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ROCKY RULE: THE IDIOSYNCRASY OF SPATIAL AND TEMPORAL SIZE VARIATION IN MAMMALS

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Mammals are predicted to vary in body size following Bergmann's rule, with individuals found at higher latitudes in colder temperatures being larger in size compared to conspecifics occurring at lower latitudes in warmer temperatures. Body size is similarly expected to vary temporally, with a decrease in size through time due to recent climate warming. While Bergmann's rule is well supported in mammals, there is increasing evidence of exceptions to the rule. Here, we present patterns of size variation in 17 North American mammal species using five morphological traits (condylobasal skull length, skull width, maxillary toothrow length, body weight, and head-and-body length) to determine if size varies predictably for each species in space and time. We found little support for a widespread Bergmannian pattern for these species at a broad spatial scale (across North America) and a contemporary temporal scale (the past 120 years). The effects of latitude or year on each trait were highly variable with three types of responses: an increase, a decrease, or no change in size across space or through time. Spatial size trends were detected more often than temporal size trends, as the temperature range was significantly larger in space than through time. Body weight (the most variable trait) and head-and-body length were more likely to conform to Bergmann's rule than craniodental measurements. We did not detect any changes in size variability with latitude, and our study species either increased or decreased in size variability over time. Our findings demonstrate that size variation in mammals is highly context dependent. As such, caution is needed when using rules of body size variation to predict the future response of species to climate warning—while valid in theory, it is likely too simplistic of an approach.

Key words: Bergmann's rule, body size, geographic variation, latitudinal gradient, mammals, morphology

INTRODUCTION

Recent climate warming has led to a cumulative increase in temperature of 0.835°C from the 1980s to 2019 (Shen et al. 2022). While organisms can tolerate environmental shifts, many species are responding to global warming by shifting or expanding their geographic range poleward (Hickling et al. 2006; Quintero and Wiens 2013; Roy-Dufresne et al. 2013; Coristine and Kerr 2015; Pacifici et al. 2017; Radchuk et al. 2019). Theory predicts that some Northern Hemisphere species might require a northward distributional shift of up to 20 kilometers per year to remain within their current fundamental thermal niche (Chen et al. 2011; McCain and King 2014; Coristine and Kerr 2015; Radchuk et al. 2019). However, species may also be able to tolerate significant environmental changes through phenotypic plasticity, local adaptation, or a combination of both (Chen et al. 2011; McCain and King 2014; Coristine and Kerr 2015; Radchuk et al. 2019). As such, studies on morphological size variation at the intraspecific level can reveal plasticity and adaptability, thereby identifying species most sensitive to climate change (Pergams and Lawler 2009; Radchuk et al. 2019; Chardon et al. 2020).

Bergmann's rule, one of the most studied ecogeographic patterns of size variation, describes predictable changes in body size of homeotherms, where species or genera in colder climates are larger in size than species or genera found in warmer climates (Bergmann 1847). Bergmann's explanation for such patterns was that larger-sized individuals have a larger surface-area-to-volume ratio, thereby limiting heat dissipation and improving heat preservation (Bergmann 1847). Yet, identification of the mechanism driving Bergmann's rule remains controversial (Blackburn et al. 1999; Shelomi & Zeuss 2017). Another source of contention surrounding Bergmann's rule is the taxonomic level at which it should apply. While Bergmann originally illustrated the rule with examples of size differences between species within genera, Bergmann's rule was later recast by Rensch (1938) and Mayr (1956) to apply to body size variation of individuals within a species, and much evidence for Bergmann's rule pertains to intraspecific variation of body size with latitude (as an implicit or explicit proxy for temperature).

Body size is also expected to vary similarly in direction and magnitude both across space and through time if the focal environmental factor such as temperature varies similarly across spatial and temporal scales (Millien et al. 2006; Gardner et al. 2011; Teplitsky and Millien 2014). As a result, a decrease in body size through time has been predicted to be a possible third response to climate warming, following changes in distribution and phenology (Gardner et al. 2011; Sheridan and Bickford 2011; Teplitsky and Millien 2014). Confirming this prediction, the warming climate was hypothesized to be a key driver of rapid morphological size changes in various rodent species across North America (Pergams and Ashley 1999; Pergams and Lacy 2008; Pergams and Lawler 2009; Holmes et al. 2016; Millien et al. 2017).

