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Research Article

Tradeoffs between brain and digestive tissues across elevations in *Typhlomys daloushanensis*: evidence for sexual dimorphism

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To cope with highly stochastic and/or heterogeneous environmental conditions, animals must balance energy resource allocation across physiological processes. The digestive tract and brain exhibit structural variations under strong developmental and selective pressures that vary across environmental gradients both between and within species. Here, we measured body mass, body length, digestive tract segments lengths (stomach, cecum, small intestine, large intestine), brain weight, and relative brain size (scale mass index, SMI residuals) for 67 Chinese pygmy dormice *Typhlomys daloushanensis* (29 females and 38 males), an ancient, small, arboreal rodent species with echolocation abilities, captured at 37 sites between 414 and 1757 m a.s.l. From standardized major axis (SMA) regressions, we found no significant relationship between body size (SMI) and elevation. Notably, neither digestive tract segment lengths and their residuals nor brain weight (absolute and residual) correlated significantly with elevation in either sex, and slopes did not differ between males and females, providing no support for the digestive tract theory (DTT) or the cognitive buffer hypothesis (CBH). However, brain–digestive tract relationships exhibited sex-specific differences, partially supporting the expensive tissue hypothesis (ETH), suggesting that energy allocation to high-cost organs is sex-dependent. Males maintained relatively heavier brain weight under comparable digestive tract lengths, likely to meet cognitive demands associated with mate competition, territorial defense, and exploratory behavior, whereas females tended to prioritize digestive tract investment to meet the energetic demands of gestation and lactation. Thus, classical predictions

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of body size–environment relationships may be overridden by sex-specific physiological tradeoffs in specialized species, providing new insights into how small mammals may adapt to rapid environmental change.

Keywords: cognitive buffer hypothesis, digestive tract theory, elevation gradient, expensive tissue hypothesis, sexual size dimorphism, *Typhlomys daloushanensis*

Introduction

In complex and changeable ecosystems, environmental heterogeneity is universally acknowledged as a primary factor driving developmental phenotypic plasticity and the adaptive evolution of species (Edelaar et al. 2023). High latitude, temperature extremes, and seasonal and stochastic variations in resources not only shape the behavioral patterns and life history strategies of animals (Bright Ross et al. 2020) but can also profoundly influence their physiology and energy allocation budgets (Bright Ross et al. 2025). Genotypic adaptation, via Darwinian selection, takes generations to occur (Barnosky and Kraatz 2007). Consequently, behavioral and physiological plasticity provide the most immediate tactical response to changing conditions, where animals attempt to maintain their survival and reproductive rates through a combination of mechanisms including behavioral adjustments (i.e. migration and foraging strategies; Noonan et al. 2018), physiological regulation (i.e. changes in metabolic rate and fat storage; Bright Ross et al. 2021), and even developmental organ structure remodeling (Hildebrandt 2023).

Ecophysiology posits that organ systems serve as a crucial bridge between the external environment and internal physiological regulation in adaptive phenotypic responses (Burraco et al. 2025). Given the fundamental relationship expressed by Kleiber's law (Kleiber 1975, Ballesteros et al. 2015), where an animal's basal metabolic rate tends to scale to the ¾ power of mass (Rao 2021), changes in animal body size have been recognized to constitute a third universal response to contemporary climate change (Gardner et al. 2011), in addition to changes in distribution and phenology. Generally, within species, body size is often taken as a proxy for specific underlying factors, such as metabolic resource availability, body surface area and total muscle mass (Schoenemann 2004). Although structural size and body mass result from different genetic, physiological and ecological mechanisms and represent energy allocation to different functions (Piersma and Van Gils 2011), these are used interchangeably in studies evaluating population responses to environmental change, especially in trait-based demographic models (Canale et al. 2016).

Differences in diet composition can have a profound effect on intestinal morphology (Langer and Clauss 2018). The digestive tract theory (DTT; Penry and Jumars 1987, Wang et al. 2003) posits that structural adjustments in the digestive system are driven mainly by the digestibility of food consumed: when the proportion of indigestible components in food is relatively high, such as in poorer habitats, animals tend to have longer intestines to increase retention time, thereby enhancing digestive efficiency and energy acquisition rate (Chapman and McLean 2023, Duque-Correa et al. 2025). More specifically, different functional segments of the digestive tract respond differently to environmental factors: low temperatures usually promote an increase in small intestine length to enhance its chemical digestive capacity, while the cecum, as the main site for microbial fermentation in non-ruminant mammals, tends to increase in volume when consuming high-fiber foods (Wang et al. 2003). This can result in a relationship between body size, diet quality and digestive strategy, such that smaller animals (especially herbivores) require a richer diet than larger animals, as formulated by the Jarman–Bell principle (Bell 1971, Jarman 1974, Potter and Pringle 2023).

The effects of environmental conditions on energy-intensive organs are not limited to the digestive tract. The brain also exerts substantial and continuous energy demands and exhibits variations in size and structure in response to environmental complexity, resource predictability, home-range size, habitat stability and sociality (Gonda et al. 2013). The cognitive buffer hypothesis (CBH) posits that a relatively larger brain can enhance an animal's cognitive abilities and behavioral flexibility, enabling it to respond more effectively to environmental stressors such as unpredictable spatiotemporal food scarcity, increased predation pressure, or unstable climatic conditions (Sol et al. 2016). Therefore, individuals with relatively larger brains may have a phenotypic, and possibly a selective, advantage. For instance, Schuck-Paim et al. (2008) found that among Neotropical parrots brain size increased with greater climate variability. In terms of survival strategies, individuals with larger brains mitigate the need for crypsis (e.g. coat color, spots or stripes, etc.) because enhanced cognitive abilities allow them to evade predators through active behavior (Liao et al. 2022); regarding reproductive strategies, brain size promotes nest-building behavior and reproductive success (Bialas et al. 2024); in male–male competition, brain size is positively associated with competitive success (Liao et al. 2025); and in social and mating systems, larger-brained birds show more stable pair bonds and lower rates of extra-pair paternity (Liu et al. 2023).

Because of their high metabolic requirements, the brain and digestive tract are particularly prone to phenotypic adaptation arising from energy reallocation strategies (Heldstab et al. 2022). Consequently, structural and functional changes in these organs reflect how animals respond to various ecological pressures, such as social interactions and foraging resource landscapes (Hartwig et al. 2011). Similarly, because the vertebrate brain requires a continuous and stable energy supply to maintain physiological homeostasis, homeorhesis, sensory information processing, and shaping individual identity through integration, learning, memory, emotion and cognition (Pereira 2021), this can impose serious constraints on brain size evolution, despite concomitant cognitive benefits (Tsuboi et al. 2015). The expensive tissue hypothesis (ETH), initially proposed by Aiello and Wheeler in (1995), therefore posits that brain size can only increase through a reduction in the mass of other energetically costly organs, such as the digestive tract. This results in a redistribution of metabolic resources among organ systems (Isler and Van Schaik 2006, Liao et al. 2016), which generally requires an improvement in foraging efficiency or nutrient availability in the environment. Isler and Van Schaik (2009) further expanded this hypothesis and proposed a more comprehensive framework for metabolic energy allocation, extending the tradeoff range from the intestine to other high-energy-consuming systems such as somatic growth and maintenance (Isler and van Schaik 2006), locomotion (Saxena et al. 2022), and reproduction (Isler and Van Schaik 2009), while emphasizing the regulatory role of life history traits on brain evolution (Song et al. 2023).

