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Geographical variation of organ size in Andrew's toad (*Bufo andrewsi*)

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Phenotypic variation of morphological and physiological traits is assumed to be generated from spatial heterogeneity in environments, and it has been regarded as an important concern domain in evolutionary biology. Organs display markedly size variation among populations along environmental gradients and this variation is associated with changes in oxygen supply and energy demands. Here, we investigated geographical variation in the relative size of organs (i.e., brain, heart, lung, gallbladder, livers, spleen, kidneys, and digestive tract) among 14 populations of Andrew's toad (*Bufo andrewsi*) transcending an elevational range from 864 to 2,367 m, and spanning 8° latitude. We found that although the relative sizes of the eight specific organs varied significantly among populations, none organ size was affected by altitude and latitude. However, based on the combined the new data and published data we found a negative relationship between the relative size of the heart and latitude, contrasting to the Hesse's rule. We also found that the relative size of livers was positively linked to latitude, suggesting that more energy demands and intakes due to slower metabolism in high latitude shaped the evolution of larger livers.

KEYWORDS

phenotypic plasticity, Hesse's rule, organ size, *Bufo andrewsi*, oxygen supply

Introduction

The theory of phenotypic plasticity states that organisms change their morphology and physiological function as an adaptive response to environmental conditions (Stearns, 1989; Clifton et al., 2020; Peng et al., 2022). Phenotypic plasticity in morphological and physiological traits is a common phenomenon across animal taxa (Tucker and Horvath, 1973; Hammond et al., 1999; Piersma et al., 1999; Naya et al., 2009; Zhong et al., 2017; Balciauskas et al., 2020; Donihue et al., 2021; Huang et al., 2021; Liang et al., 2021; Zamora-camacho, 2021; Zedda et al., 2021; Giacomini et al., 2022; Hinds et al., 2022). Organ's size can reflect the traits of structures with certain morphology and independent physiological functions within an organism, and its variation also

undergo certain adaptations to respond to environmental changes (Hammond et al., 2001; Chen et al., 2021; Jiang et al., 2022a). Adaptive strategies of organs responding to the change in temperature and rainfall across geographical gradients were related to food ingestion and the distribution of nutrition digested from food and oxygen consumption in metabolism (Hansson, 1971; Bonnet et al., 1998; Piersma et al., 1999; Dudczak et al., 2022). Indeed, there is evidence that environmental changes affect the development of organ sizes in vertebrates (Piersma et al., 1999; Liu et al., 2011, 2014; Lou et al., 2013; Jin et al., 2016; Ma et al., 2016; Yang et al., 2017; Zhong et al., 2017; Tang et al., 2018; Bláha et al., 2021).

Variation of organ sizes are positively associated with the energetic storage because organisms need energy to reproduce and survive over periods when the available food is limited (Jonsson et al., 1997). Many studies have shown that organ sizes are correlated with the changes in energetic status based on the short-term and long-term sustainable metabolic rates (Chappell et al., 1988; Daan et al., 1990; Hammond and Wunder, 1991; Loeb et al., 1991). Several hypotheses have suggested to explain the relationship between energetic status and organ size. For instance, the brain was regarded as an important costly organ, and two main hypotheses have been proposed to explain the relationship between brain size variation and environmental selection pressures (Striedter, 2005; Liu et al., 2022). The cognitive buffer hypothesis (CBH) predicts a major cognitive advantage of a relatively large brain for foraging and avoiding predators in changing environments (Lefebvre et al., 1997). By contrast, the expensive brain framework (EBF) states that relative brain size is reduced in fluctuating environments when the developmental costs are over the cognitive benefits of large brains (van Woerden et al., 2010; Luo et al., 2017). Moreover, the Hesse's rule also explains variation in heart size among populations where individuals living in colder and hypoxic conditions have larger hearts than individuals inhabiting warmer and hyperoxic conditions (Hesse et al., 1937). Indeed, following the prediction of the Hesse's rule, the size of the heart displays pronounced size variation in species along altitudinal gradients (Hock, 1964; Hammond et al., 1999, 2001; Naya et al., 2009; Müller et al., 2014).