The general consensus is that measurements of morphological traits used as a proxy for overall body size conform to Bergmann's rule, with an increase in size with latitude and a decrease in size over time (e.g., Villar and Naya 2018). However, such conformity to Bergmann's rule both across space and over time may be the exception rather than the rule (Villar and Naya 2018). It has been proposed that such inconsistent patterns of size variation across space and over time stem from the significantly larger temperature gradient across latitudes (up to 35°C in some studies) compared to the recent increase in temperature observed over the past decades (La Sorte et al. 2014; Teplitsky and Millien 2014; Shen et al. 2022). Additionally, species occurring in the Northern Hemisphere and undergoing poleward range shifts may display increased levels of trait variability at high latitudes, towards the edge of their distribution (Naya et al. 2008; Aguilar-Kirigin and Naya 2013;

Forsman et al. 2016). Such increased variability in size may in turn modulate the response of a species to climate warming through phenotypic plasticity, local adaptation, or a combination of both. Finally, other factors such as food availability that vary with latitude may have a relatively larger effect on morphological traits related to resource acquisition than on overall body size (e.g., Millien et al. 2017).

Support for Bergmann's rule may also depend on the measurement used as a proxy for body size. Body weight is thought to comply with the expected size patterns more than other external or craniodental measurements, which may be due to lower rates of change in size for linear or craniodental metrics than for body weight, a cubic measure (Meiri and Dayan 2003; Teplitsky and Millien 2014). However, changes in the surface-area-to-volume ratio of an individual due to thermoregulatory shifts may have a greater impact on body weight than other two-dimensional or linear metrics (Yom-Tov and Geffen 2011; Teplitsky and Millien 2014).

While Bergmann's rule provides a theoretical framework for the study of size variation in mammals and their adaptation to climate warming, more and more exceptions are reported (Millien 2004; Soutu-Lima and Millien 2014; Sargis et al. 2018; Juman et al. 2022). Additional studies using empirical data are needed to tease apart the multiple drivers of size variation, especially in the context of climate warming. Here, we analyzed size variation using three craniodental measurements, body weight, and head-and-body length at a broad geographic scale (across North America) and a recent temporal scale (the past 120 years). Morphological traits were measured directly from museum specimens or retrieved from specimen tags from over 2,000 specimens of 17 North American mammal species. Our study is thus the first to combine a large empirical dataset with consistent data for multiple homeothermic species and phenotypic traits. We tested for widespread Bergmannian patterns of variation for these species with increases in size across space *or* decreases in size through time. Our work highlights the need for careful study design and sampling to limit biases when assessing size variation in mammals, as the complex mechanisms behind this variation are still not fully understood. Particular caution is warranted given the recent revival of Bergmann's rule as a tool to predict the response of mammal species to climate warming.

MATERIAL AND METHODS

Sample. —We sampled 17 North American mammal species belonging to five orders and nine families representing a wide range of body size. The study species included two shrews (*Blarina brevicauda*, *Sorex cinereus*), an opossum (*Didelphis virginiana*), three carnivorans (*Mephitis mephitis*, *Procyon lotor*, *Vulpes vulpes*), a lagomorph (*Sylvilagus floridanus*), and ten rodents (*Marmota monax*, *Tamias striatus*, *Tamiasciurus hudsonicus*, *Napaeozapus insignis*, *Zapus hudsonius*, *Microtus pennsylvanicus*, *Myodes gapperi*, *Peromyscus gossypinus*, *P. leucopus*, and *P. maniculatus*).

A total of 2,293 museum specimens were sampled from the Field Museum of Natural History (FMNH; *n* = 1,382), the Musée de la nature et des sciences de Sherbrooke (MS; *n* = 22), the Canadian Museum of Nature (CMN; *n* = 500), and the Redpath Museum (RM; *n* = 389). The sampled localities for specimens ranged from 16.62°N to 58.82°N latitude with collection years ranging from 1887 to 2017 (Supplementary Data SD1).

Specimens were selected from localities across North America including Quebec in Canada (*n* = 766) and 16 states of the United States (Florida, Georgia, Illinois, Indiana, Maine, Michigan, Minnesota, New York, North Carolina, Pennsylvania, South Carolina, Tennessee, Vermont, Virginia, West Virginia, and Wisconsin; *n* = 1,447). The distributions of six of the study species (*D. virginiana*, *M. mephitis*, *P. lotor*, *S. floridanus*, *P. leucopus*, *P. maniculatus*) extended into Mexico, for which a small sample of specimens was also included (*n* = 80). Most parts of the range of our study species were thus fully sampled. Data were lacking at the low latitudes of the distribution of some of our study species (e.g., *D. virginiana*, *P. lotor*, and *S. floridanus*), but consistent patterns of body size variation should be detectable both at the continental scale and within all parts of the species range.