The tradeoff between larger brain size and reduced digestive tract length is complex, as the digestive system must be scaled to fulfill metabolic demands and thus exhibits considerable plasticity in response to the availability of nutritional resources and environmental variability (Secor 2001). The ETH has subsequently been applied to various animal groups. Among endothermic species, the ETH has been used as a framework to study the energy tradeoffs between the brain and other tissues in birds (Isler and Van Schaik 2006) and bats (Jones and MacLarnon 2004). Among ectotherms, similar investigations have been conducted in amphibians (Liao et al. 2016, Luo et al. 2017) and fish (Tsuboi et al. 2015). The accumulation of empirical studies across different groups has provided support for the ETH, but studies have also shown that its applicability may be influenced by ecological conditions, life history strategies and evolutionary backgrounds.

Capacity to trade off expensive tissues may also be sex dependent, as an extension of sexual size dimorphism (SSD) theory (Hedrick and Temeles 1989, Isaac 2005, Tombak et al. 2024, Winkler et al. 2024), where the extent to which males must compete for access to females determines male body size, aggression and armaments, with females preferentially selecting larger, stronger males, i.e. the Darwin–Bateman-Trivers paradigm (Dewsbury 2005; versus the Ghiselin–Reiss small-male hypothesis in systems dominated by scramble competition; Blanckenhorn et al. 1995). Simultaneously, in mammals, minimal energy intakes for females are determined by the elevated costs of gestation and lactation (Fokidis et al. 2007). When female size matches of exceeds that of males, this is typically due to selection pressures that affect homeothermy during pregnancy, good-quality milk production, offspring protection and transport, and other forms of parental care, (i.e. the big mother hypothesis; Ralls 1976), or arises when species are more social, for example, due to environmental or resource pressure (Firman et al. 2020).

High-elevation habitats are typically characterized by lower temperatures, shorter growing seasons with lower primary productivity, shifts in vegetation composition, and reduced oxygen concentrations (Xu et al. 2024). These factors can exacerbate pressures on energy acquisition and utilization substantially. Such constraints may, in turn, drive developmental and adaptive selection for longer and more efficient digestive systems. However, this energetic reallocation may come at a potential cost to maintaining investment in brain size, which serves as a proxy for cognitive capacity at both structural and functional levels. The responses of montane species thus provide excellent indicators of vulnerability to climate change and thus forecast likely future impacts on biodiversity (Vitasse et al. 2021).

In this study, we examined relative organ size in the Chinese pygmy dormouse (hereafter *Typhlomys daloushanensis*) – an ancient, small, arboreal rodent species (Qian et al. 2024) that occurs among a guild of 38 other rodent species in the forested, mountainous Shennongjia region of Hubei Province, in sub-tropical China (Zhou and Lei 2019). The genus *Typhlomys* has diminished vision and relies instead on echolocation capabilities (Qian et al. 2024), foraging for leaves, stems, fruits and seeds (Smith and Xie 2008). The majority of previous studies on *T. daloushanensis* have mainly focused on its taxonomy, phylogeny, distribution, species differentiation and echolocation (Hu et al. 2021, Qian et al. 2024), whereas research on the relationships between its physiological traits and environmental factors remains limited. However, the biology and elevational distribution of *T. daloushanensis* make it ideally suited for investigating the potential tradeoffs among organ systems as environmental conditions change with elevation. Cui et al. (2020) observed substantial heterogeneity in the morphometric traits of *T. daloushanensis* with elevation in the same study population as used in this current study (these individuals were originally recorded as *T. cinereus*, but following taxonomic revisions, they have been reclassified as *T. daloushanensis*; Qian et al. 2024), although they observed no ecogeographical clines in relation to Bergmann's, Allen's (except ear size), or Hesse's rule. In terms of body-size, Qin et al. (2024) established a significant male-biased sexual size dimorphism (SSD) in *T. daloushanensis*, with males exhibiting notably greater body length (+4.3%) and body mass (+16.7%) compared to females. In relation to a link between body-size and reproductive capacity through SSD, *T. daloushanensis* typically produces just one litter per annum of two to four offspring, which is relatively low, for a small rodent species (Smith and Xie 2008).

Building on existing knowledge of morphological organ variation in *T. daloushanensis* (Cui et al. 2020), here we examined its relative energy allocation to brain weight and digestive tract length along an elevational gradient. We first re-tested and confirmed Cui et al.'s (2020) assessment that overall body mass in this population does not increase with elevation (i.e. with cooler conditions). Subsequently, we integrated the digestive tract theory (DTT), the cognitive buffer hypothesis (CBH), and the expensive tissue hypothesis (ETH) to investigate potential tradeoffs between energy allocation and ecological adaptation and whether effects differ between the sexes.

We tested four hypotheses/theories:

1) The digestive tract theory (DTT), predicting an increase in digestive tract length with higher (colder) elevation to cope with poorer food quality/availability and to maintain energy allocation to brain tissue;
2) The cognitive buffer hypothesis (CBH), predicting an increase in brain weight with higher elevation to enhance cognitive and adaptive abilities; that is, that larger brain size may enhance foraging efficiency and compensate for shorter digestive tract length;
3) The expensive tissue hypothesis (ETH), predicting a negative tradeoff between brain weight and digestive tract length, where an energy uptake insufficiency could compromise either or both organ systems; and
4) Sexual size dimorphism (SSD), predicting that the demands of gestation and lactation may influence female energy allocation with a bias toward DTT effects, whereas males may benefit from investing in intelligence with a bias toward CBH effects.

Material and methods

Study area

This study was conducted at the Shennongjia World Natural Heritage Site (31°15′–31°57′N, 109°56′–110°58′E), a biodiversity hotspot and conservation priority area (Xie et al. 2017), and in Yichang (29°56′–31°34′N, 110°15′–112°04′E), both in Hubei Province, central China. Here, elevation ranges from 50 m a.s.l. in the deepest valleys to 3106 m at Shennong Peak, the highest point in central China. The Köppen–Geiger climate classification for the Shennongjia region is transitional between Cwb – temperate monsoon climate (dry winter, cool summer) and Cfa – subtropical monsoon climate zones (Wu et al. 2025). The region experiences a mean annual precipitation of 1381 mm, which is evenly distributed throughout the year and increases with elevation from 400 to 2000 mm (Xiang et al. 2025). Annual temperature averages 10.4°C, with a mean of –0.6°C for the coldest month (January), and the frost period typically extends from late September to the end of the following April. Both mean temperature and temperature seasonality decrease with elevation (Cui et al. 2020, Supporting information). These climatic data were obtained from 27 standard meteorological stations distributed across the study area for the period 2012–2018 (nine stations operated by the Shennongjia Forestry District Meteorological Bureau, 13 by the Xingshan County Meteorological Bureau, and 5 by the National Field Research Station for Forest Ecosystem of Shennongjia). The elevational distribution of *T. daloushanensis* typically ranges from 400 to 2000 m (Zhou and Lei 2019). Within this range, below 900 m, vegetation consists of evergreen broadleaf forests, dominated by species such as *Quercus serrata* and *Q. aliena*. These forests are widely distributed, but plant species diversity is relatively low. Between 900 and 1500 m, there is a mixed forest zone of evergreen and deciduous broadleaf trees. From 1500 to 2000 m, the vegetation transitions to deciduous broadleaf forests, with a complex plant species composition, commonly including species such as various Fagaceae spp. (Xiang et al. 2025).

