 | 88.52% |
| LEW | 0.0009 | 0.006 | 0.0088 | 5.73 | 38.22 | 56.05 | 86.96% |
| REW | 0.0008 | 0.0063 | 0.0082 | 5.23 | 41.18 | 53.59 | 88.73% |
| BW | 1.8954 | 0.1418 | 19.1651 | 8.94 | 0.67 | 90.39 | 6.96% |
| CRL | 0.1136 | 0.056 | 1.1489 | 8.62 | 4.25 | 87.14 | 33.02% |
| CBL | 0.0978 | 0.0222 | 0.9892 | 8.82 | 2 | 89.18 | 18.50% |
| PNL | 0.0568 | 0.025 | 0.5742 | 8.66 | 3.81 | 87.53 | 30.56% |
| ZW | 0.0252 | 0 | 0.2551 | 8.99 | 0 | 91.01 | 0.00% |
| LD | 0.0033 | 0 | 0.0329 | 9.12 | 0 | 90.88 | 0.00% |
| SKW | 0.0061 | 0.0215 | 0.0614 | 6.85 | 24.16 | 68.99 | 77.90% |
| CH | 0.0076 | 0.0286 | 0.0772 | 6.7 | 25.22 | 68.08 | 79.01% |
| EBL | 0.0029 | 0.0036 | 0.0298 | 7.99 | 9.92 | 82.09 | 55.38% |
| UCL_L | 0.0214 | 0 | 0.2162 | 9.01 | 0 | 90.99 | 0.00% |
| LCL_L | 0.0435 | 0 | 0.4401 | 9 | 0 | 91 | 0.00% |
| Mean | | | | 6.92318182 | 23.1668182 | 69.9104545 | 57.46% |

Note: BW: Body weight; BL: Body length; TL: Tail length; TL/BL: Tail-to-Body ratio; LFL: Length of left forelimb; RFL: Length of right forelimb; LHL: Length of left hindlimb; RHL: Length of right hindlimb; LEL: Length of left ear; REL: Length of right ear; LEW: Width of left ear; REW: Width of right ear; CRL: Cranial length; CBL: Cranial base length; PNL: Occipitonasal length; ZW: Zygomatic width; LD: Interorbital width; SKW: Cranial width; CH: Cranial height; EBL: Ear bulla length; UCL_L: Upper tooth row length (Left); LCL_L: Lower tooth row length (Left).

**Table 3:** Coefficients of variation (CV) of phenotypic traits in long-tailed dwarf hamster (*Cricetulus longicaudatus*) populations.