We retrieved latitude and longitude data associated with each specimen from online museum catalogues or directly from specimen tags. When exact coordinates were lacking, we used locality names to extract the geographic coordinates using Google Earth (Google Inc 2017). Geographic coordinates were converted to latitude and longitude decimal degrees from the Universal Tranverse Mercator (UTM) system by using the Coordinate Conversion Tool from the West Virginia Department of Environmental Protection (2011) and from degrees, minutes, and seconds by the Geographic Unit Converter from Montana State University (2014).

We considered only adult specimens in our study. If the specimen tag indicated the specimen was a juvenile, it was removed from the dataset. Adults were identified based on the fusion of basicranial sutures of the skull and fully erupted molars (Martin et al. 2000). For cranial measurements and head-and-body length, adults with any reproductive condition remained in the dataset, as this condition should not affect these traits. However, to analyze body weight, only adults that were not recorded as lactating or pregnant were included.

Data acquisition.—We measured three craniodental measurements on each skull in mm using either calipers or digital capture (see below): (1) condylobasal length (CBL) was measured from the anterior points of the premaxilla anterior to the first incisors to the posterior surface of the occipital condyles along the midline of the ventral surface; (2) skull width (SW) was defined as the largest width of the skull, which was either the greatest distance between the outer margins of the zygomatic arches, or, in shrews, the greatest width measured at the level of the braincase; and (3) maxillary toothrow length (MTR) was defined as the alveolar length of the maxillary toothrow (Supplementary Data SD2; Martin et al. 2000; Sargis et al. 2018). MTR was measured on the left side of the maxilla unless broken or incomplete.

For *D. virginiana*, *M. mephitis*, *M. monax*, *P. lotor*, and *V. vulpes*, CBL and SW were measured using digital calipers (Mitutoyo Absolute Digimatic Caliper CD-6” CX) to the nearest 0.01 mm (Martin et al. 2000). To measure MTR, the calipers were placed from the anterior surface of the alveolus of the first premolar to the posterior surface of the alveolus of the last molar (Martin et al. 2000). For the remaining species, CBL, SW, and MTR were obtained using photographs taken with a Nikon D3100 with a macro lens (Nikon AS-F Micro Nikkor 85 mm 1:3.5 G). Skulls were photographed with a scale while lying dorsally flat with the occlusal surface of the molars parallel to the camera lens. Some specimens in the RM collection were photographed using a Lumenera Infinity 1 digital camera mounted on a Leica MS5 stereomicroscope. Using photographs, three pairs of endpoints associated with the craniodental measurements were digitized for each specimen on the ventral surface of the skull using the *digitize2d* function in the R package *geomorph* (Supplementary Data SD2, SD3; Adams et al. 2017). Distances between endpoints were calculated using the *interlmkdist* function (Adams et al. 2017) and converted into length measurements using the photographed scale. For each specimen, body weight (BW) and head-and-body length (HBL) were recorded from specimen tags (Appendix I). Several species had limited sample sizes for BW (n < 15), including *S. floridanus*, *D. virginiana*, *M. monax*, *M. mephitis*, *P. lotor*, and *V. vulpes*.

Data analysis

All statistical analyses were performed in R (R Core Team 2020).

Morphological variability.—All measurements were log-transformed. We investigated trait correlation across all study species using the *ggpairs* function in the GGally package (Schloerke et al. 2020). The overall amount of variability in each morphological trait of each species was evaluated using the coefficient of variation (CV) calculated as a percentage using the raster package (Hijmans 2017).

Sexual size dimorphism.—For each species, we then tested for the presence of sexual size dimorphism for each trait, while considering the effects of latitude and year using a linear model with Sex, Latitude, and Year as factors. We then ran post-hoc Tukey pairwise mean comparison tests using the *glht* function in the multcomp package, with single step *P*-value adjustments based on the *t* distribution of the linear function (Hothorn et al. 2008). If sexual dimorphism was detected for some traits in a species, all further analyses included Sex as a factor.