Data collection

The individuals analyzed in this study correspond with those used by Cui et al. (2020), and thus all trapping localities and climatic conditions align with those described in that study. Trapping for *T. daloushanensis* (synonym *T. cinereus*; IUCN: Least Concern, ver. 3.1, 2017) was conducted sequentially over 25 nights at 4–6 sites per night, transcending an elevational gradient from 45 to 2900 m. At each site, 150 snap traps (155 × 85 mm) were placed at intervals of 2–3 m (total $n = 115$ sites × 150 traps × 1 [night site^{-1}]). Traps were baited with chestnuts *Castanea mollissima* (Cui et al. 2020) that occur naturally and extensively across the study region and have been shown to produce high capture rates in regional rodent–seed dispersal studies (Chen et al. 2019). Traps were inspected at around 7:00 h on the following morning, and the species and sex of each captured individual were documented with respect to elevation using a GPSmap 60CSx device. The primary purpose of this lethal trapping was to examine the role of *T. daloushanensis* in the transmission of lethal pathogens such as lymphocytic choriomeningitis virus, plague and hemorrhagic fever (Wong and Qiu 2018), and thus our study leveraged these necropsy data as an existing resource. This study was formally approved by the Ethics Committee of China Three Gorges University (no. 2022025A) and all trapping procedures were carried out in full compliance with the provisions of the National Wildlife Conservation Law of China. For more detailed information see Cui et al. (2020).

Only adult specimens were necropsied, as established from their reproductive status. For males, individuals were considered reproductively mature when testes were clearly descended into the scrotum. Female maturity was determined by the presence of an unfused, open vagina. Females showing clear signs of pregnancy were not included in the analysis. For all individuals captured, body was measured using an electronic balance accurate to 0.01 g and body length (BL; from snout to anus) was measured with a ruler. Individuals were then dissected. The brain was carefully removed and weighed using an electronic balance accurate to 0.1 mg, as a metric of brain size. The entire digestive tract was then carefully extracted, and all surrounding mesenteric tissues were removed. The total length of the relaxed digestive tract was measured using a ruler (Muise et al. 2016), where digestive tract length, rather than mass, is most closely related to nutrient (energy) absorption capacity (Weaver et al. 1991). Finally, the digestive tract was separated into four principal parts – stomach, small intestine, large intestine and cecum – each of which was fully extended to its maximum length and measured with the same ruler. All measurements were carried out by a single researcher to reduce inter-observer variation. Given that all specimens were collected from a geographically restricted region, it can be reasonably inferred that they constitute a single genetic population subjected to comparable regional selective pressures (Müller et al. 2014).

Statistical analyses

To characterize the elevational trend of temperature as a background environmental gradient, we incorporated the lapse rate reported by Cui et al. (2020). In that study, the authors quantified the relationships of mean annual temperature, mean temperature of the coldest and warmest three months, and temperature seasonality with elevation using a generalized additive model (GAM), to allow for non-linear responses. Their fitted lapse-rate functions were used here to represent the temperature–elevation pattern for the region (Supporting information).

Establishing parametric morphological variables is vital in the assessment of allometric responses (Cui et al. 2020). Although body length is commonly used for standardization, several studies have noted its limitations (Müller et al. 2014, Cui et al. 2020). Furthermore, body mass is subject to seasonal fluctuations in calorific intake and fat storage relating to resource availability, and to cyclical changes in energy expenditure (e.g. mating and reproduction) (Bright Ross et al. 2021), making direct use unreliable. In contrast, using a scale mass index (SMI) provides a more effective method to normalize inter-individual body size differences by quantifying the scaling relationship between body mass and body length, thereby capturing their inter-dependence (Peig and Green 2009).

$$\mathrm{SMI} = \mathrm{M_i}\left(\frac{\mathrm{L0}}{\mathrm{L_i}}\right)b_{\mathrm{SMA}}$$

Where M_i and L_i represent the actual measured body mass and body length of the individual i, L_0 represents the arithmetic mean body length of the study population, and b_{SMA} provides the regression slope of ln (body mass) on ln (body length) obtained from a standardized major axis (SMA).

All data, including body mass, BL, as well as total intestine length, stomach, small intestine, large intestine, and cecum lengths, SMI, brain weight, and elevation were $\log_{10}$-transformed to reduce skew and better meet the assumptions of normality. To control for the effects of body size, digestive tract lengths and brain weight were standardized using the SMI. Residuals from linear regressions with SMI as the predictor were used as size-corrected values for subsequent analyses.

To investigate the effects of elevation on digestive tract length and brain weight, we utilized standardized major axis (SMA) regression (following Cui et al. 2020). Initially, SMA regressions were conducted with elevation as the independent variable and both brain weight and DT length actual values and their corresponding residuals as dependent variables, generating estimates of slopes, intercepts, and coefficients of determination (R^2), along with results from significance tests. Subsequently, SMA analyses were carried out using total digestive tract length as the predictor variable and brain weight as the response variable to explore the relationship between these two traits and to identify any potential sex-based differences.

Four theoretical frameworks were employed for hypothesis testing: 1) under the DTT, total digestive tract length and its components – including the stomach, large intestine, small intestine and cecum – were treated as response variables to investigate trends in both actual and residual digestive tract lengths, with elevation as the predictor variable; 2) under the CBH, brain weight, including both actual and residual values, was modeled in response to elevation; 3) under the ETH, both actual digestive tract length and its residual values were utilized as response variables, with brain weight and its residuals as predictors, to explore the potential tradeoff between neural and digestive tissue investment; and 4) under SDD, separate SMA regressions were performed for males and females, and likelihood-ratio tests were applied to assess heterogeneity in slope parameters between the two sexes. All statistical analyses were conducted using R ver. 4.3.3.

Results

Trait variation

A total of 67 adult *T. daloushanensis* (females, n = 29; males, n = 38) were captured at 37 sites ranging in elevation from 414 to 1757 m. Over this sample we observed substantial variation in morphological, brain, and digestive tract traits: body mass = 13.60–26.28 g; body length = 66–93 mm; total digestive tract length = 40.83–87.52 mm; stomach length = 13.47–34.5 mm; large intestine length = 4.5–16.52 mm; small intestine length = 10.10–43.25 mm; cecum length = 1.99–5.80 mm; and brain weight = 0.420–0.748 g. There were no significant differences in total digestive tract length between the sexes or in any of its components (total digestive tract: t = –1.18, p = 0.241; stomach: t = –0.16, p = 0.871; small intestine: t = –1.13, p = 0.262; large intestine: t = –0.83, p = 0.412; cecum: t = 0.29, p = 0.772).

