



Functional adaptation rather than ecogeographical rules determine body-size metrics along a thermal cline with elevation in the Chinese pygmy dormouse (*Typhlomys cinereus*)

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ABSTRACT

Phenotypic plasticity is crucial for how organisms respond to variation in their environment, affecting their diversity and distribution, especially in the light of rapid environmental change. Ecogeographical rules predict an association between specific adaptive morphological and physiological traits with cooler conditions due to higher latitude, elevation, or climate change. Such ecogeographical effects are often most evident in ancient species due to continuous selective adaptation occurring over long periods of time. Here, we use the suitably ancient Chinese pygmy dormouse (*Typhlomys cinereus*) to test whether body-size, appendage length and heart size vary in accordance with Bergmann's, Allen's and Hesse's rule, respectively. Based on a sample of 67 adult individuals (female, $n = 29$; male $n = 38$) trapped at 37 sites transcending an elevational range from 414 to 1757 m, we tested for trait concordance with Bergmann's rule (body mass, length and SMI), Allen's rule (length of tail, foot, ear, snout), and Hesse's rule (wet and dry heart mass). Effects of elevation (and thus temperature lapse rate; calculated as 0.61 °C per 100 m) on body size, appendage length and heart size, were tested by fitting Standardized Major Axis (SMA) models. We observed substantial heterogeneity in morphometric traits allowing for the detection of ecogeographical clines. However, none conformed with Bergmann's, Allen's (except ear size), or Hesse's rule. However, our results indicate some support for Geist's rule of net primary productivity. We conclude that pervasive functional life-history adaptations in this blind, arboreal, echolocating ancient species exceeded selection for morphological energy efficiency constraints, with the notable exception of reduced ear pinnae size at colder, elevated sites. This is an important consideration for predicting how species, and populations in general, may adapt to human induced rapid environmental change, contrary to expectations of warming driving selection for smaller body-size.

1. Introduction

There is growing conservation concern that species and populations may not be capable of adapting their physiology quickly or sufficiently enough to cope with Human Induced Rapid Environmental Change (HIREC; Mawdsley et al., 2009; Sih et al., 2011), particularly climate

change (Gardner et al., 2011). This concern hinges substantially on there being distinct differences between individuals linked to the temperature and weather conditions they experience (Yom-Tov and Geffen, 2006). As a result the morphology, physiology and genetics of a species (or broader taxon) often trend systematically across their biogeographical range (central-marginal hypothesis; Weiner, 1992; Millien et al., 2006; Eckert

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et al., 2008; Naya et al., 2009), defining an ecotypic cline (Endler, 1977; Badgley and Fox, 2000).

Environmental conditions are principally associated with geophysical phenomena, such as cooler conditions occurring at higher latitudes (reduced solar insolation and photoperiod) and adiabatic lapse rates in temperature (and pressure related weather) with elevation/altitude (Fleming et al., 1990). Due to scale law allometries (West et al., 1999), metabolism typically scales to the $\frac{3}{4}$ power with mass (Kleiber's law, Kleiber, 1932, see Dodds et al., 2001), imposing elastic criteria on biological proportions (McMahon, 1973). Consequently, individuals living in colder environments tend to be larger (Bergmann's rule, Bergmann, 1847; Rensch, 1938; Shelomi, 2012; Salewski and Watt, 2017); tend to have shorter appendages (e.g., ears, feet, etc.) (Allen's Law, Allen, 1877); and to have larger hearts relative to their body size (Hesse's Law, Hesse et al., 1937). Rapid climate change may, however, expose populations to altered weather regimes, with the potential to destabilize their morphological fit with their environment. Millien et al. (2006) propose that rules of geographical variation in response to changes in the local environment can apply to morphological adaptation even in response to contemporary climate change, where Gardner et al. (2011) predict that declining body-size may occur as a third universal response to global warming (alongside changing phenology and distribution).