Latitudinal and temporal size variation.—For each species, we tested the effects of latitude and year on each of the five measurements. We ran linear models with Size as a response variable and Latitude, Year, Trait (a factor with five levels: CBL, SW, MTR, BW, HBL), and Sex as dependent variables. These models were not run for BW for six species due to small sample sizes ($n < 15$). We then ran post-hoc Tukey pairwise mean comparisons with multiplicity adjustment to compare the slopes of the size-latitude and size-time relations between traits using the *lsmeans* package (Lenth 2016). Finally, to test whether spatial and temporal variation were comparable in direction and magnitude, we checked for a significant interaction between Latitude and Year on each trait within each species and calculated the Pearson's product-moment correlation between the slopes of the size-latitude and size-time linear regressions.

Latitudinal and temporal trends in morphological variability.—We evaluated whether the amount of trait variability varied with latitude or over time by extracting the residual values from our models. Within each species, we tested for a significant relation between the absolute residuals and Latitude or Year for each trait.

Phylogenetic effect.—We tested for the presence of a phylogenetic signal in our data on spatial and temporal size variation. Using the TimeTree database (Kumar et al. 2017), we built a phylogenetic tree of the 17 species using the estimated date of divergence from one species to its closest relative among those being studied (Supplementary Data SD4). We then tested whether the species-level differences in the slopes of the latitudinal and temporal size trends may be the result of evolutionary history. The K statistic (Blomberg et al. 2003) and Pagel's λ (1999) were calculated using the *phylosig* function in the phytools package (Revell 2012) to estimate the phylogenetic signal in the slope coefficient from our linear models, with 1000 permutations to assess significance levels.

RESULTS

Morphological variability.—CV ranged from 1.0% to 15.3%, where BW had larger CV values than any other morphological traits that we measured (all $P < 0.001$; Supplementary Data SD3).

Sexual size dimorphism.—We found evidence of sexual size dimorphism in seven of the 17 species, with only 13 significant cases out of the 79 Tukey pairwise comparisons (Supplementary Data SD5). No sexual dimorphism was detected for BW for any of the species, while HBL was only larger in males for *S. cinereus*. The remaining 12 cases of sexual size dimorphism were for craniodental traits in seven species (Supplementary Data SD5). Overall, males tended to be larger than females (nine out of 12 significant cases), with exceptions in *S. cinereus* (SW and MTR) and *T. hudsonius* (MTR). As we detected sexual size dimorphism in over 40% of our species and traits, Sex was included as a factor in all further analyses.

Latitudinal size trends within species.—Overall, a significant effect on size of Latitude alone or in interaction with Trait was detected in all species except for *V. vulpes* and *P. gossypinus* (Table 1, Supplementary Data SD6). The interaction term between Latitude and Trait was significant in seven species, indicating that the latitudinal trend varied across traits within these species (Supplementary Data SD6). Over half of the species (10 out of 17) significantly changed in size with latitude independent of the morphological trait (Fig. 1). Overall, only 17 latitudinal size trends were significant, with an equal number of positive and negative trends (nine cases and eight cases, respectively). An increase in size with latitude was apparent in *B. brevicauda* (CBL, MTR, and BW), *T. striatus* (MTR), *N. insignis* (SW), *Z. hudsonius* (HBL), *M. pennsylvanicus* (BW), *P. leucopus* (BW), and *D. virginiana* (SW). A decrease in size with latitude was observed in five species: *M. monax* (CBL, SW, and MTR), *M. pennsylvanicus* (CBL and MTR), *P. leucopus* (HBL), *P. maniculatus* (HBL), and *M. mephitis* (HBL). Finally, significant latitudinal trends were more often detected for craniodental measurements (10 of 17 trends) than for BW and HBL.

Generally, latitudinal size variation was consistent across traits within species. However, we did detect some species-level discrepancies (e.g., *M. pennsylvanicus* and *P. leucopus*) across traits in the direction of the size change with latitude (Supplementary Data SD7). Supporting these findings, we found that the majority of post-hoc comparisons did not reveal any significant differences in the slope value of the size-latitude relations between traits (Supplementary Data SD8). A few exceptions were observed in *B. brevicauda*, *M. pennsylvanicus*, and *P. leucopus* for which BW increased relatively more (i.e., a steeper slope) than all other traits, as well as for *M. mephitis* and *P. leucopus*, for which HBL had a significantly smaller slope value than other morphological traits.

