Received: 5 January 2023 | Revised: 18 June 2023 | Accepted: 21 June 2023
DOI: 10.1111/gcb.16860

RESEARCH ARTICLE

Global Change Biology WILEY

A global assessment of Bergmann's rule in mammals and birds

Jiekun He | Jiahao Tu | Jiehua Yu | Haisheng Jiang

Spatial Ecology Lab, School of Life Sciences, South China Normal University, Guangzhou, China

Correspondence
Jiekun He and Haisheng Jiang, Spatial Ecology Lab, School of Life Sciences, South China Normal University, 510631 Guangzhou, China.
Email: jiekunhe@m.scnu.edu.cn and jhs@scnu.edu.cn

Funding information
Guangdong Basic and Applied Basic Research Foundation, Grant/Award Number: 2023A1515011045; National Natural Science Foundation of China, Grant/Award Number: 31900324 and 32271733; Science and Technology Projects in Guangzhou, Grant/Award Number: 2023A04J0121

Abstract

Bergmann's rule states that endotherms have a large body size in high latitudes and cold climates. However, previous empirical studies have reported mixed evidence on the relationships between body size and latitude, raising the question of why some clades of endotherms follow Bergmann's rule, whereas others do not. Here, we synthesized the interspecific relationships between body size and latitude among 16,187 endothermic species (5422 mammals and 10,765 birds) using Bayesian phylogenetic generalized linear mixed models to examine the strength and magnitude of Bergmann's rule. We further assessed the effect of biological and ecological factors (i.e., body mass categories, dietary guild, winter activity, habitat openness, and climate zone) on the variations in the body mass–latitude relationships by adding an interaction term in the models. Our results revealed a generally weak but significant adherence to Bergmann's rule among all endotherms at the global scale. Despite taxonomic variation in the strength of Bergmann's rule, the body mass of species within most animal orders showed an increasing trend toward high latitudes. Generally, large-bodied, temperate species, non-hibernating mammals, and migratory and open-habitat birds tend to conform to Bergmann's rule more than their relatives do. Our results suggest that whether Bergmann's rule applies to a particular taxon is mediated by not only geographic and biological features, but also potential alternate strategies that species might have for thermoregulation. Future studies could explore the potential of integrating comprehensive trait data into phylogenetic comparative analysis to re-assess the classic ecogeographic rules on a global scale.

KEYWORDS
biogeography, body size, ecogeographic rule, endotherm, phylogenetic comparative analysis, thermoregulation

1 | INTRODUCTION

Naturalists have long noticed geographic variations in animal traits such as body size (Bergmann, 1847), color (Gloger, 1833), appendage size (Allen, 1877), range size (Rapoport, 1982), and clutch size (Lack, 1947). In endotherms, the tendency for body size to increase toward high latitudes and cold temperatures is an ecogeographic phenomenon known as Bergmann's rule (Bergmann, 1847; James, 1970; Mayr, 1956; Meiri, 2011; Pincheira-Donoso, 2010). This pattern was originally considered to be the result of better heat conservation in large species because they have lower surface-area-to-volume ratios (Mayr, 1956; Meiri, 2011), followed by other explanations involving phylogeny (Blackburn & Gaston, 1996), resource availability (Geist, 1987), and starvation resistance (Lindstedt & Boyce, 1985). Regardless of debatable explanatory mechanisms, Bergmann's rule has received revived interest in recent decades and

---

Jiekun He and Haisheng Jiang should be considered joint senior authors.

has been extensively assessed, both within and between species, among a range of taxa in multiple geographic regions (e.g., endothermic vertebrates: Alhajeri et al., 2020; Meiri & Dayan, 2003; Riemer et al., 2018; ectothermic vertebrates: Johnson et al., 2023; Slavenko et al., 2019; and invertebrates: Gérard et al., 2018; Shelomi, 2012).

Previous studies on latitudinal clines in body size following Bergmann's rule reported discrepant results. Empirical support for Bergmann's rule has been found in comparative studies within species (James, 1970; Romano et al., 2020), global interspecific analyses of mammals (Clauss et al., 2013) and birds (Olson et al., 2009), and at the assemblage level on a continental scale (Blackburn & Hawkins, 2004; Ramirez et al., 2008). Nevertheless, many exceptions have been reported (e.g., Gohli & Voje, 2016; Hendges et al., 2021; Riemer et al., 2018; Rodríguez et al., 2008). In addition, several meta-analyses revealed inconsistent patterns with regard to Bergmann's rule across species within a taxonomic group (Olson et al., 2009). For example, non-passerines showed higher conformity to Bergmann's rule than do passerines (Meiri & Dayan, 2003). For mammals, species among some orders (e.g., Chiroptera, Primates, and Artiodactyla) tend to have larger body sizes in colder climates (Clauss et al., 2013), whereas some lineages exhibit patterns in contrast to Bergmann's rule (Hendges et al., 2021). These variations in the relationships between body mass and latitude/temperature raise the question of why some clades of endothermic organisms follow Bergmann's rule, whereas others do not.

A range of biological and ecological factors likely influence the generality of Bergmann's rule. The heat conservation hypothesis predicts that small-bodied species would have weaker thermal conservation and, thus, should follow stronger latitude-body size clines than do their large-bodied relatives (Steudel et al., 1994). Nevertheless, empirical evidence demonstrated a reverse of this pattern (Freckleton et al., 2003) and revealed that conformity to Bergmann's rule may depend on life-history strategies, such as winter activity (e.g., migration, hibernation; Meiri & Dayan, 2003), nest design (Mainwaring & Street, 2021), and activity times (Feldman & Meiri, 2013; Hantak et al., 2021). For example, migratory birds and hibernating mammals would not show a pattern in accord with Bergmann's rule, because these inherent biological features might facilitate them to cope with extremely cold climates (Meiri & Dayan, 2003). Similarly, enclosed nesting birds and burrowing mammals can prevent heat dissipation by exploiting microclimate refugia rather than having larger body sizes (Mainwaring & Street, 2021; Mayr, 1956). This was indeed documented by Medina et al. (2007) for subterranean rodents of the genus Ctenomys. In addition, animal trophic levels might differentiate the strength of Bergmann's rule among species, owing to the latitudinal changes in the primary production of terrestrial communities and prey–predator relationships (Ho et al., 2010; Rodríguez et al., 2006).

Species may follow Bergmann's rule more strongly in specific environments and biogeographic contexts, in addition to biological effects. Compared to tropical species, temperate species are more exposed to environmental fluctuations, show a higher tendency to strengthen their ability to preserve body heat, and thus are more likely to conform to Bergmann's rule (Rodríguez et al., 2006, 2008). Moreover, the climate zone may interact with other factors, such as the "island rule" effect, in mediating the latitudinal clines in body size (Lomolino, 2005). For example, Benítez-López et al. (2021) documented a tendency of exacerbated gigantism and diminished dwarfism for both insular mammals and birds in response to the colder and harsher environments on islands. Body size–latitude relationships also likely vary across habitat types (Bro-Jørgensen, 2008), in which species living in dense habitats might show weaker conformity to Bergmann's rule than the open-habitat species owing to better heat conservation. Notably, the validity of Bergmann's rule is likely driven by multiple non-mutual exclusive factors from biology and biogeography, as several species traits highly covary with specific environments and biogeographic contexts (Sheard et al., 2020). To date, there is a lack of comprehensive assessment of how Bergmann's rule varies among different lineages of endotherms worldwide; in particular, how biological and ecological factors among taxa mediate the effects of latitude on body size remains unknown.

In this study, we used a comprehensive database of 16,187 endothermic species (5422 mammals and 10,765 birds) to assess whether interspecific variations in body mass follow predictions in accordance with Bergmann's rule. We focused on mammals and birds, as this rule was originally attributed to a thermoregulatory adaptation of homeotherms despite several assessments on ectothermic species. Specifically, we first tested Bergmann's rule using phylogenetic mixed-effects models to obtain the overall mean slopes of the body mass–latitude correlations across all mammal and bird species. Next, we assessed whether the strength of Bergmann's rule varies among endotherm orders, between metatherian and eutherian mammals, and between passerine and non-passerine birds. Finally, we used a series of phylogenetic mixed-effects models to examine the extent to which body mass–latitude relationships are influenced by biological and ecological factors (i.e., body mass categories, dietary guild, winter activity, habitat, and climate zone; Table S1).