DTT

Inconsistent with the predictions of the DTT, elevation had no significant effect on either the actual or residual lengths of the stomach, cecum, small intestine or large intestine (Table 1, Fig. 1).

CBH

Inconsistent with the CBH, neither actual nor residual brain weight exhibited correlated significantly with elevation (Table 1, Fig. 2).

ETH

Inconsistent with the predictions of ETH, neither the actual nor the residual values of digestive tract length and brain weight showed significant correlations across the full sample (Table 1, Fig. 3).

Table 1. Standardized major axis (SMA) regression results for digestive tract length and its components, as well as brain weight (actual and residual values, from the standardized major axis index, SMI) as predictor variables, sex as a grouping variable, and elevation, and actual and residual values (SMI) of digestive tract length as response variables. Statistical significance (in bold) was set at $p < 0.05$.

Hypothesis/theories	Response variables	Independent variable	Male			Female			Sexual size dimorphism (SSD)	
			Intercepts	R^2	p	Intercepts	R^2	p	Likelihood rate	p
The digestive tract theory (DTT)	Digestive tract length	Elevation	101.260	0.031	0.287	93.753	0.021	0.448	0.277	0.598
	Residual digestive tract length (SMI)	Elevation	0.216	0.035	0.262	0.172	0.005	0.715	0.595	0.440
	Stomach length	Elevation	8.026	0.042	0.216	35.239	0.005	0.726	0.001	0.970
	Residual stomach length (SMI)	Elevation	−0.267	0.056	0.153	0.276	0.003	0.762	0.071	0.789
	Large intestine length	Elevation	16.994	0.013	0.489	0.819	0.084	0.127	0.644	0.422
	Residual large intestine length (SMI)	Elevation	0.298	0.012	0.514	−0.385	0.105	0.086	1.333	0.248
	Small intestine length	Elevation	57.966	0.096	0.058	55.027	0.064	0.184	0.001	0.974
	Residual small intestine length (SMI)	Elevation	0.408	0.100	0.052	0.334	0.045	0.268	0.481	0.483
	Cecum length	Elevation	7.229	0.002	0.796	0.468	0.016	0.511	0.065	0.796
	Residual cecum length (SMI)	Elevation	0.444	0.007	0.606	−0.385	0.025	0.408	0.154	0.695
The cognitive buffer hypothesis (CBH)	Brain weight	Elevation	0.415	0.019	0.402	0.920	0.036	0.324	3.338	0.067
	Residual brain weight (SMI)	Elevation	−0.147	0.042	0.219	0.228	0.013	0.545	3.291	0.069
The expensive tissue hypothesis (ETH)	Brain weight	Digestive tract length	0.174	0.025	0.343	1.387	0.002	0.826	5.403	**0.020**
	Residual brain weight (SMI)	Residual digestive tract length (SMI)	0.009	0.008	0.586	−0.013	0.021	0.454	5.341	**0.021**

SSD

Although males had significantly heavier brains than females ($t = -2.08$, $p = 0.044$), indicating SSD, the sex-specific slopes of brain weight in relation to elevation were not statistically different (Table 1, Fig. 2). In relation to the ETH, however, slopes differed significantly between sexes (actual: $t = 5.403$, $p = 0.020$; residual: $t = 5.341$, $p = 0.021$; Table 1, Fig. 3) indicating that energy allocation to high-cost organs differed between the sexes, with males maintaining relatively larger brain weight relative to DT length, whereas female brain weight decreased with DT length.

Discussion

Overall, we established that neither the lengths of digestive tract segments (refuting DTT) nor brain weight (refuting CBH) varied significantly with elevation, nor were digestive tract segment lengths and brain weight inversely correlated, suggesting no tradeoff was occurring (refuting EBH). Interestingly, however, distinct patterns were evident when separating these data by sex, supporting SSD.

The consistent lack of support for DTT (Table 1, Fig. 1) may arise because there was no overall increase in *T. daloushanensis* body-size with elevation (Cui et al. 2020); that is, the Jarman–Bell principle did not apply (Müller et al. 2013), where DT length may instead be linked to other dietary and behavioral strategies in this species. Although digestive tract theory predicts that any decline in diet quality or food digestibility with increasing elevation should favor longer intestines, *T. daloushanensis* preferentially forages for and consumes high-energy, easily digestible seeds and engages in food caching behavior (Smith and Xie 2008). This diet apparently buffers any differences in resource availability linked to changing habitat conditions with elevation (Penry and Jumars 1987, Russo et al. 2025), obviating the need for digestive tract elongation to meet metabolic demands. Indeed, recent studies indicate that DT morphology is influenced not only by food digestibility but also by bioclimatic zone, phylogeny and life-history traits (Chapman and McLean 2023, Duque-Correa et al. 2025).

In relation to the CBH, brain size is closely linked to cognition (Gonda et al. 2013) and can provide a proxy for intelligence (i.e. cognitive performance) across and within species, enabling individuals to utilize the resources in their habitat more efficiently and to exploit novel assets (Heldstab et al. 2022). For example, larger-brained and thus more intelligent vertebrate species tend to live in more complex habitats, linked to superior spatial memory and use more sophisticated foraging techniques to gain continuous access to difficult-to-extract but nutrient-rich food resources (Heldstab et al. 2016) or, in the case of bird species with relatively larger brains, achieve greater nest-building complexity (Li et al. 2023). Furthermore, higher intelligence is associated with lower mortality rates, presumably because of superior predator and parasite avoidance (Stankowich and Romero 2017).