| Trait | KL | LC | LF | QX | SY | WT | WZ | XX | ZQ | Mean |
|---|---|---|---|---|---|---|---|---|---|---|
| BL | 11.33 | 7.20 | 7.74 | 6.66 | 12.84 | 8.63 | 9.81 | 8.43 | 6.69 | 8.82 |
| TL | 18.58 | 13.56 | 7.76 | 9.91 | 19.96 | 13.39 | 16.98 | 16.81 | 8.17 | 13.90 |
| TL/BL | 15.16 | 12.50 | 4.63 | 9.19 | 16.57 | 16.90 | 18.48 | 22.15 | 8.37 | 13.77 |
| LFL | 10.78 | 8.55 | 7.06 | 10.67 | 12.45 | 11.36 | 7.52 | 14.22 | 6.31 | 9.88 |
| RFL | 10.52 | 8.47 | 7.15 | 9.90 | 12.18 | 11.05 | 7.21 | 13.57 | 6.49 | 9.62 |
| LHL | 6.10 | 6.26 | 9.17 | 3.86 | 8.32 | 9.24 | 6.89 | 15.25 | 4.32 | 7.71 |
| RHL | 5.66 | 5.72 | 9.08 | 4.13 | 8.48 | 9.00 | 5.82 | 11.59 | 3.63 | 7.01 |
| LEL | 12.64 | 7.88 | 14.07 | 5.51 | 9.62 | 5.98 | 13.91 | 10.68 | 12.35 | 10.29 |
| REL | 11.99 | 7.57 | 13.68 | 5.84 | 9.86 | 6.33 | 13.83 | 11.02 | 13.07 | 10.35 |
| LEW | 2.99 | 3.61 | 11.44 | 10.02 | 6.37 | 7.23 | 9.16 | 8.42 | 5.49 | 7.19 |
| REW | 2.13 | 3.69 | 11.23 | 9.84 | 5.87 | 7.14 | 8.49 | 8.38 | 4.62 | 6.82 |
| BW | 22.76 | 20.48 | 18.24 | 11.75 | 27.03 | 18.23 | 21.75 | 14.80 | 16.64 | 19.08 |
| CRL | 3.53 | 4.50 | 2.14 | 5.16 | 5.32 | 3.08 | 5.72 | 1.95 | 6.08 | 4.17 |
| CBL | 3.79 | 4.81 | 0.93 | 4.90 | 4.05 | 2.89 | 6.71 | 2.73 | 6.90 | 4.19 |
| PNL | 2.62 | 3.02 | 2.24 | 5.78 | 3.40 | 3.28 | 6.47 | 2.09 | 5.67 | 3.84 |
| ZW | 4.41 | 3.61 | 2.65 | 2.08 | 4.41 | 3.76 | 6.23 | 2.67 | 3.63 | 3.72 |
| LD | 3.29 | 2.50 | 0.76 | 4.54 | 4.23 | 3.67 | 6.24 | 4.16 | 6.74 | 4.01 |
| SKW | 2.51 | 3.51 | 1.64 | 1.55 | 1.53 | 2.76 | 2.00 | 1.95 | 2.06 | 2.17 |
| CH | 2.81 | 3.51 | 1.61 | 3.05 | 2.19 | 2.36 | 3.87 | 2.85 | 5.27 | 3.06 |
| EBL | 3.85 | 6.69 | 4.71 | 6.18 | 3.87 | 6.85 | 4.78 | 8.31 | 7.32 | 5.84 |
| UCL_L | 3.62 | 3.60 | 2.28 | 3.70 | 5.41 | 3.34 | 7.42 | 3.14 | 4.93 | 4.16 |
| LCL_L | 2.16 | 2.23 | 2.70 | 3.04 | 5.47 | 13.33 | 7.04 | 2.26 | 4.17 | 4.71 |
| Mean | 7.42 | 6.52 | 6.50 | 6.24 | 8.61 | 7.72 | 8.92 | 8.52 | 6.77 | 7.47 |

Note: BW: Body weight; BL: Body length; TL: Tail length; TL/BL: Tail-to-Body ratio; LFL: Length of left forelimb; RFL: Length of right forelimb; LHL: Length of left hindlimb; RHL: Length of right hindlimb; LEL: Length of left ear; REL: Length of right ear; LEW: Width of left ear; REW: Width of right ear; CRL: Cranial length; CBL: Cranial base length; PNL: Occipitonasal length; ZW: Zygomatic width; LD: Interorbital width; SKW: Cranial width; CH: Cranial height; EBL: Ear bulla length; UCL_L: Upper tooth row length (Left); LCL_L: Lower tooth row length (Left).

traits. Upper and lower tooth row lengths were lowest (2.63% and 2.54%).

**Principal component analysis and cluster analysis of morphological indices**

PCA revealed PC1, PC2 and PC3 explained 51.24%, 28.01% and 8.99% of variation (cumulative 88.24%, Fig 2). In PC1-PC2 space (Fig 2A), populations formed concentrated clusters with distinct shifts (especially PC1) and some overlap (PC2), suggesting phenotypic similarities. PC1-PC3 (Fig 2B) was consistent with PC1-PC2, with PC3 reflecting secondary trait differences. Hierarchical clustering (Fig 3) divided populations into Group I (QX, ZQ, LC, SY, WT) and Group II (WZ, LF, KL, XX); Group I (except SY) were mainly in the Taihang Mountains, Group II in the Lvliang Mountains.