2 | MATERIALS AND METHODS

2.1 | Body size, latitude, and temperature

Body mass was used as an index of body size, and we obtained the body mass for each species from the PHYLACINE 1.2 database for mammals (Faurby et al., 2018) and the AVONET database for birds (Tobias et al., 2022). These datasets were based largely on Dunning (2007) and Smith et al. (2003) for birds and mammals, respectively, with updates from primary and secondary literature sources. Given that the body mass values of some species (including 970 mammals and 868 birds) were not obtained originally from direct measurement of specimens or published sources but were instead estimated by morphologically similar correlates or phylogenetic imputation (Faurby et al., 2018; Tobias et al., 2022), we performed our analyses based on two alternative datasets (see Sensitivity analysis below). We standardized species taxonomy following the

International Union for Conservation of Nature (IUCN) Red List Version 2016-3 for mammals and obtained species geographic ranges from the present-natural range maps of the PHYLACINE 1.2 database (Faurby et al., 2018). For birds, species taxonomy and geographic ranges were extracted from BirdLife International and NatureServe (http://www.birdlife.org). We omitted predominately pelagic and marine species (e.g., mammals: pinnipeds, dugongs, and manatees; birds: albatrosses, alcids, and petrels) from the analyses because these groups exclusively feed and nest on marine ecosystems. We also excluded non-breeding migrants, and only considered areas where a species was native and resident or occurred regularly during the breeding season (i.e., breeding range). We tested the strength of Bergmann's rule by quantifying the relationships between the body mass of species and the latitude and temperature of their breeding ranges. The latitude of each species was calculated using the midpoint latitude of their breeding range polygon in a geographic information system (ArcInfo version 10.2, ESRI, 2013). The median temperature of each species was quantified by intersecting species breeding range with the mean annual temperature data (BIO1) from the WorldClim dataset at 2.5 arc min spatial resolution (version 2.0; Fick & Hijmans, 2017).

2.2 | Predictor variables

We compiled several biological and ecological factors (i.e., body mass categories, dietary guild, winter activity, habitat, and climate zone) for each species that have been hypothesized to cause variations in body size–latitude correlations (Dataset S1). Each species was classified as having a large, medium, or small body size when the mammals' body mass is <500, 500–5000, >5000 g and that of birds is <20, 20–500, >500 g, respectively. Dietary guilds of birds were obtained from Tobias et al. (2022), in which each species was subdivided into carnivores (≥70% of food resources by consuming invertebrates and/or vertebrates), herbivores (≥70% of food resources from plants), and omnivores (obtaining resources from multiple trophic levels). Following this classification, each species of mammal was classified as carnivores, herbivores, or omnivores based on the percentage of a species' diet (i.e., plant, vertebrate, and invertebrate) obtained from Faurby et al. (2018). We used the complete dataset (including 1540 species' diets that were estimated or inferred) because these coarse dietary categories can be accurately imputed phylogenetically (Faurby et al., 2018). Winter activity included hibernation in mammals and migratory behavior in birds, and both types of adaptations indicate species avoidance of adverse climatic conditions. Each mammal species was assigned to hibernation or not based on the COMBINE database (Soria et al., 2021) that was compiled from several studies. Hibernation is defined by bouts of inactivity lasting from some days to several weeks (Ruf & Geiser, 2015; Soria et al., 2021). The migratory behavior of birds was based on data from Tobias et al. (2022), and sedentary species were scored as non-migrant category, while all other species (including partially migratory and migratory) were scored as migrants. Habitat openness data of birds were extracted directly from Tobias et al. (2022), in which each species was scored as dense, semi-open, and open based on general habitat types extracted from literature, such as *Handbook of the Birds of the World*. To maximize consistency, the habitat openness of mammals was classified into four categories (dense, semi-open, open, and caves and subterranean) according to non-mutually exclusive binary habitat types obtained from the IUCN Red List database (http://www.iucnredlist.org). Dense habitats include forests; semi-open habitats include savannah and shrubland; and open habitats include grasslands, wetlands, rocky areas, and deserts. Any species belonging to a single habitat type or that with more than 50% of its habitat preference in one type and <50% in all others was classified as belonging to that major category. Each species was classified into either tropical or non-tropical species using the absolute midpoint latitude of its geographic range (cutoff set at 23.5°).

2.3 | Statistical analyses

To quantify the overall association between species' body mass and latitude and/or temperature, we fitted Bayesian phylogenetic generalized linear mixed models using the “MCMCglmm” package (Hadfield, 2010) in R (version 4.0.4; R Development Core Team, 2021). We fitted Bayesian models across the whole sample of species and two separate mammal and bird subsets, in which body mass was the response variable and the species' range absolute latitude midpoint or mean temperature was the predictor variable. The body mass was log10-transformed to improve linearity. To control for non-independence owing to shared ancestry among species, we included a phylogenetic covariance matrix as a random effect (Freckleton et al., 2002). The phylogenetic variance–covariance matrix was produced using the “vcv” function via the R package “phytools” (Revell, 2012), which contains the pairwise shared evolutionary history among species measured by branch lengths of the phylogenetic trees. The phylogenetic tree including all endothermic species was generated using the R package “V.PhyloMaker” (Jin & Qian, 2019). The backbone phylogenies were obtained from Upham et al. (2019) for mammals ($n=5911$) and Jetz et al. (2012) for birds ($n=9993$) using the Hackett constraint (http://vertlife.org/phylosubsets) for the posterior distribution of trees ($n=100$). The species that were not present in the backbone were randomly inserted into their relevant genera or families via the “phylo.maker” function.

To account for phylogenetic uncertainty, we performed models across a random sample of 100 phylogenetic trees and summarized the phylogenetically controlled slope estimates using mean values across these 100 models. We quantified the phylogenetic signal by estimating the heritability (h^2), which measures the proportion of residual variance attributable to phylogeny like Blomberg's K (Blomberg et al., 2003) or Pagel's λ (Pagel, 1999). The h^2 value varies from 0, indicating no phylogenetic effect and species can be treated as independent, to 1, indicating that similarity between species is directly proportional to their phylogenetic relationships (Freckleton et al., 2002). We specified a commonly implemented prior variance

(V) and degrees of freedom (nu) for the phylogenetic and residual variances ($V=1$, nu $=0.002$) following the recommendations in Hadfield (2010). We ran each model for 11,000 iterations with a burn-in (the number of initial MCMC iterations were discarded) of 1000 and a thinning interval of 100 to obtain an effective sample size of 1000 iterations and ensure adequate model convergence.

As Bergmann's rule was originally formulated to describe variations in body size among closely related species, we first fitted Bayesian phylogenetic mixed-effect models to calculate interspecific variations in body mass across latitudes within each genus and family. To ensure the feasibility of the body mass–latitude correlations, we used genera and families with more than 5, 10, and 30 species for this analysis. To test whether the strength of Bergman's rule differs among taxonomic groups, we performed models by adding animal order as an interaction term. Similarly, to investigate the effect of biological and ecological factors on the variations in the body mass–latitude relationships, we included an interaction term, allowing the slopes of body mass on latitude to vary between species with different body mass categories, dietary guild, winter activity, habitat openness, and climate zone (Mainwaring & Street, 2021).

We reported the means and 95% credible intervals of all parameters estimates from posterior distributions and considered the significance of the estimate if the 95% credible interval for the coefficient did not overlay with zero. We also reported pMCMC values for slope estimates to assess the probability of the slope being zero. The differences between pairwise predictor levels were determined using the Wilcoxon rank-sum test on the mean values of posterior slope estimates across 100 phylogenetic trees. The percentage of variance explained by the fixed effects (marginal R^2, R^2_m) and that by both the fixed and phylogenetic effects (conditional R^2, R^2_c) were calculated to assess the explained heterogeneity (Nakagawa & Schielzeth, 2013). The percentage of the remaining, nonphylogenetic variance explained by the fixed effects was calculated as $R^2_c/(1-(R^2_c-R^2_m))$.

2.4 | Sensitivity analysis

To test whether our results were robust, we performed sensitivity analyses with alternative datasets and categories of predictor variables, as well as different breakpoints of body size. First, our main dataset comprised all mammals and birds with body mass information to maximize taxonomic coverage. Alternatively, we only considered species whose body masses were obtained originally from direct measurements of specimens or published sources and excluded 947 and 833 species of mammals and birds, respectively, whose body masses were estimated by morphologically similar correlates or phylogenetic imputation. Second, we omitted the species with missing DNA data and repeated our analyses based on the subsets of phylogenies reconstructed by molecular data. For avian migratory information, we assessed whether our results shift if the partial migrants were included as non-migrants. We also obtained another scoring system for the migratory data from Dufour et al. (2020) to test whether different scoring systems influenced our results. Finally, as splitting species into different size classes might yield different results, we conducted sensitivity analyses of different breakpoints of body size. For mammals, species with body mass <100, 100–1000, and >1000 *g* were designated as “small,” “medium,” and “large,” respectively. For birds, species were designated as “small,” “medium,” and “large” if their body size is <50, 50–500, and >500 *g*, respectively.