In terms of previous investigations of ecogeographical rules, our Google Scholar search (conducted January 2019) found 419 articles discussing Bergmann's rule, 126 for Allen's rule, but only 4 for Hesse's rule. There is strong support for Bergmann's rule in birds (Ashton, 2002), but while among reptiles testudines follow Bergmann's rule, lizards and snakes invert it (Ashton and Feldman, 2003). For mammals, Ashton et al. (2000) report a significant positive correlation between body size and latitude for 78 of 110 species examined, and a negative correlation between size and temperature in 48 of 64 species. Although it has been proposed (McNab, 1971) that smaller endotherms may be bound by scale allometries (greater rates of heat loss) to follow these rules more tightly, Ashton et al. (2000) was not able to corroborate this for mammals. Furthermore, Bergmann's rule is often more evident in the fossil record (Smith and Lyons, 2011) than across contemporary populations.

Support for Allen's rule (Allen, 1877) has proven more equivocal (Cardilini et al., 2016). Nudds and Oswald (2007) avian-based study reports that reduced surface area of appendages can provide energetic savings sufficient to make this morphological trend truly adaptive; although this benefit is most important through the coldest season experienced. Among terrestrial ectothermic vertebrates, Allen's rule applies to turtles and amphibians (Alho et al., 2011), while snakes and lizards follow the inverse cline (Ashton and Feldman, 2003). Allen's rule has also been found to apply to several larger mammal species (Weaver and Ingram, 1969; Paterson, 1996). Nevertheless, ontogenetic variation on smaller mammalian taxa, particularly among rodents, has been largely ignored.

Hesse's rule (Hesse et al., 1937) has been less studied. Wiersma et al. (2007) discovered that heart mass in subtropical birds was significantly smaller in contrast to temperate individuals, while Müller et al. (2014) found that relative heart weight of two rodent species (*Myodes glareolus* and *Apodemus flavicollis*) was significantly greater at higher elevation. In contrast, Cardilini et al. (2016) found that starlings, *Sturnus vulgaris*, in Australia, exhibited no heart ratio trends in accord with any geographic or climatic variables, while Zhao et al. (2019) found that the relative heart size of Andrew's toad (*Bufo andrewsi*) did not increase with elevation or latitude across ten populations.

Here we use an ancient species, with a long evolutionary history – the Chinese pygmy dormouse – to ascertain if indeed body-size, relative limb proportions and relative heart size varied across an elevational and temperature range, or whether these predicted physiological relationships (e.g., Kleiber's Law; Ballesteros et al., 2015) are opposed by other forces of selection. The Chinese pygmy dormouse is distributed across a wide elevation range (here 414–1757 m), while being relatively sessile,

and thus reliant upon in-situ physiological adaptation to adverse conditions. Support for the null-hypothesis of no effect would therefore imply that climatic warming, per se, may not have a dominant impact on the adaptive fit of body-size related physiology, but instead is exceeded by selection pressures for other fitness criteria (Scholander et al., 1950).

2. Methods

2.1. Study sites and sampling technique

Data were collected at the Shennongjia World Natural Heritage Site (31°15'–31°57'N, 109°56'–110°58'E) and Yichang (29°56'–31°34'N, 110°15'–112°04'E), with subsequent post-mortems conducted in Xingshan County, located in north-west Hubei Province, central China. The study area lies in the transitional belt between middle and northern subtropical zones and is characterized by 4 distinct seasons, including a hot, humid summer (June–August, monthly mean temperature > 25 °C, monthly mean precipitation >250 mm) and a cold winter (December–February, monthly mean temperature <−4 °C; Cui et al., 2018; Su et al., 2019). Elevation ranges from 50 m in the deepest gorges to 3106 m at Shennong Peak, the highest mountain in central China, with rugged terrain and topography. Weather records were obtained from Records from 27 standard meteorological stations (2012–2018) across the study area (9 in Shennongjia Forestry District Meteorological Bureau, 13 in Xingshan County meteorological bureau and 5 in National Field Research Station for Forest Ecosystem of Shennongjia).

Trapping for Chinese pygmy dormice (IUCN, Least Concern ver 3.1, 2017) was conducted at 115 sites across an elevational range from 45 to 2900 m, with specimens snap trapped successfully at 37 sites between 414 and 1757 m. This lethal trapping was primarily conducted to investigate the role *T. cinereus* plays in the transmission of the lethal lymphocytic choriomeningitis virus, plague and haemorrhagic fever, and our study took secondary benefit from these existing necropsy data (Raoul et al., 2008; Meerburg, 2015; Wong and Qiu, 2018). Given that all these specimens were collected from a small region, we infer they should belong to a single genetic population, subject to the same regional genetic selection pressures (Müller et al., 2014).