Previous studies have shown that environmental factors such as temperature and rainfall can promote variations in organ sizes among populations in anurans (Jönsson et al., 2009; Jiang et al., 2015; Zhao et al., 2019). For example, supporting the prediction of the EBF, there is a positive correlation between brain size and activity season length among *Bufo andrewsi* populations (Jiang et al., 2015). The common frogs (*Rana temporaria*) from the north have larger livers than southern conspecifics due to more requirement of energy (Jönsson et al., 2009). The digestive tract length in Andean toads (*Bufo spinulosus*) declines with increasing altitude (Naya et al., 2009) whereas the Yunnan frog (*Pelophylax pleuraden*) exactly shows the opposite direction (Lou et al., 2013). Besides, the heart and

lung mass increase with altitude in the spot-legged treefrog (*Polypedates megacephalus*) among populations, supporting the prediction of the Hesse's rule (Zhong et al., 2017). Hence, the environmental pressures leading to differences in requirement of energy were regarded as the key powers in shaping variations in organ sizes across populations in species of frogs.

The Andrew's toad (*B. andrewsi*) is a medium-sized anuran species that lives in the subtropical forests of the Hengduan Mountains, China, at elevations ranging from 750 to 3,500 m (Fei and Ye, 2001). Toward high altitudes, this species attains a larger size at metamorphosis, longer longevity, and larger body size at slower growth rates (Liao and Lu, 2012; Liao et al., 2015, 2016). Although ecological factors have been suggested to shape variations in brain size and limb muscles among populations along an altitudinal gradient (Jiang et al., 2015; Yang et al., 2017; Zhao et al., 2019), the variation in organ size (e.g., brain, heart, lung, gallbladder, livers, spleen, kidneys, digestive tract) in this species across total geographical ranges at the intraspecific level is as yet unexplored. Here, we investigated patterns and possible causes of geographical variation in organ size among *B. andrewsi* populations. We first examined the predictions of the CBH and EBF by investigating the relationship between brain size and altitude and/or latitude. We further tested whether the heart size variation followed the Hesse's rule. Finally, we tested geographical variations in other organ size (e.g., lung, gallbladder, livers, spleen, kidneys, digestive tract) among populations.

Materials and methods

Data collection

A total of 355 male toads were collected from 14 populations in southwestern China between 2017 and 2019 (Figure 1 and Supplementary Table 1). All the toads were sampled each year between the end of March and the beginning of April during the breeding season. We captured all individuals within each sampling site at night using a 12-V flashlight, and confirmed their sexes through their secondary sexual traits (e.g., nuptial pads in males and eggs in females). After being kept at room temperature for 12–24 h in the rectangular tank (1 × 0.5 × 0.8 m, L × W × H) filled with fresh water (2 cm deep) in the laboratory, all individuals were sacrificed by single-pithing (Yu et al., 2018; Zhao et al., 2019). The body size (snout–vent length, SVL) of each individual was measured to the nearest 0.1 mm using a vernier caliper. Subsequently, all specimens were fixed in 4% phosphate-buffered formalin (Zeng et al., 2016). All measurements were taken blindly by identifying specimens by ID number without knowledge of the species' identity. After a maximum of 2 months of preservation, the brain, heart, lungs, gallbladder, liver, spleen,

kidneys, digestive tract were dissected. All organs except the digestive tract and brain were placed in a thermostat drier (60°C) for 48 h and measured their dry mass to the nearest 0.1 mg with an electronic balance. The digestive tract length was measured to the nearest 0.1 mm using a vernier caliper. There is evidence that the length of preservation time has a non-significant effect on organ size in a frog of species (Zhong et al., 2017). The Animal Ethics Committee at China West Normal University (AECCWNU) approved the sacrifice of animals for the reported experiments.