3 | RESULTS

3.1 | Generality of Bergmann's rule

Our dataset comprised the body mass and breeding range latitude of 16,187 endothermic species, including 5422 terrestrial mammals and 10,765 birds (Dataset S1). Overall, the posterior mean slope estimates for body mass–latitude correlations were significantly positive for all endothermic species ($\beta=.0007$, 95% CI = [.0004, .0011], pMCMC < .001; Table 1), mammals ($\beta=.0009$, 95% CI = [.0000, .0017], pMCMC = .043), and birds ($\beta=.0007$, 95% CI = [.0004, .0010], pMCMC < .001). This result, combined with the significantly negative body mass–temperature correlations (all pMCMC < .001), supported the overall validity of Bergmann's rule in endotherms. The fixed effects of breeding range latitude and temperature explained a negligible amount of the variation in body mass (all $R^2_m < 1\%$), whereas the fixed effects combined with phylogenetic random effects explained the majority (all $R^2_c > 96\%$) of variances (Table 1). The high heritability of models (all $h^2 > 0.96$) indicated that most variations in body mass were explained by the ancestor descendant relationship. Latitude and temperature only accounted for 0.7% and 2.1%, respectively, of the non-phylogenetic variance for all endothermic species (Table 1). Sensitivity analysis, excluding species whose phylogenetic positions and body masses were imputed ($n=2128$ mammals and $n=4483$ birds), showed that the body mass increased with latitude ($\beta=.0009$; 95% CI = [.0005, .0012], pMCMC < .001) and decreased with breeding range temperature ($\beta=-.0027$; 95% CI = [−.0035, −.0019], pMCMC < .001; Table S2). This trend was also verified among mammals and birds, which corroborated our main results (compare Table 1 to Table S2).

3.2 | Taxonomic variations in Bergmann's rule

Phylogenetic and frequency distribution of the body mass–latitude relationships per genus showed that the strength of Bergmann's rule varied substantially among taxa (Figure 1). When testing body mass–latitude relationships within each genus with more than five species, 265 of 284 for mammals and 546 of 577 for birds were not significant ($p > .05$; Table S3). Positive body mass–latitude correlations were significant only within 13 mammalian and 17 avian genera, whereas

TABLE 1 Summary of statistics from Bayesian phylogenetic generalized linear mixed models predicting the body size by species range latitude or temperature.

Model	K	β	95% CI	pMCMC	R^2_m	R^2_c	Prop.Fixed	h^2
Latitude								
All	16,187	.0007	[0.0004, 0.0011]	<.001	.0001	.9836	.007	.9836
Mammals	5422	.0009	[0.0000, 0.0017]	.043	.0001	.9798	.007	.9798
Birds	10,765	.0007	[0.0004, 0.0010]	<.001	.0004	.9638	.012	.9638
Temperature								
All	16,187	−.0026	[−0.0033, −0.0019]	<.001	.0004	.9836	.021	.9836
Mammals	5422	−.0032	[−0.0049, −0.0016]	<.001	.0004	.9799	.022	.9799
Birds	10,765	−.0022	[−0.0029, −0.0016]	<.001	.0012	.9639	.031	.9638

Note: R^2_m (Marginal R^2) indicates the proportion of variation explained by fixed effects, and R^2_c (conditional R^2) indicates the proportion of variation explained by fixed and random effects. Prop.fixed indicates the proportion of non-phylogenetic variance explained by the fixed effects and was calculated as $R^2_m/(1-(R^2_c-R^2_m))$. h^2 (heritability) indicates the proportion of residual variance attributable to phylogenetic relationships.

Abbreviations: CI, credible interval; K, sample size; pMCMC, p values from Bayesian phylogenetic generalized linear mixed models; β, posterior mean slope estimates.

six mammalian and 14 avian genera showed a significantly negative correlation (Table S3). Similarly, among 240 body mass–latitude correlations within families, only 7.9% for mammals (7/89) and 6.6% for birds (10/151) were significantly positive (Table S3). Notably, sensitive analyses with larger sample sizes within each genus and family ($n \geq 10$ or $n \geq 30$) yielded more significantly positive body mass–latitude relationships (Table S3). For example, considering the species richness ≥30, the positive body mass–latitude correlations were significant among 17.7% of families (6/34) and 16.7% of genera (3/18) for mammals (Table S3).

When animal order was included as an interaction term in the models estimating body mass–latitude relationships, the fixed effects explained 43.9% and 54.3% of the total variance in body mass for mammals and birds (Table S4), respectively, indicating a substantial variation in Bergmann's rule among animal orders. The body mass of species within most orders showed an increasing trend toward higher latitude (Figure 2; Table S4). However, only a few animal orders significantly followed Bergmann's rule. For mammals, three (i.e., Cingulata, Cetartiodactyla, and Primates) of 15 examined orders showed significant adherence to Bergmann's rule. The largest order Rodentia showed a deviation from this rule, as its mean slope estimates and 95% credible interval overlapped marginally with zero ($\beta = .015$, 95% CI = [−.0001, .0030]; pMCMC = .064; Figure 2). Notably, the rodents showed marginally significant conformity to Bergmann's rule when the imputed species were excluded (Table S5; Figure S1). For birds, five of the 15 avian orders significantly followed the prediction of Bergmann's rule, including Galliformes, Pelecaniformes, Strigiformes, Accipitriformes, and Piciformes. The body mass within the largest group Passeriformes did not exhibit significant conformity to Bergmann's rule ($\beta = -.0001$, 95% CI = [−.0005, .0003]; pMCMC = .596; Figure 2). Of note, eutherian mammals and non-passerine birds showed significantly stronger adherence to Bergmann's rule than metatheria mammals and passerines, respectively (Wilcoxon rank-sum test, $p < .05$; Figures S2 and S3; Table S4).

3.3 | Predictors for Bergmann's rule

Results from a series of Bayesian models revealed that body mass emerged as a significant predictor underpinning the strength of Bergmann's rule for both mammals and birds (Figure 3; Tables S6 and S7). The posterior slope estimates for large-bodied species ($\beta = .0030$, 95% CI = [.0014, .0045] for mammals; $\beta = .0014$, 95% CI = [.0010, .0018] for birds) were significantly higher than those for medium- and small-bodied species (Wilcoxon rank sum test, $p < .05$; Figure 3). Sensitivity analysis conducted without imputed species (Figure S4; Tables S8 and S9) and with different breakpoints for designating body mass classes (Table S10) yielded consistent results. In addition, conformity to Bergmann's rule for non-tropical species ($\beta = .0031$, 95% CI = [.0013, .0049] for mammals; $\beta = .0011$, 95% CI = [.0004, .0018] for birds) was significantly stronger than that for tropical species ($\beta = .0000$, 95% CI = [−.0015, .0015] for mammals, and $\beta = -.0002$, 95% CI = [−.0008, .0004] for birds; $p < .05$; Figure 3; Tables S6 and S7).

Winter activity was also identified as an important predictor for Bergmann's rule (Figure 3). For mammals, the effect size of non-hibernating mammals was significantly positive with latitude ($\beta = .0015$, 95% CI = [.0003, .0027]), whereas that of hibernating species did not differ from zero ($\beta = .0045$, 95% CI = [−.0002, .0094]), with significant difference between these two predictor levels ($p < .05$; Figure 3; Table S6). Similarly, adherence to Bergmann's rule for migratory birds ($\beta = .0011$, 95% CI = [.0006, .0017]) was significantly stronger than that for non-migratory species ($\beta = .0007$, 95% CI = [.0003, .0011], $p < .05$; Figure 3; Table S7). This result was supported by the results of sensitivity analysis conducted based on two different scoring systems of migratory data (Table S11).

The effects of trophic level and habitat openness on the body mass–latitude relationships for birds differed from those for mammals (Figure 3). For example, conformity to Bergmann's rule was the strongest for open-habitat birds ($\beta = .0011$, 95% CI = [.0006,