At each site, 150 snap traps (155 × 85 mm) were spaced at 2–3 m (total $n = 115 \text{ sites} \times 150 \text{ traps} \times 1 \text{ [night/site]}$) (Hu et al., 2017; Wen et al., 2018a), and baited with chestnuts (*Castanea mollissima*). Traps were checked at 7:00 a.m. the following morning and the species and sex of each *T. cinereus* caught was logged against elevation using *GPSmap 60CSx*. All trapping was carried out in strict accordance with the National Wildlife Conservation Law in China, also trapping *Apodemus draco*, *Niviventer confucianus*, among other endemic rodents (Chen et al., 2019; Wu et al., 2019).

2.2. Species biology and morphological measurements

Typhlomys spp. are not true dormice (Gliridae) but are members of the Platycanthomyidae (distinguished by having no premolars). *T. cinereus* is arboreal, living in bamboo stands, although it will also burrow. The reproductive capacity of *T. cinereus* is relatively low, with typically just one litter per annum of two to four offspring, and its diet consists of leaves, stems, fruits, and seeds (Smith and Xie, 2008).

Using rulers, we measured body length (excluding tail), tail length, foot length, ear length and snout length to the nearest millimetre, along with body mass to the nearest 0.01 g, and wet and dry heart mass to the nearest 0.1 mg. Following Smith and Xie (2008), body length was defined as distance from nose to anus; tail length as anus to tail tip; foot as heel to the top of the third digit of the right rear foot; ear length as base to tip; and snout length as tip of snout to the anterior edge of the right eye. Only adults were measured, as determined from reproductive condition.

Establishing parametric morphological variables is vital in the assessment of ecogeographical responses, as established by previous

studies examining this source of variation (Müller et al., 2014; Cardilini et al., 2016). Therefore, simple body mass cannot be used because it can fluctuate inter-annually with seasonal resource availability. To address this we used a Scaled Mass Index (SMI, after Peig and Green, 2009, 2010; noting the limitations of body-length described by Müller et al., 2014; Cardilini et al., 2016):

$$SMI = M_i \left[\frac{L_0}{L_i} \right]^{b_{SMA}}$$

where M_i = the body mass of individual i ,

- L_i = body length of individual i ,
- L_0 = arithmetic mean body-length across of study population, and
- b_{SMA} = the slope of an standardized major axis (SMA) regression of \ln (study population mass) = \ln (study population length) + β + ϵ .

This SMI procedure better enabled us to examine the relationship between body mass and body length, by quantifying the scaling exponent between these two inter-dependent variables.

We investigated conformity with Bergmann’s rule with elevation as predictor and SMI as response variable; also modelling simple body mass and length for comparison (see Appendix A for details). For Allen’s rule, we used four appendage metrics (e.g. tail, foot, ear and snout) as response variables, testing both actual lengths and length residuals (calculated as the residual observed value minus the predicted value, based on the regression of observed value on SMI controlling body size effects using Linear Models). For Hesse’s rule, we tested actual wet and dry heart weight (i.e., heart weight after full desiccation in a hot air oven) as well SMI residuals. We also tested the effect of elevation on the residual values of all appendage and heart metrics scaled to body mass and body length for comparison (see Appendix A).

2.3. Statistical analysis

To explore the relationship between temperature and elevation, Generalized Additive Models (GAM, ‘mgcv’ package) were employed with mean annual temperature, mean temperature in the coldest and warmest 3 months as the dependent response variables and elevation as an independent variable. Similarly, GAM was also used for temperature seasonality.

Prior to statistical analysis we explored the extent of heterogeneity in measures between individuals to establish if there was sufficient variation within metric ranges to detect inter-individual variation along elevation clines. All measurements were made by a single investigator to minimize inter-observer bias.

Table 1

Results from standardized major axis (SMA) regressions with elevation as the predictor variable, sex as a group variable, with Scaled Mass Index (SMI), the actual and relative size (residuals to SMI) of appendage length, and heart size as response variables. Significance (bold) was set at $p < 0.05$.