**Bergmann's rule testing and analysis of *C. longicaudatus* morphology**

Phenotypic indicators were grouped by function and morphology into body surface traits (BL, TL, TL/BL, BW, LIMBS, EAR_SIZE) and skull traits (further integrated into length, width, height and functional axes) to reduce single-indicator interference.

Spearman correlations between 22 traits and 6 environmental factors (altitude, humidity, latitude, longitude, temperature, wind speed) are shown in heatmap (Fig 4). Trait responses varied significantly. Wind speed and latitude showed relatively concentrated correlations with multiple traits ($P$<0.05), while altitude, humidity, longitude and temperature showed no correlations with most traits. Latitude was significantly negatively correlated with cranial height ($P$<0.01, $R$ = -0.46), skull width ($P$<0.05, $R$ = 0.30), ear length ($P$<0.01, $R_{LEL}$ = -0.29, $R_{REL}$ = -0.08), ear width ($P$<0.01, $R_{LEW}$ = -0.41, $R_{REW}$ = -0.34) and forelimb length ($P$<0.01, $R_{LFL}$ = -0.30, $R_{RFL}$ = -0.31). Wind speed was significantly positively correlated with skull width ($P$<0.05, $R$ = -0.30), tail length ($P$<0.01, $R$ = 0.27), tail-to-body ratio ($P$<0.01, $R$ = 0.29), ear width ($P$<0.01, $R_{LEW}$ = 0.38, $R_{REW}$ = 0.43) and limb length ($P_{LFL}$ < 0.05, $R_{LFL}$ = 0.26; $P_{RFL}$ < 0.01, $R_{RFL}$ = 0.27; $P_{LHL}$ < 0.01, $R_{LHL}$ = 0.44; $P_{RHL}$ < 0.01, $R_{RHL}$ = 0.43),

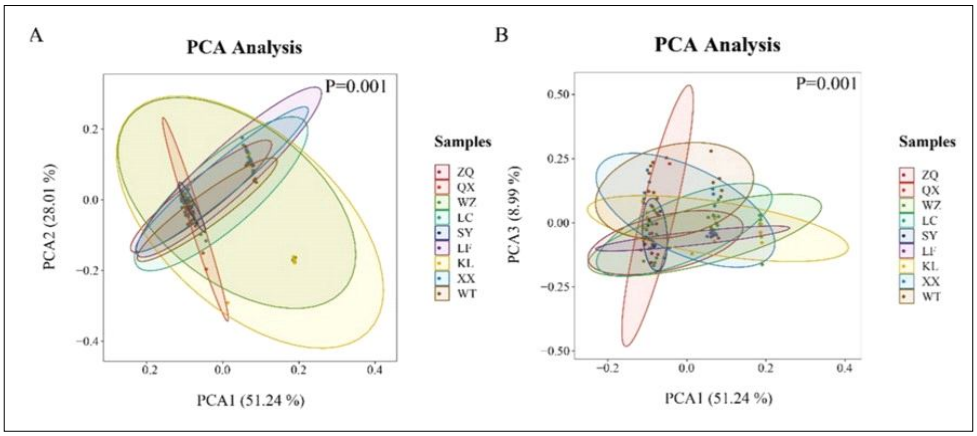



**Fig 2:** Principal component analysis (PCA) of phenotypic traits in long-tailed dwarf hamsters (*Cricetulus longicaudatus*).