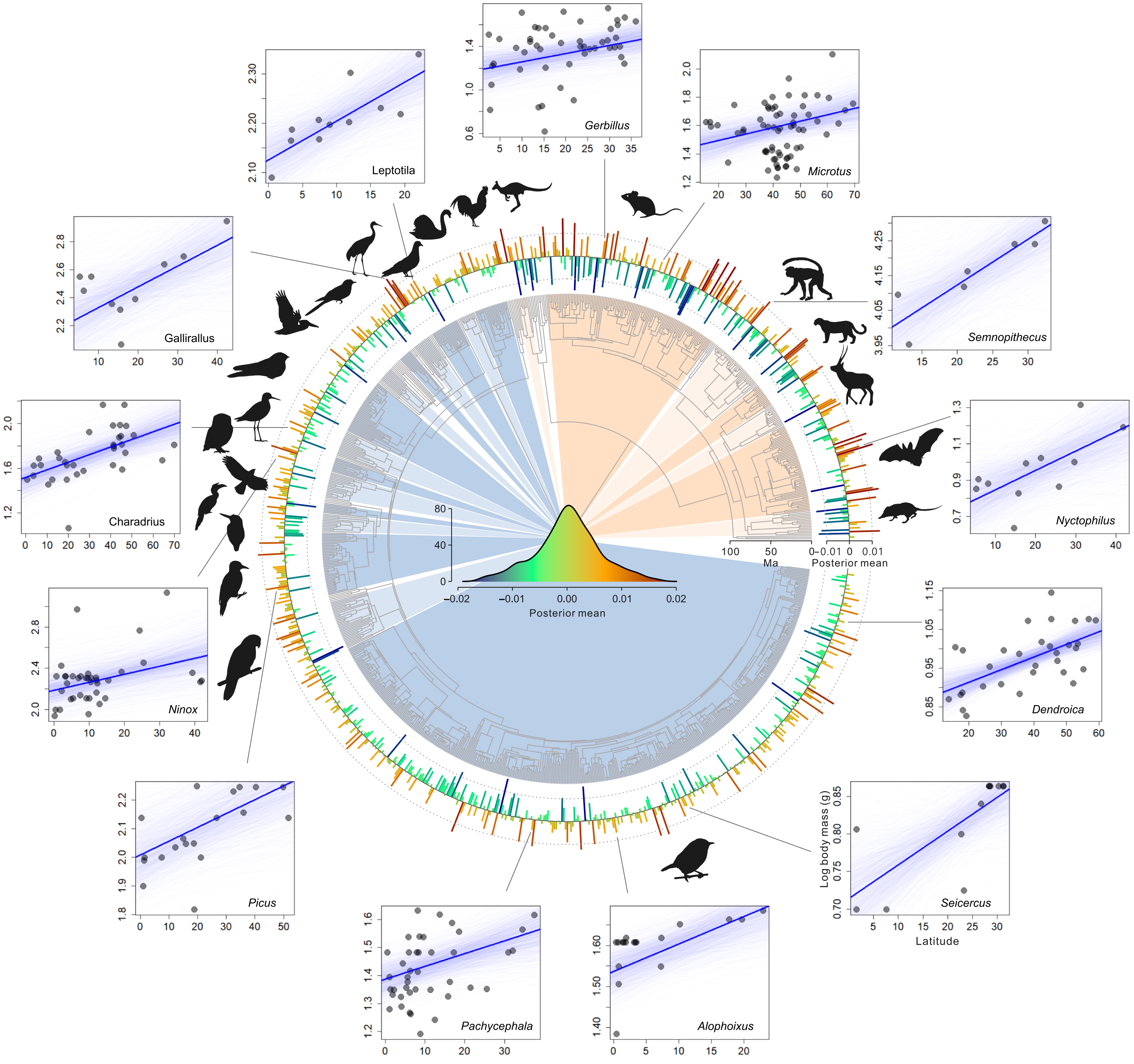

FIGURE 1 Phylogenetic distribution of body size–latitude relationships across mammals and birds. For each genus, posterior mean estimates of body mass–latitude relationships are represented by bar lengths and gradient colors at branch tips of the phylogenies. This phylogeny was generated using the R package "V.PhyloMaker" (Jin & Qian, 2019) based on the backbone of phylogenies from Upham et al. (2019) and Jetz et al. (2012) and was randomly drawn from 100 phylogenetic trees. The inset in the center of phylogeny shows the frequency distribution of posterior mean estimates of body mass–latitude relationships across each genus. The scatter plots show examples of the significant relationships between species body size ($\log_{10}$, g) and breeding range latitude midpoint from Bayesian phylogenetic generalized linear mixed models. Animal silhouettes for representative species in species-rich orders are shown and are downloaded from phylopic.org under public domain license.

.0017], pMCMC < .001), which tended to become weaker with decreasing habitat openness. For mammals, however, only the species living in dense habitats significantly followed this rule (β = .0015, 95% CI = [.0002, .0030], pMCMC < .05; Figure 3). Furthermore, the body sizes of both avian herbivores and carnivores tended to increase significantly toward high latitudes (both pMCMC < .05), whereas only those of herbivorous mammals significantly followed Bergmann's rule (β = .0020, 95% CI = [.0007, .0034], pMCMC < .01; Figure 3).

4 | DISCUSSION

By conducting a comprehensive interspecific comparison of the body mass–latitude correlations of nearly all species of mammals and birds, we documented weak support for Bergmann's rule. In total, 48.7–54.7% of body mass–latitude correlations within genera and 60.3–62.5% within families (considering different sample sizes) were positive, but only a fraction of them were statistically significant. After conducting Bayesian phylogenetic generalized linear mixed

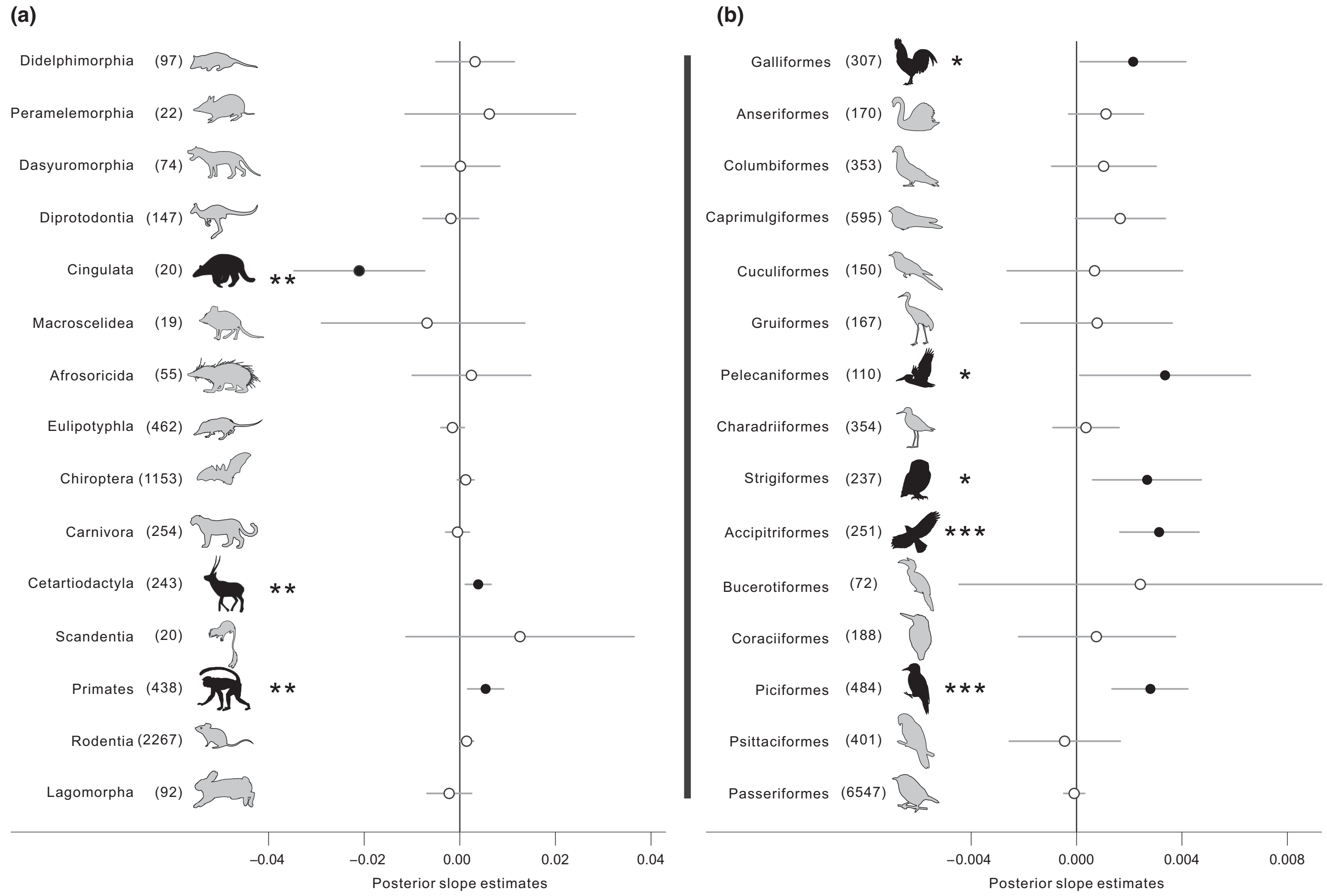

FIGURE 2 Posterior slope estimates for the body mass–latitude relationships within the main orders of mammals (a) and birds (b) derived from Bayesian phylogenetic generalized linear mixed models. Dots represent the mean slope estimates for the body mass–latitude correlations with 95% credible intervals. Animal silhouettes and dots in black indicate the significance level of slope estimate (*pMCMC < .05, **pMCMC < .01, and ***pMCMC < .001). The number of species included in each order is shown in parentheses. The solid line showing the location of posterior mean slope estimate equals zero.

models across all endothermic species to estimate the overall association, we observed a significant but weak tendency toward large body size in a high latitude for both mammals and birds. This finding is consistent with that of a previous meta-analysis on intraspecific comparisons (Riemer et al., 2018), as well as interspecific studies on mammals (Gohli & Voje, 2016) and birds (Olson et al., 2009). In contrast to previous studies supporting Bergmann's rule, this inconsistency may have resulted from at least three factors. First, many studies have tested the body size–latitude relationships in some particular taxonomic groups and/or biogeographic regions, and this sampling bias may obscure the generality of Bergmann's rule. Second, despite previous meta-analyses incorporating studies of multiple lineages, our understanding of the generality of Bergmann's rule may suffer from publication bias (Ashton & Feldman, 2003; Meiri et al., 2004), given that significant results are more likely to be accepted for publication. Third, previous global-scale studies tested whether the significant body size–latitude correlations were higher than 50% and relied on this statistical summary to determine the generality of Bergmann's rule (Riemer et al., 2018). To control for these biases, in this study, we incorporated a large database of nearly all endothermic species into a phylogenetic comparative framework, and our results provide a comprehensive view of how the generality of Bergmann's rule varies among endothermic organisms.