Response variable(residuals)	Male				Female				Sex	
	Estimate	Intercepts	R ²	p	Estimate	Intercepts	R ²	p	likelihood rate	p
Bergmann’s rule										
SMI	-19.671	79.695	0.002	0.812	-15.191	64.087	0.041	0.291	1.035	0.309
Allen’s rule										
Tail length	5.492	-5.507	0.016	0.450	-4.191	23.792	0.034	0.337	1.121	0.290
Residual tail length (SMI)	3.474	-10.564	0.006	0.638	-4.188	12.664	0.037	0.315	0.536	0.464
Foot length	-1.067	5.366	0.073	0.102	0.758	-0.240	0.041	0.289	1.861	0.173
Residual foot length (SMI)	-0.900	2.738	0.037	0.248	0.467	-1.413	0.010	0.598	6.541	0.011
Ear length	-1.366	5.597	0.211	0.004	-1.307	5.405	0.119	0.066	0.035	0.852
Residual ear length (SMI)	-1.122	3.412	0.133	0.024	-0.754	2.281	0.049	0.248	2.592	0.107
Snout length	0.844	-1.431	0.012	0.521	0.991	-1.755	0.001	0.853	0.384	0.535
Residual snout length (SMI)	0.699	-2.129	0.011	0.530	-0.716	2.167	0.000	0.939	0.008	0.929
Hesse’s rule										
Wet heart mass	0.248	-0.568	0.009	0.577	0.229	-0.518	0.001	0.901	0.094	0.759
Residual wet heart (SMI)	0.148	-0.448	0.000	0.917	0.121	-0.365	0.001	0.880	0.604	0.437
Dry heart mass	0.058	-0.128	0.006	0.644	0.048	-0.098	0.000	0.969	0.513	0.474
Residual dry heart (SMI)	-0.035	0.105	0.000	0.998	0.048	-0.145	0.000	0.964	1.425	0.233

For analyses of morphometric variation with elevational gradient, all mass and body-length data, all limb lengths, all SMIs and all elevations were log10 transformed to reduce data skew and conform to a normal distribution. Site was used as a transformed factor and date as a continuous variable. To control for allometry, we then constructed a series of Standardized Major Axis (SMA, package *smatr*) models that included elevation as an independent variable, and sex as a group variable, along with the dependent response variables described in Table 1 and Appendix A. The sexes were analyzed separately in these SMA regressions. The slopes of these relationships for male and female were further compared in SMA regressions using the likelihood-ratio method based on the Chi-squared test. The SMA slope (i.e. ordinary regression slope/ r) can minimize the variance perpendicular to the fit of a line after transformation so that $\text{var } y = \text{var } x$ (King et al., 2009; Warton et al., 2012). All statistical analyses were performed in R 3.5.0.

3. Results

3.1. Decreasing temperature with elevation

Temperature (mean annual) declined with elevation ($F = 776.5, p < 0.001$). Similarly mean temperature declined with elevation in the coldest ($F = 329.5, p < 0.001$) and warmest 3 months ($F = 957.7, p < 0.001$), as did temperature seasonality ($F = 22.7, p < 0.001$) (Fig. 1). This provides a robust ecogeographical basis for testing the effects of a thermal cline with elevation on morphological traits.

3.2. Trait heterogeneity

In total, we measured 67 adult Chinese pygmy dormice (female, $n = 29$; male $n = 38$), captured at 37 sites distributed over an elevational range from 414 to 1757 m (Fig. 2). We observed substantial heterogeneity in the morphometric traits of interest: body mass = 13.60 g–26.28 g; body length = 66 mm–93 mm; tail length = 96 mm–125 mm; foot length = 17 mm–25 mm; ear length = 11 mm–18 mm; snout length = 9 mm–16 mm; wet heart mass = 0.120 g–0.268 g and dry heart mass = 0.036 g–0.068 g. Our study sample exhibited sexual size dimorphism (SSD) with body mass and SMI significantly greater for males than for females (t -test: $t = 2.43, p = 0.018$; $t = 2.82, p = 0.006$). Males had significantly longer feet than did females ($t = 2.17, p = 0.033$), but tended to have relatively shorter snouts ($t = -3.163, p = 0.003$).