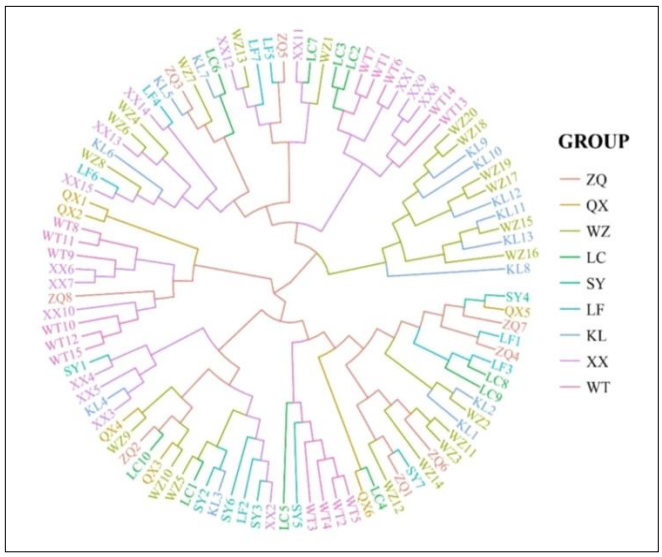



**Fig 3:** Dendrogram of hierarchical cluster analysis for long-tailed dwarf hamster (*Cricetulus longicaudatus*) populations.

but negatively correlated with body length ($P$<0.05, $R$ = -0.23). Tail length was negatively correlated with altitude ($P$ < 0.01, $R$ = -0.29). Cranial height and ear width were negatively correlated with humidity ($P$<0.05, $R_{CH}$ = -0.32; $R_{LEW}$ = -0.24, $R_{REW}$ = -0.22). Ear bulla length was negatively correlated with longitude ($P$<0.05, $R$ = -0.29), but positively correlated with temperature ($P$<0.05, $R$ = 0.26), as was body length ($P$<0.05, $R$ = 0.24). Other traits showed no significant correlations ($P$>0.05).

Mantel tests (Fig 5) showed significant correlations mainly between specific environmental gradients and composite traits. Altitude correlated positively with LIMBS and EAR_SIZE; latitude correlated with body weight (strong), body length (weak) and tail/tail-body (weak but stable). For skull traits, latitude correlated positively with all four composite axes (length, width, height, functional), indicating synchronous skull changes along latitude. Longitude and humidity showed weaker/fewer correlations. Overall, trait-environment correlations concentrated between altitude and body surface traits and latitude and skull structure, reflecting differential trait responsiveness. Bergmann's rule (body size) and Allen's rule (appendage length) (Bergmann, 1848; Allen, 1877) have species- and gradient-specific applicability (Tabh and Nord, 2023; Valladares-Gómez *et al.*, 2024). Our latitude-body size correlations align with most rodents (Ashton *et al.*, 2000; Balèiauskas *et al.*, 2025; Tomlinson and Withers, 2009), supporting Bergmann's rule and altitude-driven skull