We took digital images of the dorsal, ventral, left and right sides of the brain with a Motic Images 3.1 digital camera mounted on a Moticam 2006 light microscope at a 400 × magnification (Liao et al., 2022). For dorsal and ventral views, we ensured that the view of the brain being photographed was horizontal and that the brain was symmetrically positioned such that one hemisphere did not appear larger than the other. For paired regions, we measured only the width of the right hemisphere and the volume estimate was doubled. The length (L), width (W), and height (H) of the brain were measured from the digital photographs using a tpsDig2 Software. The definition of brain was given as the greatest distance and exhibited the used landmarks. Volumetric estimates of brains were then obtained through an ellipsoid model: $\text{volume} = (L \times W \times H) \pi / (6 \times 1.43)$; (see details in Jiang et al., 2015). The sizes of brains were measured three times and very high intra-measurer repeatability was found for anurans of species.

Statistical analyses

All analyses were performed using R software 4.2.0 (R Core Team, 2022; also see Jiang et al., 2022b). Prior to the analyses, all continuous variables were scaled by 1,000 and \log_{10} -transformed to meet the assumption of normality and enhance the homogeneity of variances. To analyze the differences in organ size among populations, we used one-way analyses of variance (ANOVA) for each organ separately, controlling for body size as a covariate. A previous study has demonstrated that latitude and/or altitude affect the differences in organ size in this species (Zhao et al., 2017). We thus used linear mixed models (LMMs) to assess the effect of geographical gradients (e.g., latitude and altitude) on organ size, with the population as a random effect, and body size as a covariate. The mean values for different organ sizes were also calculated for each population. Because we gain insight into variations in organ sizes across total distributed region of the toad, we analyzed the relationship between the average size of organs and geographical gradients (altitude and latitude) at the population level using a multiple regression analysis in combination with data extracted from previously published

literatures (Supplementary Table 2; Jiang et al., 2015; Ma et al., 2016; Zhao et al., 2019). Finally, we analyzed the relationship between the relative size of all organs and both temperature and rainfall of each site among all populations.

Results

The size of all organs with mean \pm SE for all populations was shown in Supplementary Table 2. One-way ANOVA revealed that in analyses of covariance controlling for body size (all $P < 0.001$), the size of the eight specific organs differed significantly among populations (Table 1). The LMMs revealed that variation in the relative size of all organs was independent on altitude and/or latitude at the level of individuals (all $P > 0.05$; Table 2).

We further examined altitudinal and/or latitudinal variation in organ size at the population level based on the published data. After controlling for body size, the relative size of heart was negatively correlated with latitude (Figure 2A; $t = -2.459$, $n = 24$, $P = 0.023$), but not vary significantly with altitude ($t = 0.264$, $n = 24$, $P = 0.794$). Inconsistent with the relative size of heart, we found a significant effect of latitude on the variation of the size of livers (Figure 2B; $t = 2.284$, $n = 24$, $P = 0.034$). We did not find convincing evidence for altitudinal and/or latitudinal variation in the other organ size (Table 3). Moreover, none organ size showed a correlation with both temperature and rainfall within each site among all populations (Supplementary Table 3).

Discussion

We demonstrate the significant differences in relative size of organs (brain, heart, lungs, gallbladder, livers, kidney, spleen, and digestive tract) among populations. However, we find that altitude and/or latitude are not correlated with the relative size of all organs across populations. Based on published data on the average size of organs, we find that the relative size of the heart is negatively correlated with latitude whereas the relative size of the livers increases with increasing latitude. Our findings suggest that the heart size variation of the toad contrasts with the prediction of Hesse's rule. We find that none organ size is linked to temperature and rainfall across populations. In what follows, we discuss our findings associated with what has previously been known from intraspecific studies the variation in size of organs in anurans.