3.3. Bergmann’s rule

We found no support for Bergmann’s rule. Indeed, there was a

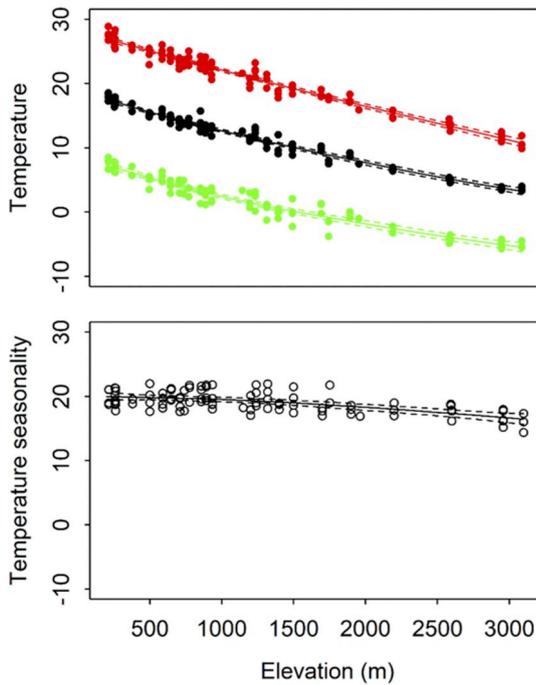


Fig. 1. Relationship between elevation and mean annual (black circles), coldest (green circles) and warmest (red circles) temperature, and temperature seasonality (open circles). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

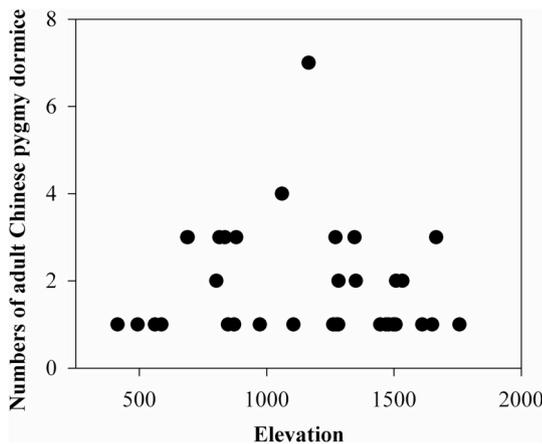


Fig. 2. Numbers of adult Chinese pygmy dormice trapped along the elevational gradient.

significant negative relationship where females living at higher elevation, and thus in colder conditions, tended to be lighter, opposing Bergmann's rule. However, no correlation was evident for males (Appendix A). Similarly, no correlation was detected between elevation and SMI where slopes did not differ between males and females (Table 1, Fig. 3).

3.4. Allen's rule

Both actual and residual ear length to SMI showed a significant negative relationship with elevation; no absolute effects of elevation on tail, foot and snout lengths were evident (Table 1, Appendix A and Fig. 4). These findings partly support Allen's rule.

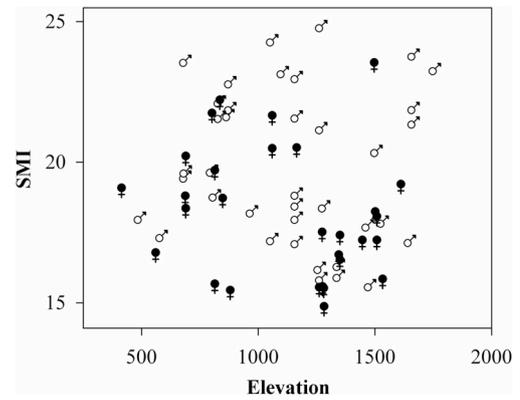


Fig. 3. Relationship between SMI and elevation across 67 adult Chinese pygmy dormice caught from 37 sampling sites between 414 to 1757 m.

3.5. Hesse's rule

Neither wet or dry heart weight or heart weights controlling for body length/weight or SMI residual were related to elevation (Table 1, Appendix A and Fig. 5), and thus we found no substantive support for Hesse's rule.