Temporal size trends within species.—We found a significant effect of Year in 15 out of 17 species (Table 1, Fig. 2), but the species differed in their pattern of temporal size variation. Out of the 79 trends, only 15 of them were significant, with 11 negative trends where size decreased over time and four positive trends where size increased over time (Fig. 2, Supplementary Data SD9). Interestingly, these significant relations were detected mostly in HBL and BW (13 of 15 trends). HBL decreased in seven species (*B. brevicauda*, *T. striatus*, *N. insignis*, *Z. hudsonius, M. gapperi*, *P. gossypinus*, and *P. maniculatus*), while BW decreased in *Z. hudsonius, M. gapperi*, and *P. leucopus* and MTR decreased in *M. pennsylvanicus*. We observed an increase in size over time in only a few cases: BW in *B. brevicauda,* CBL in *P. maniculatus*, and HBL in *P. lotor* and *V. vulpes*.

Here again, as for spatial variation, the traits within species that had a significantly different magnitude of temporal change (i.e., slope value) were BW and HBL compared to craniodental characters (Supplementary Data SD10).

Phylogenetic effect.—We evaluated the significance of phylogenetic constraints on the spatial and temporal slope values for each species. The K statistic was non-significant for all traits examined and the Pagel's λ was less than one and not different from zero in all analyses, indicating that there was no phylogenetic effect on latitudinal and temporal size variation in our study.

Comparison of the latitudinal and temporal size trends.— Overall, temporal trends were negative (mean temporal slope = -0.0003) and much weaker—by an order of magnitude—than spatial trends (mean latitudinal slope = 0.0015), but temporal and spatial trends were not significantly different (*t*-value = 1.160, $P = 0.250$). When considering all morphological traits and all species together, there was a significantly negative relation between the spatial and temporal slopes ($r = -0.319$, $P < 0.01$; Table 2). However, only two species displayed a significant increase in size with latitude together with a significant decrease in a given trait over time (HBL in *Z. hudsonius* and BW in *P. leucopus*). Results for the remaining species were ambiguous, due to the lack of significance in spatial (*M. gapperi*, *P. gossypinus, P. lotor*, and *V. vulpes*) or temporal (*M. monax, D. virginiana*, and *M. mephitis*) trends, or inconsistencies in the direction of trait size variation within species (*B. brevicauda, T. striatus*, *N. insignis*, *M. pennsylvanicus*, and *P. maniculatus*). We detected a significant negative correlation between the spatial and temporal slopes of SW for all the species together ($r = -0.580$, $P < 0.015$), but not for another trait (Table 2).

Latitudinal and temporal trends in morphological variability.—We did not detect any effect of Latitude on morphological variability estimated by the absolute value of the residuals from the linear models (Supplementary Data SD11). In general, this lack of significant increase or decrease in morphological variability with latitude held for all study species and analyzed traits. However, there was a significant effect of Latitude on the residuals of the HBL and latitude relation of *P. lotor* ($P < 0.05$).

Conversely, we found a significant effect of Year on the residual values in 18% or 14 of 79 cases, involving a total of nine species and all traits (Supplementary Data SD12). Morphological variability increased over time in *B. brevicauda* (HBL), *S. cinereus* (CBL, MTR, and BW), *T. hudsonicus* (SW), *M. gapperi* (HBL), *P. gossypinus* (HBL), *P. leucopus* (HBL), and *P. maniculatus* (HBL and BW). A decrease in variability over time was much less prevalent, and only observed in three species. For *V. vulpes*, we found decreased variability for CBL and MTR, although both trends were likely driven by a single specimen. A sampling bias is also likely for *P. maniculatus*, where CBL variability decreased over time contrasting the increased variability we observed for two other traits (HBL and BW) in this species. Lastly, MTR decreased in variability over time in *Z. hudsonius*.

DISCUSSION

We found little support for consistent spatial or temporal patterns of body size variation in 17 North American mammal species. Instead, the effects of latitude and year were highly variable and we detected all three possible types of size trends, including a size increase, a size decrease, or no change. More specifically, the direction and magnitude of body size trends differed between mammal species as well as between morphological traits for a given species. We detected significant spatial size trends more often than temporal size trends, as the temperature range was significantly larger across space than through time (La Sorte et al. 2014; Teplitsky and Millien 2014; Shen et al. 2022). We did not find changes in size variability with latitude, but variability increased or decreased over time in several species.