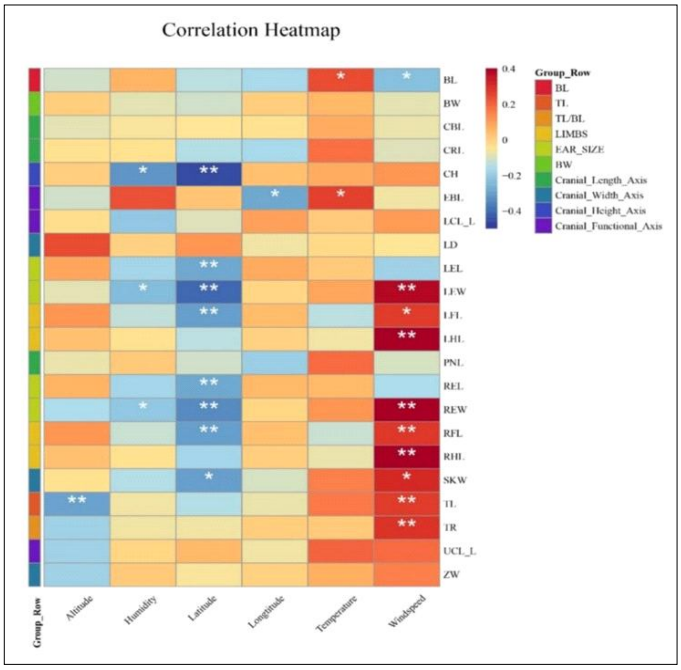



**Fig 4:** Heatmap of Spearman correlation coefficients among morphological variables.

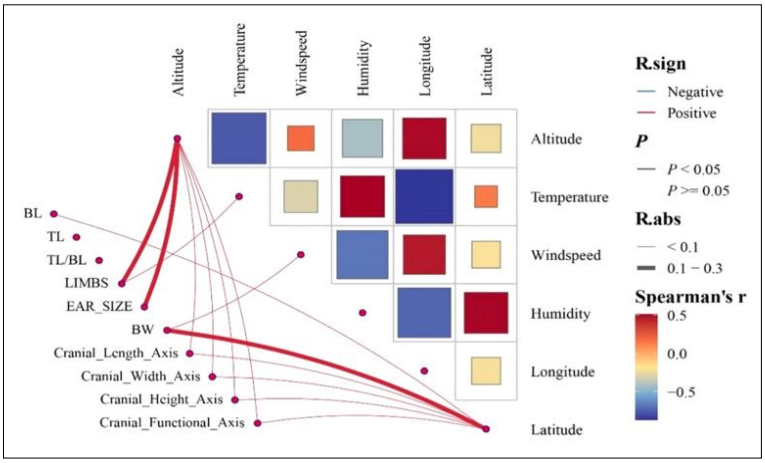



**Fig 5:** Mantel test of phenotypic and geographic distances in long-tailed dwarf hamsters (*Cricetulus longicaudatus*).

selection. However, Allen's rule was contradicted - limb/ear sizes increased with altitude, not latitude, consistent with exceptions in Chilean rodents and *A. draco* (Valladares-Gómez *et al.*, 2024; Cui *et al.*, 2020).

Differential growth rates drive morphological diversity, with plastic contributions nonlinear and energy-dependent (Tabh and Nord, 2023). The appendage-altitude positive correlation in *C. longicaudatus* may reflect allometric scaling with cooling, as in *A. agrarius*, *Rattus norvegicus* and *Niviventer confucianus*, with climate effects mediated via body size (Geng and Zhu, 2024). Bird analyses show similar variation across temperature gradients (Fröhlich *et al.*, 2023), suggesting this correlation reflects locomotor maintenance rather than thermoregulation. Allometric ratios vary among rodent groups (Rosalino *et al.*, 2013), suggesting species-specific patterns.

Environmental gradients drive differentiation via selection and gene flow (Price *et al.*, 2003; Rodríguez-Cajarville *et al.*, 2022; Cao *et al.*, 2026). High VST (>75%) in body/skull traits, with among-population variance exceeding within-population variance, mirrors patterns in *Toona ciliata* (Wang *et al.*, 2019), *Tilia mandshurica* (Mu *et al.*, 2023) and rodent skulls (Monteiro *et al.*, 2005; Kang *et al.*, 2024), indicating geographic isolation dominates. However, food/competition can outweigh temperature (Cui *et al.*, 2022), adjusting niche width (Stephens *et al.*, 2019) and foraging (Manlick *et al.*, 2021); thus ecological factors beyond climate matter. Body weight (VST = 6.96%) is season/reproduction-sensitive and not a sole indicator; food availability may drive size changes (Alston *et al.*, 2023), so multiple linear indicators are preferable.

## CONCLUSION

Phenotypic variation in *C. longicaudatus* across nine Shanxi regions supports Bergmann's rule (larger body size in colder regions) but not Allen's rule; appendage elongation with altitude likely reflects allometric growth. These findings enrich understanding of rodent adaptation to climatic gradients and provide baseline data for broader ecogeographic studies.

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### Disclaimers

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### Informed consent

All animal procedures for experiments were strictly in compliance with the People's Republic of China's Ministry of Science and Technology's Regulations on the Administration of Laboratory Animals (SXAU-EAW-2024M.JE.004022321).

### Conflict of interest

The authors declare that there are no conflicts of interest regarding the publication of this article. No funding or sponsorship influenced the design of the study, data collection, analysis, decision to publish, or preparation of the manuscript.

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