The relatively larger brains with higher cognitive abilities can deal with novel environmental challenges in animals (Sol and Lefebvre, 2000; Sol et al., 2008). However, the brain is a high metabolic organ, and its energetic costs need to be overcome to

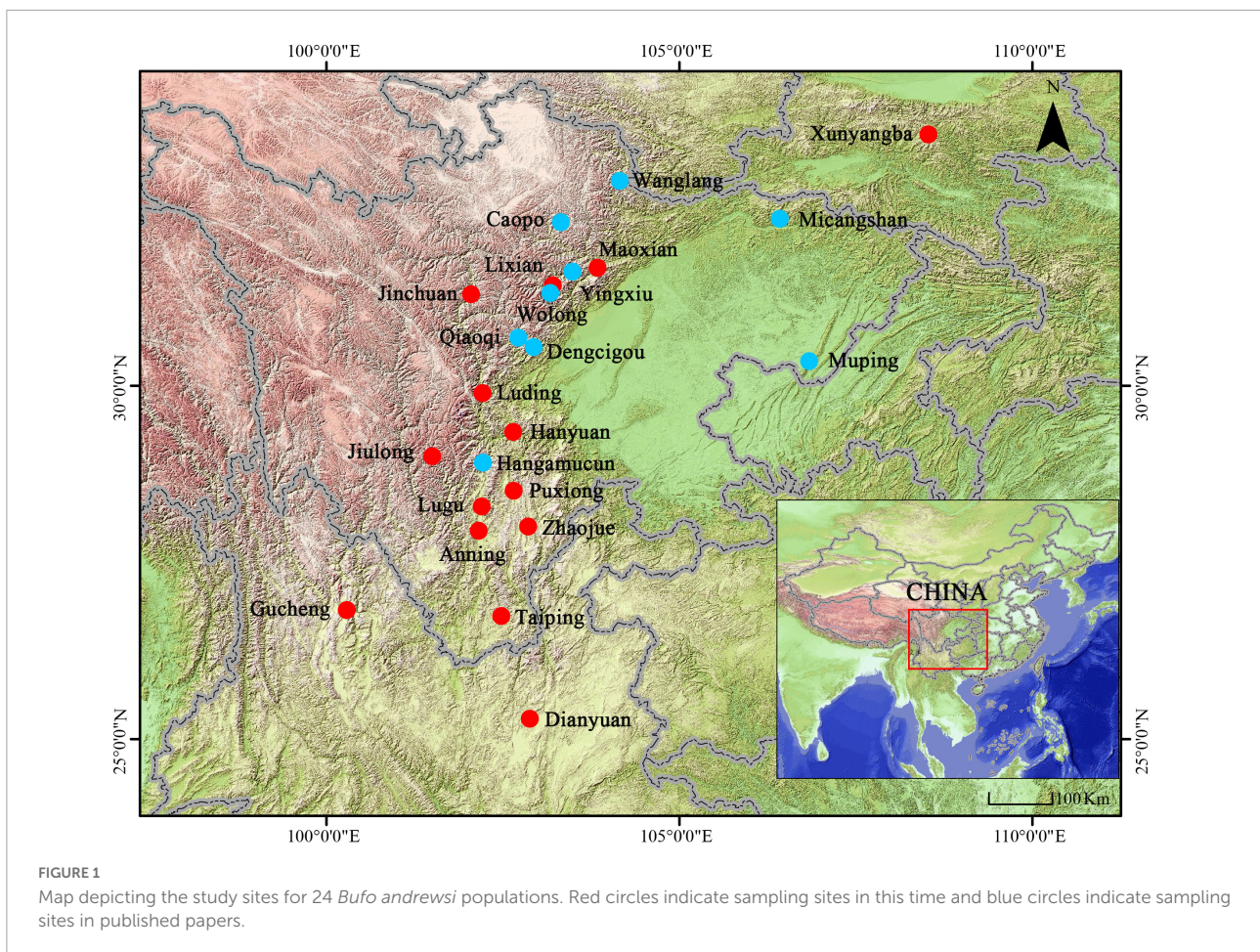


FIGURE 1 Map depicting the study sites for 24 *Bufo andrewsi* populations. Red circles indicate sampling sites in this time and blue circles indicate sampling sites in published papers.