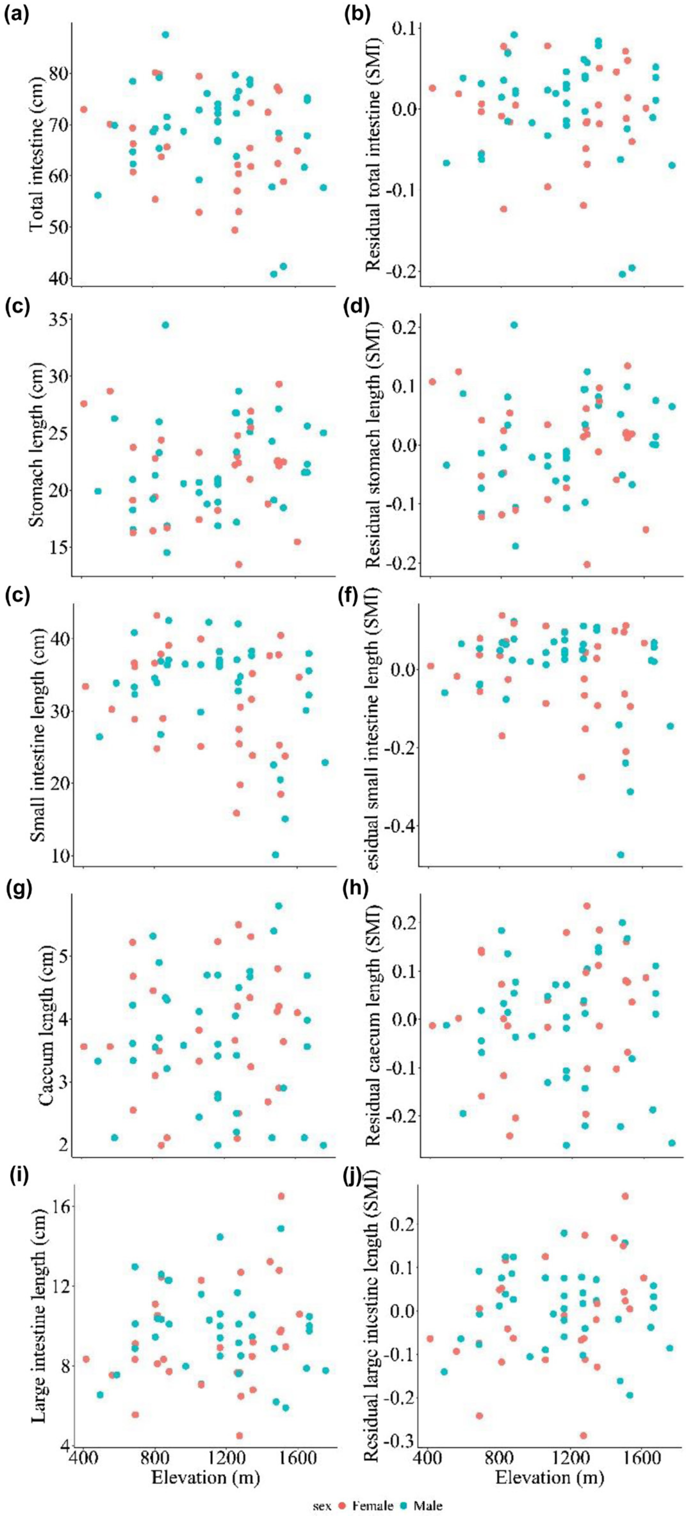

Figure 1. Testing the digestive tract theory (DTT): Responses of total digestive tract (a, b), stomach (c, d), small intestine length (e, f), cecum (g, h), and large intestine (i, j) actual and residual values (SMI) to elevation for 67 adult *Typhlomys daloushanensis*. Pink = females; Blue = males.

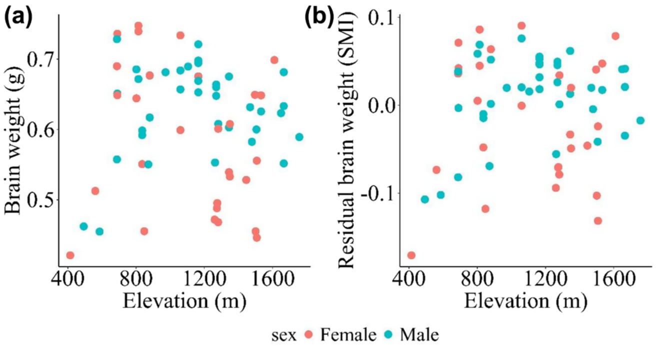

Figure 2. Testing the cognitive buffer hypothesis (CBH). Responses of brain weight actual (a) and residual values (b) (SMI) to elevation for 67 adult *Typhlomys daloushanensis*. Pink = females; Blue = males.

That we found no significant relationship between brain size and elevation in *T. daloushanensis* (Table 1, Fig. 2) may relate to its brain size being driven by other subtle factors. *Typhlomys daloushanensis* uses echolocation (Qian et al. 2024) and spends the majority of its nocturnal activity period climbing or burrowing (Vignieri 2017). This may have resulted in these drivers of encephalization eclipsing other elevation-related selection pressures; that is, the evolution of larger auditory nuclei linked to echolocation (McCurry et al. 2021), larger petrosal lobules and neocortical sizes linked to scansoriality, and a larger hippocampus linked to spatial memory (Bertrand et al. 2021). Specifically, among small mammals, Mace et al. (1981) found that forest-dwelling genera have larger brains than grassland forms; granivores, insectivores, and frugivores have larger brains than folivores or dietary specialists; arboreal genera have larger brains than terrestrial species; and that nocturnal genera have larger brains than diurnal ones. Furthermore, recent research has found that echolocation, and its cognitive demands, are generally associated with smaller body size across mammalian taxa (

Li et al. 2025), potentially constraining the potential for body size responses to elevation in *T. daloushanensis*.

In terms of support for the expensive tissue hypothesis (ETH), the application of this hypothesis is by no means universal, with particular taxa showing no, or even positive correlations (Jones and MacLarnon 2004). Certainly, additional mechanisms such as gut microbiota and fat storage may also play a role in these tradeoffs (Bright Ross et al. 2020, Cheng et al. 2025). While we found no overarching evidence for ETH tradeoffs across our full sample (Table 1, Fig. 3), we did detect a pronounced sex-specific pattern, indicating SSD effects: males maintained relatively larger brain weight relative to overall DT length, whereas female brain size decreased with DT length. This suggests that males prioritize sustaining brain investment under increasing energetic constraints with elevation to continue to support the cognitive demands associated with mate competition, territorial defense, and exploratory behavior (Qin et al. 2024). In contrast, females allocate or increase investment in the digestive system or other energy-acquisition organs to meet the energetic requirements of gestation and lactation (Corral-López et al. 2017), where their low reproductive rate for a rodent species suggests that reproduction exerts a high demand on *T. daloushanensis*. For comparison, Chapman and McLean (2023) found that the DT lengths of male and female eastern deer mice *Peromyscus maniculatus* responded in sex-specific ways to demands of reproduction.

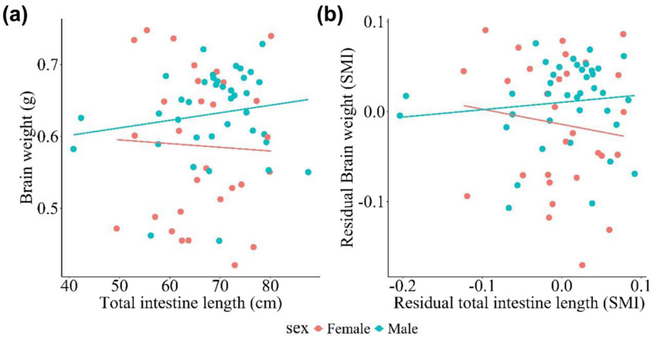

Figure 3. Testing the expensive tissue hypothesis (ETH). Relationships between (a) absolute and (b) relative sizes (SMI residuals) of digestive tract length and brain weight for 67 adult *Typhlomys daloushanensis*. Pink = females; Blue = males.