Body size has no universally accepted definition, although several size metrics such as craniodental measurements, HBL, and BW have routinely been used as proxies for body size in mammals (Kurtén 1967; Creighton 1980; Damuth and MacFadden 1990; Cuozzo 2001; Law et al. 2016; Schmidt et al. 2020; Theriot et al. 2022). However, studies on size variation using a single size metric may not accurately capture the variability in size of a species (Meiri and Dayan 2003; Teplitsky and Millien 2014). Alternatively, the first component extracted from ordination analyses such as Principal Component Analysis has often been used as a proxy for body size (McCoy et al. 2003; Björklund 2019). A drawback of using PC1 as a proxy for size to study size variation is that it only explains part of the variation in the overall "size" of individuals. More importantly, using PC1 assumes that each measured morphological trait varies at a similar rate across space or over time. Studies reviewing Bergmann's rule that used multiple morphological traits (including this study) have documented different size trends depending on the measured trait (Yom-Tov and Geffen 2011; Teplitsky and Millien 2014). Thus, the direction and magnitude of the spatial and temporal size trends of a species should be assessed simultaneously for multiple size metrics.

Additional sources of size variation are also often overlooked, downplayed, or dismissed. These can include sexual size dimorphism, simultaneous comparisons of distinct morphological traits, temporal variation (i.e., collection year in studies of spatial size trends), ontogenetic variation, or spatial variation (i.e., latitudinal or elevational range in studies of temporal size changes). If Bergmann's rule holds true across space and assuming its underlying mechanism is linked with temperature, it is predicted to similarly apply through time, with species expected to decrease in size with climate warming (Millien et al. 2006; Gardner et al. 2011; Sheridan and Bickford 2011; Teplitsky and Millien 2014). To further test the hypothesis that Bergmann's rule is valid over time and can then be used to predict species response to climate warming, we recommend the concurrent analysis of several traits, with the explicit and rigorous consideration of other potential sources of size variation such as those listed above.

Sexual size dimorphism.—Here, we detected sexual dimorphism in nearly half (41%) of our 17 study species. When significant, males were larger than females, with a few exceptions. Interestingly, we did not detect any sexual dimorphism for BW and found only one case of dimorphism in HBL, with the majority of cases being detected in craniodental measurements only.

Sexual size dimorphism was not prevalent in rodents, but we found significant dimorphism in two shrews (*B. brevicauda* and *S. cinereus*) and our three largest study species (*P. lotor*, *V. vulpes*, and *D. virginiana*). Most studies assessing sexual size dimorphism in rodents reported mixed results, likely because of reproductive seasonality (Townsend 1935; Dewsbury et al. 1980; Schulte-Hostedde 2008; Villar and Naya 2018; Heldstab 2021). Many studies on these two shrew species have found heterogeneous responses in the direction of sexual size dimorphism for different morphological traits (Guilday 1957; Choate 1972; Kirkland 1978; Kirkland and Hench 1980; Moncrief et al. 1982; van Zyll de Jong and Kirkland 1989; Innes et al. 1990; Yom-Tov and Yom-Tov 2005). Craniodental measurements in our three largest mammal species corroborated patterns of sexual dimorphism that have been consistently reported in previous studies (Allen 1901; Gardner 1973; Gingerich and Winkler 1979; Huson and Page 1979; Kennedy and Lindsay 1984; Dayan et al. 1989; Hell et al. 1989; Meiri et al. 2009a, 2009b; Astúa 2010; Gomes and Valente 2016). Given the prevalence of sexual size dimorphism we report here for a small sample of mammal species, studies on Bergmann's rule should thus account for sexual size dimorphism, as significant differences between the morphological traits of each sex could be skewing the pattern of size variation in space and time.

Latitudinal size trends.—We detected all three possible patterns of size variation with latitude (an increase, a decrease, or no changes in size). Most morphological traits (79%) that we considered in our study species did not vary with latitude. When significant spatial size trends were detected, they were either positive (11%) and increasing in size or negative (10%) and decreasing in size. These heterogeneous results reflect no clear support for predictable spatial size patterns, contrasting previous studies where up to 70% of the cases demonstrated an increase in size with latitude (Ashton and Tracy 2000; Meiri and Dayan 2003; Millien et al. 2006). For several study species, we only detected significant patterns of size variation in one of five morphological traits. In *D. virginiana*, only SW increased with latitude, similar to previous results reported for male opossums (Gardner 1973). Five other species changed in size with latitude for a single trait and either increased in size (*T. striatus*, *N. insignis*, and *Z. hudsonicus*) or decreased in size (*P. maniculatus* and *M. mephitis*). Though some of these trends are corroborated by previous studies (Drickamer and Bernstein 1972; Villar and Naya 2018), our results provide evidence for size-latitude relationships with divergent directions.