Our results confirmed that the strength of Bergmann's rule varied substantially not only among animal orders, but also between metatheria and eutheria and between passerines and non-passerines. This finding might partially explain why previous studies have yielded discrepant results that support or reject Bergmann's rule. For example, non-passerines tended to conform more strongly to the rule than passerines. This is in line with a previous intraspecies analysis by Meiri and Dayan (2003) and supports the physiological hypothesis that adverse climatic conditions acting upon non-passerines are stronger than those acting upon passerines, thus strengthening the adherence of non-passerine birds to Bergmann's rule (Kendeigh, 1969). Moreover, our results showed a high phylogenetic signal of the variation in body size, indicating that the interspecific variation in body mass was largely accounted for by the phylogeny. A previous study has suggested that the tendency to follow Bergmann's rule is likely ancestral and evolutionarily conserved for tetrapods (de Queiroz & Ashton, 2004), as evidenced by a broad range of metatherian mammals (e.g., kangaroos: Yom-Tov & Nix, 1986; koalas: Briscoe et al., 2015; and marsupials: Quin et al., 1996; Stobo-Wilson

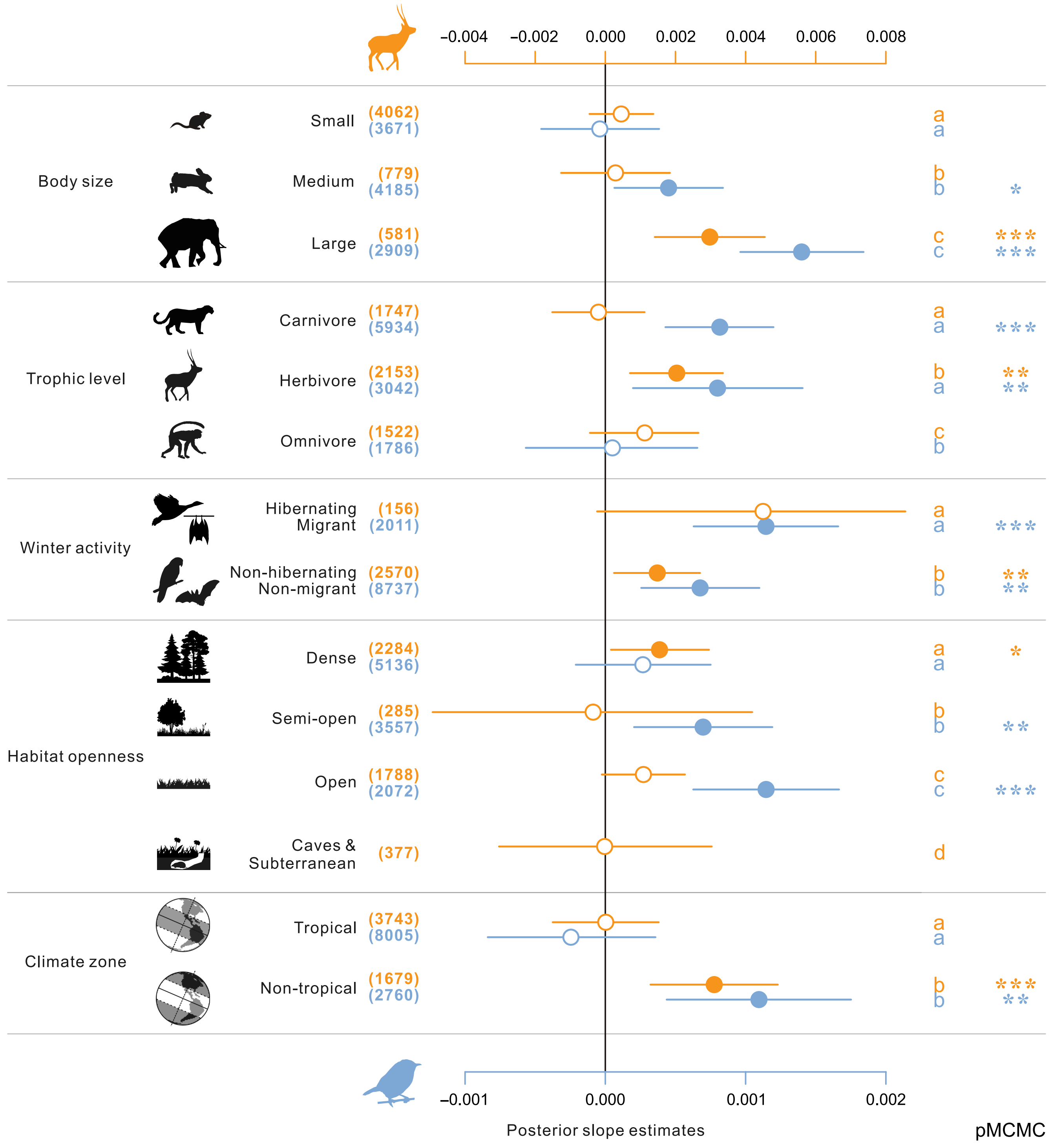

FIGURE 3 Posterior slope estimates of each predictor for the body mass–latitude relationships with 95% credible intervals. Filled dots indicate the significance level of the slope estimates (*pMCMC < .05, **pMCMC < .01, and ***pMCMC < .001). Letters indicate significant differences between levels among each predictor using Wilcoxon rank-sum test (*p* < .05). The sample size of each level of predictor is provided in parentheses. The solid line showing the location of the posterior mean slope estimate equals zero.

et al., 2020). Nevertheless, our results revealed that eutheria mammals exhibited stronger conformity to Bergmann's rule than metatherian mammals. This implies that whether a lineage follows Bergmann's rule may involve a trade-off between the deep origin of Bergmann's rule (de Queiroz & Ashton, 2004) and adaptation to current selective pressures (McNamara et al., 2016). Increasing body size is only one of the various strategies to cope with cold ambient climates. Adaptive strategies, specific habitats, and biogeographic history also play critical roles in mediating geographic variations in body size (Mainwaring & Street, 2021; Medina et al., 2007).

Our results revealed that temperate species followed Bergmann's rule more closely than tropical species. This supports the heat conservation hypothesis (Steudel et al., 1994), suggesting the need for more efficient heat conservation in cold climates during winter (Rodríguez et al., 2006); however, this demand is less prevalent in tropical species. Although our findings cannot be compared directly with those of previous studies on intraspecific comparisons (McNab, 1971; Meiri & Dayan, 2003) and species assemblages (Rodríguez et al., 2006, 2008), our results confirmed, based on the interspecific comparison, that Bergmann's rule is more evident at higher latitudes.

The heat conservation hypothesis also predicts that large species are likely to be less sensitive to cold climates than small species, because the former have lower critical temperatures in cold climates (Kendeigh, 1969). However, we observed that large species adhered to Bergmann's rule more strongly than small species, which contradicts the heat conservation hypothesis. Numerous empirical studies have also detected patterns that diverged from such a prediction (Ashton, 2002; Ashton et al., 2000; Freckleton et al., 2003), as evidenced by weak conformity to Bergmann's rule for some small-bodied species, such as passerines and rodents (Fourcade & Alhajeri, 2023; Meiri & Dayan, 2003). One possibility is that the body size of species is unevenly distributed globally and is disproportionately small at low latitudes (Harcourt & Schreier, 2009; Meiri & Thomas, 2007), which might weaken the effect of latitude on the body size of small-bodied species (Clauss et al., 2013). Another possibility is that large-bodied species have to enlarge their body sizes as an adaptive response to cold climates in high latitudes, whereas small-bodied species are more likely to be sheltered by microclimates (e.g., dense forest, caves/subterranean habitats) and/or adopt other strategies (e.g., hibernation, torpor) to cope with climatic extremes (Alhajeri & Steppan, 2016), thus obscuring the gradients of Bergmann's rule.

This explanation is enhanced by the fact that birds living in more open habitats tend to follow Bergmann's rule more strongly than those living in dense habitats. Selective pressures, such as climatic fluctuation and resource seasonality, tend to increase in open habitats, thereby making the body size of open-habitat birds more variable owing to thermoregulation in accordance with Bergmann's rule. Another piece of evidence is weak conformity to Bergmann's rule for mammals living in caves and subterranean environments, which aids burrowing species to adapt to climatic extremes by providing greater thermoregulatory benefits (Gohli & Voje, 2016; Medina et al., 2007; Rodríguez et al., 2006). Similar effects have also been documented in bird-invoked nest designs (Mainwaring & Street, 2021).