Cui et al. (2020) established significant SSD in relation to body weight and SMI among the individuals we sampled, with males larger than females. Given that the direction and extent of sexual dimorphism in body size typically relates a species' social system, where males tend to be substantially larger than females in polygynous rodent species (Wolff 2007), the extent of male-biased SSD observed in *T. daloushanensis* (Qin et al. 2024) suggests that heavier body weight may provide males with a competitive advantage when contesting access to females. Links between larger body size and larger brain size in male *T. daloushanensis* are likely driven by the need for competitive and exploratory capacities; however, this will place males under higher metabolic demands, incurring higher food acquisition and foraging expenditure costs. According with the Darwin–Bateman–Trivers paradigm, male biased SSD suggests that male *T. daloushanensis* must compete for mating opportunities, although this activity must be traded off against foraging effort (Blanckenhorn et al. 1995), thus a larger brain may allow males to forage smarter, not longer. This could be particularly advantageous in high elevation habitats with high resource diversity but low abundance.

Conclusion

The climatic variability hypothesis (CVH) posits that, due to an increase in climatic variability at higher latitudes or elevations, individuals living in these areas should exhibit increased phenotypic flexibility (Naya et al. 2012). This greater flexibility should in turn allow phenotypically flexible populations to thrive and become more widely distributed throughout those habitats (Naya et al. 2012, Wu et al. 2024). That we detected no substantive phenotypic responses to elevation for expensive organ systems in *T. daloushanensis* may arise due to this species' combination of climbing and burrowing behaviors, along with its use of echolocation – specialized traits that override simpler, direct energetic plasticity tradeoffs. This highlights the extent to which species respond differently to climatic gradients (Kingsolver and Buckley 2017) and thus will likely respond differently to ongoing rapid climate change (Fei et al. 2017).

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Author contributions

Yimei Yan: Data curation (lead); Formal analysis (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead). **Bangqing Chen**: Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Validation (equal); Writing – review and editing (equal). **Jifa Cui**: Investigation (equal). **Chris Newman**: Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Boyu Lei**: Investigation (equal). **Nan Wu**: Investigation (equal). **Jinwei Wu**: Conceptualization (equal); Methodology (equal); Writing – review and editing (equal). **Jin Zhao**: Conceptualization (equal); Methodology (equal); Writing – review and editing (equal). **Christina D. Buesching**: Writing – review and editing (equal). **Youbing Zhou**: Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Validation (equal); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.cc2fqz6kp (Yan et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Aiello, L. C. and Wheeler, P. 1995. The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. – Curr. Anthropol. 36: 199–221.

Ballesteros, F. J., Martínez, V. J., Moya, A. and Luque, B. 2015. Energy balance and the origin of Kleiber's law. – J. Biol. Phys. 3: 1–8.

Barnosky, A. D. and Kraatz, B. P. 2007. The role of climatic change in the evolution of mammals. – BioScience 57: 523–532.

Bell, R. H. V. 1971. A grazing ecosystem in the Serengeti. – Sci. Am. 225: 86–93.

Bertrand, O. C., Püschel, H. P., Schwab, J. A., Silcox, M. T. and Brusatte, S. L. 2021. The impact of locomotion on the brain evolution of squirrels and close relatives. – Commun. Biol. 4: 460.

Bialas, J. T., Dylewski, Ł. and Tobolka, M. 2024. Brain size mediates the choice of breeding strategy in the red-backed shrike *Lanius collurio*. – Integr. Zool. 19: 683–693.

Blanckenhorn, W. U., Preziosi, R. F. and Fairbairn, D. J. 1995. Time and energy constraints and the evolution of sexual size dimorphism – to eat or to mate? – Evol. Ecol. 9: 369–381.

Bright Ross, J. G., Newman, C., Buesching, C. D. and Macdonald, D. W. 2020. What lies beneath? Population dynamics conceal pace-of-life and sex ratio variation, with implications for resilience to environmental change. – Global Change Biol. 26: 3307–3324.

Bright Ross, J. G., Newman, C., Buesching, C. D., Connolly, E., Nakagawa, S. and Macdonald, D. W. 2021. A fat chance of survival: body condition provides life-history dependent buffering of environmental change in a wild mammal population. – Clim. Change Ecol. 2: 100022.

Bright Ross, J. G., Markham, A., Noonan, M. J., Buesching, C. D., Connolly, E., Pallett, D. W., Malhi, Y., Macdonald, D. W. and Newman, C. 2025. Individual mechanical energy expenditure regimens vary seasonally with weather, sex, age and body condition in a generalist carnivore population: support for inter-individual tactical diversity. – Animals 15: 1560.

Burraco, P., Hawkes, L., Pilakouta, N., Angelier, F., Brans, K. I. and Orizaola, G. 2025. Evolutionary ecophysiology in extreme environments under a global change scenario. – Conserv. Physiol. 13: coaf059.

Canale, C. I., Ozgul, A., Allainé, D. and Cohas, A. 2016. Differential plasticity of size and mass to environmental change in a hibernating mammal. – Global Change Biol. 22: 3286–3303.

Chapman, O. S. and McLean, B. S. 2023. Seasonal and sex-specific changes in the gastrointestinal tracts of *Peromyscus maniculatus*. – J. Mammal. 104: 1364–1376.

Chen, W., Zhong, J., Carson, W., Tang, Z., Xie, Z., Sun, S. and Zhou, Y. 2019. Proximity to roads disrupts rodents' contributions to seed dispersal services and subsequent recruitment dynamics. – J. Ecol. 107: 2623–2634.

Cheng, C., Zhai, H., Feng, J. and Zhang, Z. 2025. Host phylogeny and feeding habit jointly govern mammalian gut microbiota composition. – Integr. Zool. 20: 1–11.

Corral-López, A., Bloch, N. I., Kotrschal, A., van der Bijl, W., Buechel, S. D., Mank, J. E. and Kolm, N. 2017. Female brain size affects the assessment of male attractiveness during mate choice. – Sci. Adv. 3: e1601990.

Cui, J., Lei, B., Newman, C., Ji, S., Su, H., Buesching, C. D., Macdonald, D. W. and Zhou, Y. 2020. Functional adaptation rather than ecogeographical rules determine body-size metrics along a thermal cline with elevation in the Chinese pygmy dormouse (*Typhlomys cinereus*). – J. Therm. Biol. 88: 102510.

Dewsbury, D. A. 2005. The Darwin–Bateman paradigm in historical context. – Integr. Comp. Biol. 45: 831–837.

Duque-Correa, M. J., Clauss, M., Meloro, C. and Abraham, A. J. 2025. Does intestine length explain digesta retention times in birds and mammals? – Comp. Biochem. Physiol. 300: 111789.

Edelaar, P., Otsuka, J. and Luque, V. J. 2023. A generalised approach to the study and understanding of adaptive evolution. – Biol. Rev. 98: 352–375.

Fei, S., Desprez, J. M., Potter, K. M., Jo, I., Knott, J. A. and Oswalt, C. M. 2017. Divergence of species responses to climate change. – Sci. Adv. 3: e1603055.