4. Discussion

Changing climatic conditions are often invoked intuitively as a stressor driving physiological adaptation, but this requires mechanistic proof (Gardner et al., 2011; Huey et al., 2012), where the expectation is that warming trends should (if unopposed by other selective forces) drive smaller body-sizes, as a universal response (Millien et al., 2006; Porter and Kearney, 2009; Gardner et al., 2011). Here we found no link between body-size and relative limb (except ear) and heart size with a gradient in temperature with elevation. This shows that, at least in this species (contrasting Brown and Lee, 1969), other factors, such as environmental net primary productivity (eNPP) and selection for general adaptive traits, exceed any effects driving scale-law related adaptation. From this, we would predict that, in the Chinese pygmy dormouse, functional adaptations will continue to take precedence, even under conditions of projected regional climate change (Zhu et al., 2008; Yang et al., 2015), illustrating limits to the predictive power of ecotypic rules (Millien et al., 2006).

While metabolic rate typically scales with body mass to the $3/4$ power (Glazier, 2008; a concept implicit to the ecogeographical rules tested), it remains that smaller individuals have lower absolute energy requirements, which may provide a selective advantage under conditions of food constraint, especially for females that must also support offspring development (Gardner et al., 2011; Wen et al., 2018b). For instance, in the context of sexual size dimorphism, Noonan et al. (2016) proposed that selection for small body-size in females reduced competition with their offspring as they matured in their mother's territory (see also Johnson et al., 2017). Similarly, the 'Ghiselin-Reiss small-male hypothesis' posits that when male reproductive success is a function of encounter rate with females, as a scramble rather than a competitive contest, small males may be favoured when food is limiting because they require lower absolute amounts of food (Blanckenhorn et al., 1995). *T. cinereus* also climbs and burrows (Panyutina et al., 2017; Vignieri, 2017), where smaller animals require relatively less energy to climb (Garber, 1992; Cartmill, 2017), and short limbs are advantageous for scansoriality and fossoriality in terms of leverage (Rubin and Lanyon, 1984), yielding energetic advantages to shorter limbed individuals. We thus propose that absolute energy efficiency in this relatively slow lifestyle species (Careau et al., 2009) exerts a stronger influence than adaptation to Bergmann's rule.