Winter activity emerged as an important predictor underlying the strength of Bergmann's rule. Mammals that exhibit specific winter behaviors (i.e., torpor and hibernation) can reduce their metabolic demands in response to extremely cold climates (Ruf & Geiser, 2015), and, thereby, would not benefit from better heat conservation by increasing their body size. A previous study found a lack of conformity to Bergmann's rule for many heteromyid rodents and attributed this to their winter behavior (Meiri & Dayan, 2003), which supports this hypothesis. Unexpectedly, we found that migratory birds showed stronger conformity to Bergmann's rule than sedentary species, which is in contrast to our prediction and that of a previous study (Mainwaring & Street, 2021; Meiri & Dayan, 2003). One putative explanation is that sedentary birds interact with other factors, such as inhabiting dense forests or living in the tropics, to buffer species against extreme climates and, therefore, mediate the effects of latitude on body size variations. Another possibility is that we only considered the breeding ranges of migratory birds that are always in higher latitudes. Although migratory species can escape adverse climates in high latitudes during non-breeding seasons, they would remain large-bodied to better limit heat loss in breeding areas (Henry et al., 2022).

This study had some limitations. First, we only focused on the effect of latitude and/or temperature on body size but did not evaluate whether the spatial variations in body size are related to resource limitation (Geist, 1987; Rosenzweig, 1968), starvation resistance (Lindstedt & Boyce, 1985), and water availability (Yom-Tov & Geffen, 2006). In addition, our findings depended on the inclusion of the hypothesized predictors examined. Other factors potentially mediate the strength of Bergmann's rule, such as social behavior (Ferguson & Larivière, 2008), nest structure (Mainwaring & Street, 2021; Martin et al., 2017), and predator–prey interactions (Ho et al., 2010); however, this is beyond the scope of our study. Second, our data on body mass were estimated by averaging across sexes and geographic populations. It should be noted that sexual size dimorphism may cause heterogeneity in Bergmann's rule, because males and females of the same species may have different latitudinal clines in body mass (Ashton, 2002). Moreover, given that sexual size dimorphism exhibits not only a global latitude trend, but also a strong phylogenetic signal (Friedman & Remeš, 2016), the true association between body size and latitude may be complicated. Similarly, using mean body size per species may be problematic, particularly for those with large intraspecific body size variations across space and time (Zheng et al., 2023). Unfortunately, we could not test Bergmann's rule on intraspecific and intersexual levels because the body mass of each individual was not available for a substantial number of species; thereby, our conclusions are limited to the interspecific comparison of Bergmann's rule.

Taken together, this study provides a global assessment of Bergmann's rule for a comprehensive group of endothermic species. We concluded that latitudinal clines in body size, which were compared within closely related species, received weak but significant support, in line with Bergmann's rule. The strength of Bergmann's rule varied among taxonomic groups, and depended on not only their biological traits, but also the climatic conditions inhabited by specific clades of endotherms. This finding can provide some implications for how species' body size would respond to global climate change (Gardner et al., 2011; Millien et al., 2006; Tian & Benton, 2020). For example, a decline in animal body size is among the most significant changes in light of future global warming (Dubiner & Meiri, 2022; Møller et al., 2018; Weeks et al., 2020). It can be expected that, based on our findings, such a size reduction is particularly intense for large-bodied and temperate species because of their stronger adherence to Bergmann's rule and rapid climatic warming at high latitudes (Intergovernmental Panel on

Climate Change, 2018). Furthermore, our finding that the latitudinal clines in body size, in accordance with Bergmann's rule, are mediated by species' traits and behavioral strategies suggests that a decline in body size would not necessarily be a universal phenomenon for endothermic species in response to global warming (Tian & Benton, 2020). Instead, they might also adapt to the changing thermal environments by adopting behavioral strategies (Beever et al., 2017) or shifting their geographic ranges (Rushing et al., 2020). Further studies should investigate the temporal variation in body size interaction with species' thermoregulatory characteristics to better understand the morphological, behavioral, and geographic responses of endothermic species to climate change. Our study demonstrated how the integration of species-level functional traits and phylogenetic mixed-effects models may provide deep insights into the generality of the interspecific form of classic ecogeographic rules on a global scale.

AUTHOR CONTRIBUTIONS

Jiekun He and Haisheng Jiang designed the research; Jiekun He, Jiahao Tu, and Jiehua Yu collected the data; Jiekun He and Haisheng Jiang performed the analyses; and Jiekun He and Haisheng Jiang wrote the first draft of the manuscript, with substantial contributions from all coauthors.

ACKNOWLEDGMENTS

We gratefully thank Meiri Shai and three anonymous reviewers for their reviews and insightful comments that significantly enhanced the earlier version of this manuscript. This work was supported by grants from the National Natural Science Foundation of China (grant no. 32271733; 31900324), Guangdong Basic and Applied Basic Research Foundation (grant no. 2023A1515011045), and Science and Technology Projects in Guangzhou (grant no. 2023A04J0121).

CONFLICT OF INTEREST STATEMENT

There are no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data regarding species geographic ranges, functional traits, phylogenetic trees, and relevant environmental variables were derived from different datasets, as described in the Materials and Methods section. The data that support the findings of this study are available in the supplementary material of this article and Dryad at https://doi.org/10.5061/dryad.fxpnvx0xq.

ORCID

Jiekun He https://orcid.org/0000-0001-9401-4208

Haisheng Jiang https://orcid.org/0000-0002-4793-1924

REFERENCES

Alhajeri, B. H., Porto, L. M., & Maestri, R. (2020). Habitat productivity is a poor predictor of body size in rodents. *Current Zoology*, *66*(2), 135–143. https://doi.org/10.1093/cz/zoz037

Alhajeri, B. H., & Steppan, S. J. (2016). Association between climate and body size in rodents: A phylogenetic test of Bergmann's rule. *Mammalian Biology*, *81*(2), 219–225. https://doi.org/10.1016/j.mambio.2015.12.001

Allen, J. A. (1877). The influence of physical conditions in the genesis of species. *Radical Review*, *1*, 108–140.

Ashton, K. G. (2002). Patterns of within-species body size variation of birds: Strong evidence for Bergmann's rule. *Global Ecology and Biogeography*, *11*(6), 505–523. https://doi.org/10.1046/j.1466-822X.2002.00313.x

Ashton, K. G., & Feldman, C. R. (2003). Bergmann's rule in nonavian reptiles: Turtles follow it, lizards and snakes reverse it. *Evolution*, *57*(5), 1151–1163. https://doi.org/10.1111/j.0014-3820.2003.tb00324.x

Ashton, K. G., Tracy, M. C., & de Queiroz, A. (2000). Is Bergmann's rule valid for mammals? *The American Naturalist*, *156*(4), 390–415. https://doi.org/10.1086/303400

Beever, E. A., Hall, L. E., Varner, J., Loosen, A. E., Dunham, J. B., Gahl, M. K., Smith, F. A., & Lawler, J. J. (2017). Behavioral flexibility as a mechanism for coping with climate change. *Frontiers in Ecology and the Environment*, *15*(6), 299–308. https://doi.org/10.1002/fee.1502

Benítez-López, A., Santini, L., Gallego-Zamorano, J., Mila, B., Walkden, P., Huijbregts, M. A. J., & Tobias, J. A. (2021). The island rule explains consistent patterns of body size evolution in terrestrial vertebrates. *Nature Ecology & Evolution*, *5*(6), 768–786. https://doi.org/10.1038/s41559-021-01426-y

Bergmann, C. (1847). *Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse* (Vol. 3). Göttinger Studien.

Blackburn, T. M., & Gaston, K. J. (1996). Spatial patterns in the body sizes of bird species in the New World. *Oikos*, *77*(3), 436–446. https://doi.org/10.2307/3545933

Blackburn, T. M., & Hawkins, B. A. (2004). Bergmann's rule and the mammal fauna of northern North America. *Ecography*, *27*(6), 715–724. https://doi.org/10.1111/j.0906-7590.2004.03999.x

Blomberg, S. P., Garland, T., & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution*, *57*(4), 717–745. https://doi.org/10.1111/j.0014-3820.2003.tb00285.x

Briscoe, N. J., Krockenberger, A., Handasyde, K. A., & Kearney, M. R. (2015). Bergmann meets Scholander: Geographical variation in body size and insulation in the koala is related to climate. *Journal of Biogeography*, *42*(4), 791–802. https://doi.org/10.1111/jbi.12445

Bro-Jørgensen, J. (2008). Dense habitats selecting for small body size: A comparative study on bovids. *Oikos*, *117*(5), 729–737. https://doi.org/10.1111/j.0030-1299.2008.16069.x

Clauss, M., Dittmann, M. T., Müller, D. W. H., Meloro, C., & Codron, D. (2013). Bergmann's rule in mammals: A cross-species interspecific pattern. *Oikos*, *122*(10), 1465–1472. https://doi.org/10.1111/j.1600-0706.2013.00463.x

de Queiroz, A., & Ashton, K. G. (2004). The phylogeny of a species-level tendency: Species heritability and possible deep origins of Bergmann's rule in tetrapods. *Evolution*, *58*(8), 1674–1684. https://doi.org/10.1111/j.0014-3820.2004.tb00453.x

Dubiner, S., & Meiri, S. (2022). Widespread recent changes in morphology of Old World birds, global warming the immediate suspect. *Global Ecology and Biogeography*, *31*(4), 791–801. https://doi.org/10.1111/geb.13474

Dufour, P., Descamps, S., Chantepie, S., Renaud, J., Guéguen, M., Schiffers, K., Thuiller, W., & Lavergne, S. (2020). Reconstructing the geographic and climatic origins of long-distance bird migrations. *Journal of Biogeography*, *47*(1), 155–166. https://doi.org/10.1111/jbi.13700

Dunning, J. B., Jr. (2007). *CRC handbook of avian body masses*. CRC press.