TABLE 1 The variations of organs size in *Bufo andrewsi* among 14 populations when correcting for body size using one-way analyses of variance.

Source	Heart	Lungs	Gallbladder	Livers	Kidneys	Spleen	Digestive tract	Brain
Population								
<i>F</i>	32.98	23.70	7.20	38.87	21.90	25.12	15.40	31.75
<i>P</i>	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
SVL								
<i>F</i>	150.27	185.50	13.07	136.91	123.20	62.44	17.88	98.64
<i>P</i>	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

maintain a larger brain (van Woerden et al., 2011; Jiang et al., 2021). A previous study has indicated that there is significant seasonality-dependent population variation in absolute and relative brain size in *B. andrewsi* (Jiang et al., 2015). In this study, we found that relative brain size differed significantly among populations. Amphibians living at lower altitudes and/or latitudes have more access to food than amphibians living at higher altitudes and/or latitudes, which can be explained by the CBH (Luo et al., 2017). As a result, individuals with lower altitudes and/or latitudes for foraging, growth, and reproduction by decreasing hibernation were expected to have relatively larger brains. Indeed, Jiang et al. (2015) found that higher altitudes

and/or latitudes lead to smaller brain sizes in *B. andrewsi* due to the short active season. However, the observed variation in relative brain size was not correlated with altitude and latitude among *B. andrewsi* populations, which do not support both the CBH and EBF.

Animals may experience limitations to aerobic activities (i.e., exercise and heat production) to adapt to the less oxygen supply at higher altitudes (Chappell et al., 1988). There are evidences for the Hesse's rule that hearts are larger at high altitudes than at low altitudes (Hock, 1964; Hammond et al., 1999; Zhong et al., 2017). However, the relative size of heart does not increase with increasing altitudes

TABLE 2 The effects of altitude, latitude, and population on variation in organ size across 14 populations of the Andrew's toads when correcting for snout–vent length (SVL) using linear mixed models (LMMs).

Source	Random		Fixed				
	VAR	SD	Estimate	SE	df	<i>t</i>	<i>P</i>
Heart							
Population	0.009	0.097					
Residual	0.019	0.138					
Latitude			−1.032	0.869	10.876	−1.188	0.260
Altitude			−0.009	0.232	11.162	−0.038	0.970
SVL			2.546	0.198	348.743	12.849	< 0.001
Lung							
Population	0.004	0.066					
Residual	0.015	0.122					
Latitude			0.387	0.606	10.720	0.638	0.537
Altitude			−0.182	0.163	11.210	−1.120	0.286
SVL			2.498	0.173	343.086	14.411	< 0.001
Gallbladder							
Population	0.021	0.144					
Residual	0.065	0.255					
Latitude			0.754	1.315	10.665	0.573	0.578
Altitude			0.111	0.352	10.975	0.314	0.759
SVL			1.354	0.374	327.114	3.621	< 0.001
Liver							
Population	0.021	0.146					
Residual	0.022	0.148					
Latitude			1.131	1.279	10.821	0.884	0.396
Altitude			−0.299	0.341	10.988	−0.876	0.400
SVL			2.568	0.213	349.232	12.041	< 0.001
Kidneys							
Population	0.005	0.070					
Residual	0.017	0.132					
Latitude			0.804	0.642	10.844	1.253	0.237
Altitude			0.081	0.172	11.346	0.470	0.647
SVL			2.209	0.187	341.979	11.816	< 0.001
Spleen							
Population	0.025	0.158					
Residual	0.043	0.208					
Latitude			−1.499	1.402	10.857	−1.069	0.308
Altitude			0.742	0.375	11.115	1.981	0.073
SVL			2.334	0.299	348.999	7.813	< 0.001
Digestive tract							
Population	0.006	0.079					
Residual	0.010	0.102					
Latitude			−0.041	0.700	10.676	−0.059	0.954
Altitude			−0.179	0.187	10.952	−0.957	0.359
SVL			0.664	0.147	348.965	4.529	< 0.001
Brain							
Population	0.009	0.097					
Residual	0.006	0.078					
Latitude			0.929	0.841	10.584	1.104	0.294
Altitude			−0.073	0.224	10.731	−0.324	0.752
SVL			1.463	0.144	291.742	10.195	< 0.001