Firman, R. C., Rubenstein, D. R., Moran, J. M., Rowe, K. C. and Buzatto, B. A. 2020. Extreme and variable climatic conditions drive the evolution of sociality in Australian rodents. – Curr. Biol. 30: 691–697.e3.

Fokidis, H. B., Risch, T. S. and Glenn, T. C. 2007. Reproductive and resource benefits to large female body size in a mammal with female-biased sexual size dimorphism. – Anim. Behav. 73: 479–488.

Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L. and Heinsohn, R. 2011. Declining body size: a third universal response to warming? – Trends Ecol. Evol. 26: 285–291.

Gonda, A., Herczeg, G. and Merilä, J. 2013. Evolutionary ecology of intraspecific brain size variation: a review. – Ecol. Evol. 3: 2751–2764.

Hartwig, W., Rosenberger, A. L., Norconk, M. A. and Owl, M. Y. 2011. Relative brain size, gut size, and evolution in new world monkeys. – Anat. Rec. 294: 2207–2221.

Hedrick, A. V. and Temeles, E. J. 1989. The evolution of sexual dimorphism in animals – hypotheses and tests. – Trends Ecol. Evol. 1989: 136–138.

Heldstab, S. A., Kosonen, Z. K., Koski, S. E., Burkart, J. M., Van Schaik, C. P. and Isler, K. 2016. Manipulation complexity in primates coevolved with brain size and terrestriality. – Sci. Rep. 6: 24528.

Heldstab, S. A., Isler, K., Graber, S. M., Schuppli, C. and Van Schaik, C. P. 2022. The economics of brain size evolution in vertebrates. – Curr. Biol. 32: R697–R708.

Hildebrandt, J. P. 2023. Ecology meets physiology: phenotypic plasticity and the ability of animals to adjust to changing environmental conditions. – Physiologia 3: 366–380.

Hu, T., Cheng, F., Xu, Z., Chen, Z., Yu, L., Ban, Q., Li, C., Pan, T. and Zhang, B. 2021. Molecular and morphological evidence for a new species of the genus *Typhlomys* (Rodentia: Platacanthomyidae). – Zool. Res. 42: 100–107.

Isaac, J. L. 2005. Potential causes and life-history consequences of sexual size dimorphism in mammals. – Mamm. Rev. 35: 101–115.

Isler, K. and Van Schaik, C. P. 2006. Costs of encephalization: the energy trade-off hypothesis tested on birds. – J. Hum. Evol. 51: 228–243.

Isler, K. and Van Schaik, C. P. 2009. The expensive brain: a framework for explaining evolutionary changes in brain size. – J. Hum. Evol. 57: 392–400.

Jarman, P. J. 1974. The social organisation of antelope in relation to their ecology. – Behaviour 48: 215–267.

Jones, K. E. and MacLarnon, A. M. 2004. Affording larger brains: testing hypotheses of mammalian brain evolution on bats. – Am. Nat. 164: E20–E31.

Kingsolver, J. G. and Buckley, L. B. 2017. Evolution of plasticity and adaptive responses to climate change along climate gradients. – Proc. R. Soc. B 284: 20170386.

Kleiber, M. 1975. Metabolic turnover rate: a physiological meaning of the metabolic rate per unit body weight. – J. Theor. Biol. 53: 199–204.

Langer, P. and Clauss, M. 2018. Morphological adaptation of the eutherian gastrointestinaltract to diet. – Vertebr. Zool. 68: 237–252.

Li, J., Wu, N., Wang, J., Guo, J., Newman, C., Qian, Q., Buesching, C. D., Macdonald, D. W. and Zhou, Y. 2025. Global drivers of echolocating mammal species richness. – Global Change Biol. 31: e70522.

Li, S. B., Liu, Y. X., Du, X. L., Li, G. P. and Liao, W. B. 2023. Nest complexity correlates with larger brain size but smaller body mass across bird species. – Integr. Zool. 18: 278–288.

Liao, W. B., Lou, S. L., Zeng, Y. and Kotrschal, A. 2016. Large brains, small guts: the expensive tissue hypothesis supported within anurans. – Am. Nat. 188: 693–700.

Liao, W. B., Jiang, Y., Li, D. Y., Jin, L., Zhong, M. J., Qi, Y., Lüpold, S. and Kotrshal, A. 2022. Cognition contra camouflage: how the brain mediates predator-driven crypsis evolution. – Sci. Adv. 8: eabq1878.

Liao, W. B., Ma, D. L., Jiang, A., Cao, L. S. and Wu, H. 2025. Males with greater mating success during male–male competition have larger brain size in the Andrews toad (*Bufo andrewsi*). – Asian Herpetol. Res. 16: 227–235.

Liu, Y. T., Wu, Z. J. and Liao, W. B. 2023. Large-brained birds display lower extra-pair paternity. – Integr. Zool. 18: 278–288.

Luo, Y., Zhong, M. J., Huang, Y., Li, F., Liao, W. B. and Kotrschal, A. 2017. Seasonality and brain size are negatively associated in frogs: evidence for the expensive brain framework. – Sci. Rep. 7: 16629.

Mace, G. M., Harvey, P. H. and Clutton-Brock, T. H. 1981. Brain size and ecology in small mammals. – J. Zool. 193: 333–354.

Mccurry, M. R., Marx, F. G., Evans, A. R., Park, T., Pyenson, N. D., Kohno, N., Castiglione, S. and Fitzgerald, E. M. G. 2021. Brain size evolution in whales and dolphins: new data from fossil mysticetes. – Biol. J. Linn. Soc. 133: 990–998.

Muise, E. D., Tackett, J. J., Callender, K. A., Gandotra, N., Bamdad, M. C. and Cowles, R. A. 2016. Accurate assessment of bowel length: the method of measurement matters. – J. Surg. Res. 206: 146–150.

Müller, D. W. H., Codron, D., Meloro, C., Munn, A., Schwarm, A., Hummel, J. and Clauss, M. 2013. Assessing the Jarman–Bell principle: scaling of intake, digestibility, retention time and gut fill with body mass in mammalian herbivores. – Comp. Biochem. Physiol 164: 129–140.

Müller, J., Bässler, C., Essbauer, S., Schex, S., Müller, D. W. H., Opgenoorth, L. and Brandl, R. 2014. Relative heart size in two rodent species increases with elevation: reviving Hesse's rule. – J. Biogeogr. 41: 2211–2220.

Naya, D. E., Spangenberg, L., Naya, H. and Bozinovic, F. 2012. Latitudinal patterns in rodent metabolic flexibility. – Am. Nat. 179: E172–E179.

Noonan, M. J., Newman, C., Markham, A., Bilham, K., Buesching, C. D. and Macdonald, D. W. 2018. In situ behavioral plasticity as compensation for weather variability: implications for future climate change. – Clim. Change 149: 457–471.

Peig, J. and Green, A. J. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. – Oikos 118: 1883–1891.

Penry, D. L. and Jumars, P. A. 1987. Modeling animal guts as chemical reactors. – Am. Nat. 129: 69–96.