ESRI. (2013). *ArcGIS 10.2*. Environmental Systems Research Institute Inc., Redlands, CA.

Faurby, S., Davis, M., Pedersen, R. Ø., Schowanek, S. D., Antonelli, A., & Svenning, J.-C. (2018). PHYLACINE 1.2: The phylogenetic atlas of mammal macroecology. *Ecology*, *99*(11), 2626. https://doi.org/10.1002/ecy.2443

Feldman, A., & Meiri, S. (2013). Length–mass allometry in snakes. *Biological Journal of the Linnean Society*, *108*(1), 161–172. https://doi.org/10.1111/j.1095-8312.2012.02001.x

Ferguson, S. H., & Larivière, S. (2008). How social behaviour links environment and body size in mammalian carnivores. *The Open Ecology Journal*, *1*(1), 1–7. https://doi.org/10.2174/1874213000801010001

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315. https://doi.org/10.1002/joc.5086

Fourcade, Y., & Alhajeri, B. H. (2023). Environmental correlates of body size influence range size and extinction risk: A global study in rodents. *Global Ecology and Biogeography*, *32*(2), 206–217. https://doi.org/10.1111/geb.13622

Freckleton, R. P., Harvey, P. H., & Pagel, M. (2002). Phylogenetic analysis and comparative data: A test and review of evidence. *The American Naturalist*, *160*(6), 712–726. https://doi.org/10.1086/343873

Freckleton, R. P., Harvey, P. H., & Pagel, M. (2003). Bergmann's rule and body size in mammals. *The American Naturalist*, *161*(5), 821–825. https://doi.org/10.1086/374346

Friedman, N. R., & Remeš, V. (2016). Global geographic patterns of sexual size dimorphism in birds: Support for a latitudinal trend? *Ecography*, *39*(1), 17–25. https://doi.org/10.1111/ecog.01531

Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., & Heinsohn, R. (2011). Declining body size: A third universal response to warming? *Trends in Ecology & Evolution*, *26*(6), 285–291. https://doi.org/10.1016/j.tree.2011.03.005

Geist, V. (1987). Bergmann's rule is invalid. *Canadian Journal of Zoology*, *65*(4), 1035–1038. https://doi.org/10.1139/z87-164

Gérard, M., Vanderplanck, M., Franzen, M., Kuhlmann, M., Potts, S. G., Rasmont, P., Schweiger, O., & Michez, D. (2018). Patterns of size variation in bees at a continental scale: Does Bergmann's rule apply? *Oikos*, *127*(8), 1095–1103. https://doi.org/10.1111/oik.05260

Gloger, C. W. (1833). *Das Abändern der Vögel durch Einfluß des Klimas*. A. Schulz.

Gohli, J., & Voje, K. L. (2016). An interspecific assessment of Bergmann's rule in 22 mammalian families. *BMC Evolutionary Biology*, *16*(1), 1–12. https://doi.org/10.1186/s12862-016-0778-x

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, *33*(2), 1–22. https://doi.org/10.18637/jss.v033.i02

Hantak, M. M., McLean, B. S., Li, D., & Guralnick, R. P. (2021). Mammalian body size is determined by interactions between climate, urbanization, and ecological traits. *Communications Biology*, *4*(1), 972. https://doi.org/10.1038/s42003-021-02505-3

Harcourt, A. H., & Schreier, B. M. (2009). Diversity, body mass, and latitudinal gradients in primates. *International Journal of Primatology*, *30*(2), 283–300. https://doi.org/10.1007/s10764-009-9342-5

Hendges, C. D., Patterson, B. D., & Cáceres, N. C. (2021). Big in the tropics: Ecogeographical clines in peccary size reveal the converse of Bergmann's rule. *Journal of Biogeography*, *48*(5), 1228–1239. https://doi.org/10.1111/jbi.14073

Henry, E., Santini, L., Huijbregts, M. A. J., & Benítez-López, A. (2022). Unveiling the environmental drivers of intraspecific body size variation in terrestrial vertebrates. *Global Ecology and Biogeography*, *32*(2), 267–280. https://doi.org/10.1111/geb.13621

Ho, C. K., Pennings, S. C., & Carefoot, T. H. (2010). Is diet quality an overlooked mechanism for Bergmann's rule? *The American Naturalist*, *175*(2), 269–276. https://doi.org/10.1086/649583

Intergovernmental Panel on Climate Change. (2018). *Global Warming of 1.5°C (Vol. Special Report)*.

James, F. C. (1970). Geographic size variation in birds and its relationship to climate. *Ecology*, *51*(3), 365–390. https://doi.org/10.2307/1935374

Jetz, W., Thomas, G., Joy, J., Hartmann, K., & Mooers, A. (2012). The global diversity of birds in space and time. *Nature*, *491*(7424), 444–448. https://doi.org/10.1038/nature11631

Jin, Y., & Qian, H. (2019). V.PhyloMaker: An R package that can generate very large phylogenies for vascular plants. *Ecography*, *42*(8), 1353–1359. https://doi.org/10.1111/ecog.04434

Johnson, J. V., Finn, C., Guirguis, J., Goodyear, L. E. B., Harvey, L. P., Magee, R., Ron, S., & Pincheira-Donoso, D. (2023). What drives the evolution of body size in ectotherms? A global analysis across the amphibian tree of life. *Global Ecology and Biogeography*. https://doi.org/10.1111/geb.13696

Kendeigh, S. C. (1969). Tolerance of cold and Bergmann's rule. *The Auk*, *86*(1), 13–25. https://doi.org/10.2307/4083537

Lack, D. (1947). The significance of clutch-size. *Ibis*, *89*(2), 302–352. https://doi.org/10.1111/j.1474-919X.1947.tb04155.x

Lindstedt, S. L., & Boyce, M. S. (1985). Seasonality, fasting endurance, and body size in mammals. *The American Naturalist*, *125*(6), 873–878. https://doi.org/10.1086/284385

Lomolino, M. V. (2005). Body size evolution in insular vertebrates: Generality of the island rule. *Journal of Biogeography*, *32*(10), 1683–1699. https://doi.org/10.1111/j.1365-2699.2005.01314.x

Mainwaring, M. C., & Street, S. E. (2021). Conformity to Bergmann's rule in birds depends on nest design and migration. *Ecology and Evolution*, *11*(19), 13118–13127. https://doi.org/10.1002/ece3.8034

Martin, T. E., Boyce, A. J., Fierro-Calderón, K., Mitchell, A. E., Armstad, C. E., Mouton, J. C., & Bin Soudi, E. (2017). Enclosed nests may provide greater thermal than nest predation benefits compared with open nests across latitudes. *Functional Ecology*, *31*(6), 1231–1240. https://doi.org/10.1111/1365-2435.12819

Mayr, E. (1956). Geographical character gradients and climatic adaptation. *Evolution*, *10*(1), 105–108. https://doi.org/10.2307/2406103

McNab, B. K. (1971). On the ecological significance of Bergmann's rule. *Ecology*, *52*(5), 845–854. https://doi.org/10.2307/1936032

McNamara, J. M., Higginson, A. D., & Verhulst, S. (2016). The influence of the starvation-predation trade-off on the relationship between ambient temperature and body size among endotherms. *Journal of Biogeography*, *43*(4), 809–819. https://doi.org/10.1111/jbi.12695

Medina, A. I., Martí, D. A., & Bidau, C. J. (2007). Subterranean rodents of the genus Ctenomys (Caviomorpha, Ctenomyidae) follow the converse to Bergmann's rule. *Journal of Biogeography*, *34*(8), 1439–1454. https://doi.org/10.1111/j.1365-2699.2007.01708.x

Meiri, S. (2011). Bergmann's rule—What's in a name? *Global Ecology and Biogeography*, *20*(1), 203–207. https://doi.org/10.1111/j.1466-8238.2010.00577.x

Meiri, S., & Dayan, T. (2003). On the validity of Bergmann's rule. *Journal of Biogeography*, *30*(3), 331–351. https://doi.org/10.1046/j.1365-2699.2003.00837.x