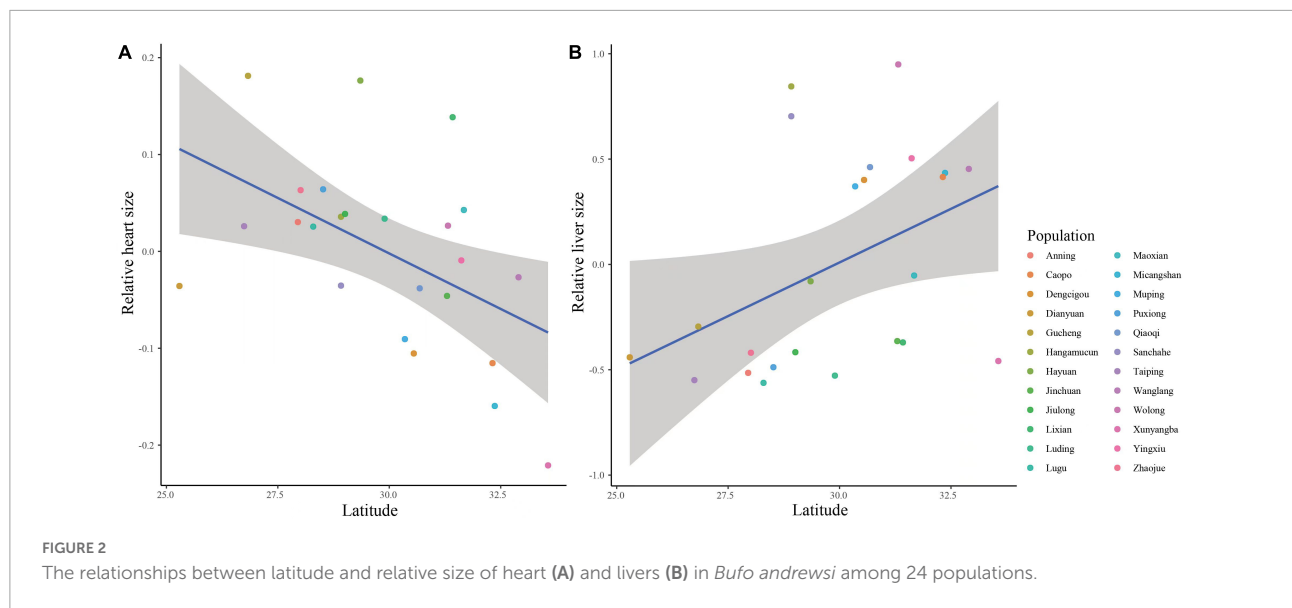


TABLE 3 The relationship between altitude and latitude and variation in mean organ size across all populations of the Andrew's toads when correcting for snout–vent length (SVL).