Rodent tails have a well-developed caudal vascular system that can

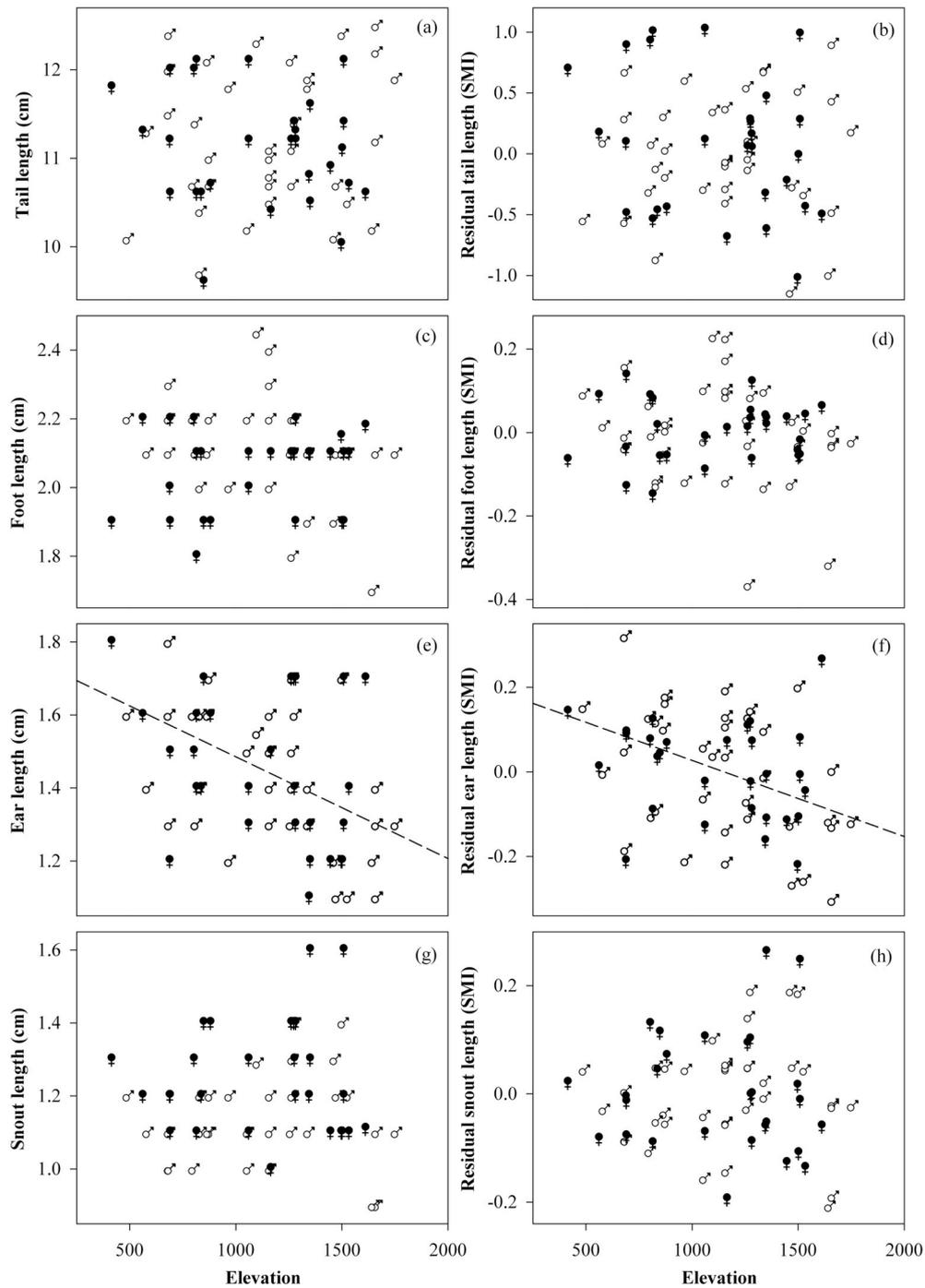


Fig. 4. Relationship between the actual and relative size (residuals to SMI) of appendage length and elevation across 67 adult Chinese pygmy dormice caught from 37 sampling sites between 414 to 1757 m. Lines depict significant relationships.

dissipate heat (Thorington, 1966; Hickman, 1979). Tail proportions are thus important to thermoregulation (Hickman, 1979; Staszuk et al., 2003) and provide a good candidate appendage for testing Allen’s rule. Nevertheless, we found no cline in tail length with elevation. Again we propose that this may be due to over-arching selection for longer (optimal) tail length to enable climbing and balancing agility in this species (Thorington, 1966; Hickman, 1979). A short tail might disadvantage *T. cinereus* when foraging and attempting to evade predators. To compensate for potential heat loss through the tail, however, Chinese pygmy dormice tails are hairy and thus well insulated. Snout and foot size also did not conform to the predictions of Allen’s rule. Given that the Chinese pygmy dormouse is functionally almost blind, acute olfactory

receptivity and acute tactile sensitivity through its feet are essential (Valkenburgh et al., 2014; Cheng et al., 2017; Vignieri, 2017; Nomoto et al., 2018). Any reduction in snout or foot size is therefore likely counteracted by selection for traits functionally necessary for survival, irrespective of elevation or temperature. Ear size did, however, conform to the predictions of Allen’s rule, suggesting that, despite echolocation, ear pinnae may be particularly vulnerable to heat loss as temperature decreases with elevation (Simmons, 1989; Ketten et al., 1992).

With regard to Hesse’s rule, we again found general incongruence. Neither actual or SMI residual wet and dry heart weight showed any relationship with decreasing temperature with elevation. Relationships with other indices (e.g. net wet or dry heart mass, wet or dry heart to