Meiri, S., Dayan, T., & Simberloff, D. (2004). Carnivores, biases and Bergmann's rule. *Biological Journal of the Linnean Society*, *81*(4), 579–588. https://doi.org/10.1111/j.1095-8312.2004.00310.x

Meiri, S., & Thomas, G. H. (2007). The geography of body size—Challenges of the interspecific approach. *Global Ecology and Biogeography*, *16*(6), 689–693. https://doi.org/10.1111/j.1466-8238.2007.00343.x

Millien, V., Kathleen Lyons, S., Olson, L., Smith, F. A., Wilson, A. B., & Yom-Tov, Y. (2006). Ecotypic variation in the context of global climate change: Revisiting the rules. *Ecology Letters*, *9*(7), 853–869. https://doi.org/10.1111/j.1461-0248.2006.00928.x

Møller, A. P., Erritzoe, J., & van Dongen, S. (2018). Body size, developmental instability, and climate change. *Evolution*, *72*(10), 2049–2056. https://doi.org/10.1111/evo.13570

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Olson, V. A., Davies, R. G., Orme, C. D., Thomas, G. H., Meiri, S., Blackburn, T. M., Gaston, K. J., Owens, I. P., & Bennett, P. M. (2009). Global biogeography and ecology of body size in birds. *Ecology Letters*, *12*(3), 249–259. https://doi.org/10.1111/j.1461-0248.2009.01281.x

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, *401*(6756), 877–884. https://doi.org/10.1038/44766

Pincheira-Donoso, D. (2010). The balance between predictions and evidence and the search for universal macroecological patterns:

Taking Bergmann's rule back to its endothermic origin. *Theory in Biosciences*, *129*(4), 247–253. https://doi.org/10.1007/s12064-010-0101-0

Quin, D. G., Smith, A. P., & Norton, T. W. (1996). Eco-geographic variation in size and sexual dimorphism in sugar gliders and squirrel gliders (Marsupialia: Petauridae). *Australian Journal of Zoology*, *44*(1), 19–45. https://doi.org/10.1071/ZO9960019

R Development Core Team. (2021). *R: A language and environment for statistical computing*. R foundation for statistical computing.

Ramirez, L., Diniz-Filho, J. A. F., & Hawkins, B. A. (2008). Partitioning phylogenetic and adaptive components of the geographical body-size pattern of New World birds. *Global Ecology and Biogeography*, *17*(1), 100–110. https://doi.org/10.1111/j.1466-8238.2007.00346.x

Rapoport, E. H. (1982). *Areography: Geographical strategies of species* (Vol. 1). Pergamon Press.

Revell, L. J. (2012). Phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*(2), 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

Riemer, K., Guralnick, R. P., & White, E. P. (2018). No general relationship between mass and temperature in endothermic species. *eLife*, *7*, e27166. https://doi.org/10.7554/eLife.27166

Rodríguez, M. A., Lopez-Sanudo, I. L., & Hawkins, B. A. (2006). The geographic distribution of mammal body size in Europe. *Global Ecology and Biogeography*, *15*(2), 173–181. https://doi.org/10.1111/j.1466-822X.2006.00206.x

Rodríguez, M. Á., Olalla-Tárraga, M. Á., & Hawkins, B. A. (2008). Bergmann's rule and the geography of mammal body size in the Western hemisphere. *Global Ecology and Biogeography*, *17*(2), 274–283. https://doi.org/10.1111/j.1466-8238.2007.00363.x

Romano, A., Séchaud, R., & Roulin, A. (2020). Generalized evidence for Bergmann's rule: Body size variation in a cosmopolitan owl genus. *Journal of Biogeography*, *48*(1), 51–63. https://doi.org/10.1111/jbi.13981

Rosenzweig, M. L. (1968). The strategy of body size in mammalian carnivores. *American Midland Naturalist*, *80*(2), 299–315. https://doi.org/10.2307/2423529

Ruf, T., & Geiser, F. (2015). Daily torpor and hibernation in birds and mammals. *Biological Reviews*, *90*(3), 891–926. https://doi.org/10.1111/brv.12137

Rushing, C. S., Royle, J. A., Ziolkowski, D. J., Jr., & Pardieck, K. L. (2020). Migratory behavior and winter geography drive differential range shifts of eastern birds in response to recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(23), 12897–12903. https://doi.org/10.1073/pnas.2000299117

Sheard, C., Neate-Clegg, M. H. C., Alioravainen, N., Jones, S. E. I., Vincent, C., MacGregor, H. E. A., Bregman, T. P., Claramunt, S., & Tobias, J. A. (2020). Ecological drivers of global gradients in avian dispersal inferred from wing morphology. *Nature Communications*, *11*(1), 2463. https://doi.org/10.1038/s41467-020-16313-6

Shelomi, M. (2012). Where are we now? Bergmann's rule sensu lato in insects. *The American Naturalist*, *180*(4), 511–519. https://doi.org/10.1086/667595

Slavenko, A., Feldman, A., Allison, A., Bauer, A. M., Böhm, M., Chirio, L., Colli, G. R., Das, I., Doan, T. M., LeBreton, M., Martins, M., Meirte, D., Nagy, Z. T., Nogueira, C. C., Pauwels, O. S. G., Pincheira-Donoso, D., Roll, U., Wagner, P., Wang, Y., & Meiri, S. (2019). Global patterns of body size evolution in squamate reptiles are not driven by climate. *Global Ecology and Biogeography*, *28*(4), 471–483. https://doi.org/10.1111/geb.12868

Smith, F. A., Lyons, S. K., Ernest, S. K. M., Jones, K. E., Kaufman, D. M., Dayan, T., Marquet, P. A., Brown, J. H., & Haskell, J. P. (2003). Body mass of late quaternary mammals. *Ecology*, *84*(12), 3403. https://doi.org/10.1890/02-9003

Soria, C. D., Pacifici, M., Di Marco, M., Stephen, S. M., & Rondinini, C. (2021). COMBINE: A coalesced mammal database of intrinsic and extrinsic traits. *Ecology*, *102*(6), e03344. https://doi.org/10.1002/ecy.3344

Steudel, K., Porter, W., & Sher, D. (1994). The biophysics of Bergmann's rule: A comparison of the effects of pelage and body size variation on metabolic rate. *Canadian Journal of Zoology*, *72*(1), 70–77. https://doi.org/10.1139/z94-010

Stobo-Wilson, A. M., Cremona, T., Murphy, B. P., & Carthew, S. M. (2020). Geographic variation in body size of five Australian marsupials supports Bergmann's thermoregulation hypothesis. *Journal of Mammalogy*, *101*(4), 1010–1020. https://doi.org/10.1093/jmammal/gyaa046

Tian, L., & Benton, M. J. (2020). Predicting biotic responses to future climate warming with classic ecogeographic rules. *Current Biology*, *30*(13), R744–R749. https://doi.org/10.1016/j.cub.2020.06.003

Tobias, J. A., Sheard, C., Pigot, A. L., Devenish, A. J. M., Yang, J., Sayol, F., Neate-Clegg, M. H. C., Alioravainen, N., Weeks, T. L., Barber, R. A., Walkden, P. A., MacGregor, H. E. A., Jones, S. E. I., Vincent, C., Phillips, A. G., Marples, N. M., Montano-Centellas, F. A., Leandro-Silva, V., Claramunt, S., & Schleuning, M. (2022). AVONET: Morphological, ecological and geographical data for all birds. *Ecology Letters*, *25*(3), 581–597. https://doi.org/10.1111/ele.13898

Upham, N. S., Esselstyn, J. A., & Jetz, W. (2019). Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biology*, *17*(12), e3000494. https://doi.org/10.1371/journal.pbio.3000494

Weeks, B. C., Willard, D. E., Zimova, M., Ellis, A. A., Witynski, M. L., Hennen, M., & Winger, B. M. (2020). Shared morphological consequences of global warming in North American migratory birds. *Ecology Letters*, *23*(2), 316–325. https://doi.org/10.1111/ele.13434

Yom-Tov, Y., & Geffen, E. (2006). Geographic variation in body size: The effects of ambient temperature and precipitation. *Oecologia*, *148*(2), 213–218. https://doi.org/10.1007/s00442-006-0364-9

Yom-Tov, Y., & Nix, H. (1986). Climatological correlates for body size of five species of Australian mammals. *Biological Journal of the Linnean Society*, *29*(4), 245–262. https://doi.org/10.1111/j.1095-8312.1986.tb00278.x

Zheng, S., Hu, J., Ma, Z., Lindenmayer, D., & Liu, J. (2023). Increases in intraspecific body size variation are common among North American mammals and birds between 1880 and 2020. *Nature Ecology & Evolution*, *7*(3), 347–354. https://doi.org/10.1038/s41559-022-01967-w

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: He, J., Tu, J., Yu, J., & Jiang, H. (2023). A global assessment of Bergmann's rule in mammals and birds. *Global Change Biology*, *00*, 1–12. https://doi.org/10.1111/gcb.16860