	Population	Variables	β	SE	<i>t</i>	<i>P</i>
Heart	24	Latitude	-1.521	0.618	-2.459	0.023
		Altitude	0.035	0.133	0.264	0.794
		SVL	2.771	0.508	5.457	< 0.001
Lungs	24	Latitude	0.575	0.475	1.211	0.240
		Altitude	-0.169	0.102	-1.660	0.113
		SVL	3.085	0.390	7.913	< 0.001
Gallbladder	14	Latitude	1.672	2.301	0.727	0.484
		Altitude	0.187	0.687	0.272	0.791
		SVL	0.570	2.764	0.206	0.841
Liver	24	Latitude	7.657	3.353	2.284	0.034
		Altitude	0.474	0.719	0.660	0.517
		SVL	1.450	2.753	0.527	0.604
Kidneys	24	Latitude	0.054	0.574	0.093	0.927
		Altitude	0.021	0.123	0.168	0.869
		SVL	2.338	0.471	4.960	< 0.001
Spleen	14	Latitude	-1.140	1.496	-0.762	0.464
		Altitude	0.990	0.447	2.215	0.051
		SVL	0.064	1.797	0.036	0.972
Digestive tract	21	Latitude	-0.524	0.659	-0.795	0.438
		Altitude	-0.153	0.137	-1.113	0.281
		SVL	0.745	0.504	1.478	0.158
Brain	14	Latitude	0.723	0.836	0.865	0.407
		Altitude	-0.291	0.249	-1.167	0.270
		SVL	2.686	1.004	2.676	0.023

or latitudes among ten *B. andrewsi* populations (Zhao et al., 2019). Here we found that relative size of heart decreased with increasing latitude among 24 populations, which contrasted the Hesse's rule.

In anurans, the mass and glycogen contents of the livers display a positive correlation with altitudes and/or latitudes because more energy stores are related to more uncertain environments (McNamara and Houston, 1990;

Jönsson et al., 2009; Zhong et al., 2017). Consequently, the larger livers at higher altitudes and/or latitudes are expected to result from the more energy storage demands during hibernation and at post-hibernation emergence. Although individuals from higher altitudes and/or latitudes do not display relatively larger livers among 10 populations (Zhao et al., 2019), we found that individuals from higher latitudes had relatively larger livers in *B. andrewsi* based on the combined the new data and published data across all populations. This pattern suggested that individuals living at higher latitudes generally had more energy demands and intakes. Moreover, the lower temperatures and oxygen supply at higher altitudes can explain the smaller kidneys because of the overall lower metabolism (Tucker and Horvath, 1973). Consistent with the previous findings (Zhao et al., 2019), we did not find larger kidneys at higher altitudes and/or latitudes in this toad, which suggested that variations in kidney size cannot be explained by the oxygen supply.

Animals can adjust digestive tract morphology to adapt to food habits and quality under changing environments (Crump and Franklin, 2005; Naya and Bozinovic, 2006; Naya et al., 2009; Lou et al., 2013; Ma et al., 2016). Indeed, individuals at higher-altitude populations consuming greater plant materials exhibit longer gut than individuals at lower-altitude populations mainly predated on seeds in rats (Hansson, 1985; Hammond et al., 1999). For *B. spinulosus*, higher temperatures result in decreasing the animal-based food availability and increasing the plant-based foods (Naya et al., 2009). Meanwhile, there is a positive correlation between the length of the digestive tract and temperature among populations in *B. andrewsi* (Zhao et al., 2019). However, the digestive tract length was not correlated with altitude and/or latitude among 21 populations, suggesting that food habits with animal-based food availability in the toads for all populations did not affect variation in digestive tract length. We also did not find the relative size of lungs, gallbladder, and spleen increasing with altitude and/or latitude across populations.

In sum, our findings indicate that altitude and/or latitude do not affect the relative size of organs except for the heart and livers. Brain size variation cannot be explained by both the CBH and EBF. The increased latitude results in relatively smaller heart, which contrasts the prediction of the Hesse's rule. The larger livers in higher-latitude individuals suggest more energy demands and intakes due to slower metabolism. Temperature and rainfall within each site do not affect the relative size of heart and livers, suggesting that the other environmental factors such as oxygen supply is likely to shape variation in heart and livers.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was reviewed and approved by the animal study was reviewed and approved by China West Normal University. All experiments were performed by the relevant guidelines and regulations.

Author contributions

XZ, CC, and YJ participated in laboratory work, data analysis, and manuscript drafting. CC, LZ, and LJ conducted data analysis and visual representation of the data. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2022.972942/full#supplementary-material>

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