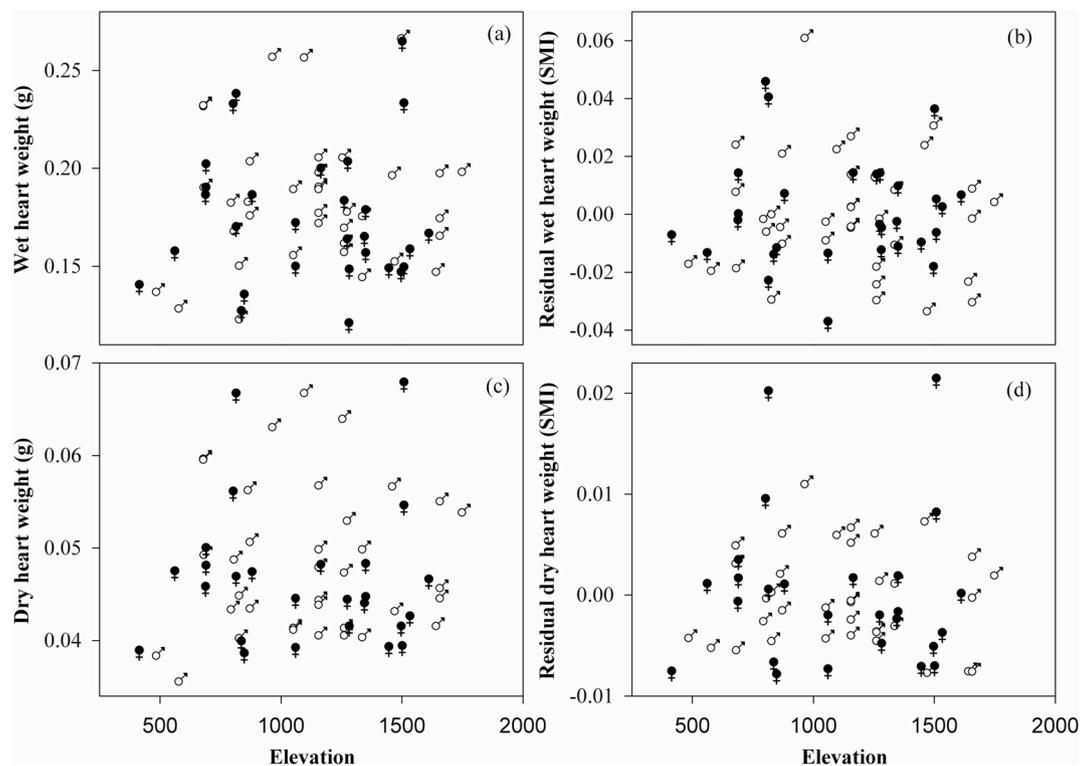


Fig. 5. Relationship between the actual and relative size (residuals to SMI) of heart size and elevation across 67 adult Chinese pygmy dormice caught from 37 sampling sites between 414 to 1757 m.

body length ratios etc) showed no significant trends. Previous work has reported patterns opposing and conforming with Hesse's rule in birds (Wiersma et al., 2007; Cardilini et al., 2016), and opposing Hesse's rule in Andrew's toad (*Bufo andrewsi*) (Zhao et al., 2019); thus far only one mammalian study (*Myodes glareolus* and *Apodemus flavicollis*) has proven consistent with the Hesse's rule (Müller et al., 2014).

By using standardized parametric relative indices (SMI) of morphological variation, our metrics for evaluating ecogeographic rules were superior to approaches based simply on raw metrics. Our relative index approach has been used only infrequently in previous ecogeographical analyses (Peig and Green, 2009, 2010; Cardilini et al., 2016), although this approach provides a more discerning way of quantifying morphological variation.

5. Conclusions

We conclude that selection for specific life-history traits linked to adaptive fitness appear to exert a stronger opposing selective pressure than ecogeographical rules of heat conservation in this specialized and ancient species across its elevational range. This trade-off between selection pressures shows that body-size reduction may not always be a universal response to warming trends (Gardner et al., 2011) and warrants further investigation in the context of what factors may be important for how resilient, or adaptable, species and populations are to HIREC.

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Declaration of competing interest

The authors declared that there are no conflicts of interest to this work.

CRediT authorship contribution statement

Jifa Cui: Methodology, Investigation, Formal analysis, Writing - original draft. **Boyu Lei:** Formal analysis, Investigation. **Chris Newman:** Methodology, Writing - original draft, Writing - review & editing. **Shengnan Ji:** Methodology, Project administration. **Huawei Su:** Investigation, Validation. **Christina D. Buesching:** Conceptualization, Writing - review & editing. **David W. Macdonald:** Conceptualization, Writing - review & editing. **Youbing Zhou:** Conceptualization, Validation, Supervision, Writing - review & editing, Project administration, Funding acquisition.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jtherbio.2020.102510>.

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