Pereira, A. 2021. Developing the concepts of homeostasis, homeorhesis, allostasis, elasticity, flexibility and plasticity of brain function. – NeuroSci 2: 372–382.

Piersma, T. and Van Gils, J. A. 2011. The flexible phenotype: a body-centred integration of ecology, physiology, and behaviour. – Oxford Univ. Press.

Potter, A. B. and Pringle, R. M. 2023. Revisiting the Jarman–bell principle. – In: Prins, H. H. T. and Gordon, I. J. (eds), The equids. Fascinating life sciences. – Springer, pp. 123–145.

Qian, Q., Li, J., Fu, M., Zou, M., Tian, T., Yan, Y., Newman, C., Zou, D. and Zhou, Y. 2024. Ultrasonic differentiation between two species of Chinese pygmy dormice (Genus *Typhlomys*) with support for the size-signal allometry hypothesis. – Integr. Zool. 2024: 1–14.

Qin, Y., Liu, J., Zou, M., Tian, T., Luo, T., Zhou, Y. and Wu, J. 2024. Male-biased sexual size dimorphism in a little-known echolocating mouse, *Typhlomys daloushanensis*. – Mamm. Biol. 104: 601–607.

Ralls, K. 1976. Mammals in which females are larger than males. – Q. Rev. Biol. 51: 245–276.

Rao, T. R. 2021. Body size matters in the lives of organisms. – Reson 26: 61–71.

Russo, D., Rebelo, H., Mata, V., Augusto, A. M., Cistrone, L., Belli, C. and Oliveira, D. 2025. Bat tongues and foraging: linking morphology to hunting strategies. – Integr. Zool. 20: 1–12.

Saxena, S., Hosken, D. J. and Dutta, T. 2022. Brain or brawn: trade-offs between brain size and flight mode in birds. – Evolution 76: 1916–1918.

Schoenemann, P. T. 2004. Brain size scaling and body composition in mammals. – Brain Behav. Evol. 63: 47–60.

Schuck-Paim, C., Alonso, W. J. and Ottoni, E. B. 2008. Cognition in an ever-changing world: climatic variability is associated with brain size in Neotropical parrots. – Brain Behav. Evol. 71: 200–215.

Secor, S. M. 2001. Regulation of digestive performance: a proposed adaptive response. – Comp. Biochem. Phys. A 128: 565–577.

Smith, A. T. and Xie, Y. 2008. A guide to the mammals of China. – Princeton Univ. Press.

Sol, D., Ducatez, S. and Sayol, F. 2016. The Cognitive buffer hypothesis. – In: Weekes-Shackelford, V., Shackelford, T. K. and Weekes-Shackelford, V. A. (eds), Encyclopedia of evolutionary psychological science. – Springer.

Song, Z., Griesser, M., Schuppli, C. and van Schaik, C. P. 2023. Does the expensive brain hypothesis apply to amphibians and reptiles? – BMC Ecol. Evol. 23: 77.

Stankowich, T. and Romero, A. N. 2017. The correlated evolution of antipredator defences and brain size in mammals. – Proc. R. Soc. B 284: 20161857.

Tombak, K. J., Hex, S. B. S. W. and Rubenstein, D. I. 2024. New estimates indicate that males are not larger than females in most mammal species. – Nat. Commun. 15: 45739.

Tsuboi, M., Husby, A., Kotrschal, A., Hayward, A., Buechel, S. D., Zidar, J., Løvlie, H. and Kolm, N. 2015. Comparative support for the expensive tissue hypothesis: big brains are correlated with smaller gut and greater parental investment in Lake Tanganyika cichlids. – Evolution 69: 190–200.

Vignieri, S. 2017. Blind climber. – Science 355: 258–259.

Vitasse, Y., Ursenbacher, S., Klein, G., Bohnenstengel, T., Chittaro, Y., Delestrade, A., Monnerat, C., Rebetez, M., Rixen, C., Strebel, N., Schmidt, B. R., Wipf, S., Wohlgemuth, T., Yoccoz, N. G. and Lenoir, J. 2021. Phenological and elevational shifts of plants, animals and fungi under climate change in the European Alps. – Biol. Rev. 96: 1816–1835.

Wang, D. H., Pei, Y. X., Yang, J. C. and Wang, Z. W. 2003. Digestive tract morphology and food habits in six species of rodents. – Folia Zool. 52: 51–56.

Weaver, L. T., Austin, S. and Cole, T. J. 1991. Small intestinal length: a factor essential for gut adaptation. – Gut 32: 1321–1323.

Winkler, L., Freckleton, R. P., Székely, T. and Janicke, T. 2024. Pre-copulatory sexual selection predicts sexual size dimorphism: a meta-analysis of comparative studies. – Ecol. Lett. 27: e14515.

Wolff, J. O. 2007. Social biology of rodents. – Integr. Zool. 2: 193–204.

Wong, G. and Qiu, X. G. 2018. Type I interferon receptor knockout mice as models for infection of highly pathogenic viruses with outbreak potential. – Zool. Res. 39: 3–14.

Wu, N., Wang, Y., Wang, J., Zhang, Y., Hu, B., Guo, J., Zheng, Z. and Zhou, Y. 2024. Recovery of small rodents from open-pit marble mining: effects on communities, populations, and individuals. – Integr. Zool. 19: 728–742.

Wu, N., Lei, B., Guo, J., Newman, C., Wang, J., Li, J., Tian, T., Buesching, C. D., Macdonald, D. W., Zhao, H. and Zhou, Y. 2025. The recovery of rodent-mediated seed dispersal processes after open-pit marble mining. – Biol. Conserv. 311: 111440.

Xiang, H., Yan, Y., Tian, T., Wu, N., Wang, J., Qian, Q., Guo, J., Newman, C., Buesching, C. D., Chen, H. and Zhou, Y. 2025. Long-term forest damage due to an extreme weather event: an ice storm mediated by elevation causes tree breakage in subtropical China. – For. Ecosyst. 13: 100301.

Xie, Z. Q., Shen, G. Z., Zhou, Y. B., Fan, D. Y., Xu, W. T., Gao, X. M., Du, Y. J., Xiong, G. M., Zhao, C. M., Zhu, Y. and Lai, J. S. 2017. The outstanding universal value and conservation of the Shennongjia World Natural Heritage Site. – Biodivers. Sci. 25: 490–497.

Xu, B., Feng, Z., Chen, Y., Zhou, Y., Shao, Y. and Wang, Z. 2024. Assessing the distribution and driving effects of net primary productivity along an elevation gradient in subtropical regions of China. – Forests 15: 340.

Yan, Y., Chen, B., Cui, J., Newman, C., Lei, B., Wu, N., Wu, J., Zhao, J., Buesching, C. D. and Zhou, Y. 2025. Data from: Tradeoffs between brain and digestive tissues across elevations in *Typhlomys daloushanensis*: evidence for sexual dimorphism. – Dryad Digital Repository, https://doi.org/10.5061/dryad.cc2fqz6kp.

Zhou, Y. and Lei, B. 2019. Checklist of terrestrial vertebrates of Shennongjia. – Science Press.