We found consistent latitudinal size trends across multiple morphological traits in only two study species—*B. blaricauda* and *M. monax*. For *B. brevicauda*, CBL, MTR, and BW increased with latitude, consistent with previous studies conducted on this species (Jones and Findley 1954; Guilday 1957; Jones and Glass 1960; Moncrief et al. 1982). However, decreases in body weight, skeletal, and cranial measurements have been previously detected at high latitudes for several shrew species, including *B. brevicauda* and *S. cinereus* (van Zyll de Jong 1976; Huggins and Kennedy 1989; Ochocińska and Taylor 2003; Yom-Tov and Yom-Tov 2005; Forsman et al. 2016; Naya et al. 2017). The heterogeneous response in the size of shrews may be related to the Dehnel phenomenon, which describes the seasonal and reversible changes in braincase size and body weight reported in several species of shrews and other small mammals (Dehnel 1949; Mezhzherin 1964; Ochocińska and Taylor 2003; Taylor et al. 2013; Lázaro et al. 2019; reviewed in Lázaro and Dechmann 2021). This seasonal decrease in size is thought to be a plastic adaptation to the upcoming winter conditions, allowing successful overwintering by providing an alternative strategy to hibernation or migration (Taylor et al. 2013; Lázaro et al. 2017; Lázaro et al. 2019). The time of capture or season may thus introduce a bias in studies of size variation for soricine shrews. For *M. monax*, CBL, MTR, and SW decreased with latitude. Only two studies on body weight and length have tested for a latitudinal size trend for this species (McNab 1971; Fenn et al. 2009), where a smaller body size at high latitudes was attributed to longer hibernation duration and shorter growing season (Zervanos et al. 2010, 2014). Neither study, however, provided any criteria used to classify individuals as "adult", and McNab (1971) did not provide a list of specimens examined.

Temporal size trends.—Overall, we found that changes in size over time were weaker, by an order of magnitude, than spatial size trends. A significant increase in size over time was apparent in only four of our study species, while another nine species decreased in size over time. For each of these species, the temporal size change was detected in only one of the five morphological traits we considered, with four exceptions (*B. brevicauda*, *M. gapperi*, *P. maniculatus*, and *Z. hudsonius*). Contrasting our finding on spatial size variation, temporal size trends were almost always detected in BW and HBL.

Adding to the growing empirical evidence for temporal size trends in mammals, our findings either confirmed previous results or opposed them. We observed temporal size trends in eight out of 10 rodent species included in our study, with HBL and BW all decreasing in size through time. Here again, some of the temporal size trends in rodents such as *M. pennsylvanicus*, *M. gapperi*, and *P. leucopus* were also reported in previous studies, yet this was not always the case, as with *P. gossypinus*, *N. insignis*, *T. striatus*, and *Z. hudsonius* (Pergams and Lawler 2009; Villar and Naya 2018). The key drivers of the rapid morphological changes previously documented in rodents were changes in human population density and temporal changes in climatic factors such as temperature or precipitation (Pergams and Lawler 2009). Two of the three carnivorans included in our dataset (*V. vulpes* and *P. lotor*) increased in HBL over time. A similar increase in body length over 50 years was found for red foxes in Israel (Yom-Tov 2003), whereas the body weight and length of male (but not female) foxes decreased over six years in Norway (Frafjord and Stevy 1998). These distinct temporal size trends for *V. vulpes* may be due to differences in resource availability across study locations and study timeframe. Increased body size over time in populations of foxes and raccoons may be related to an increased availability of food sources from proximity to anthropogenic food sources, absence of competition from larger predators, or cyclic abundances of prey, thereby fulfilling energy requirements and contributing to better body conditions (Frafjord and Stevy 1998; Yom-Tov 2003; Bateman and Fleming 2012).

Comparison of the latitudinal and temporal size trends. —Morphological changes in body size in mammals are often attributed to environmental factors that vary across space or in time, such as latitudinal temperature gradient or climate warming (Gardner et al. 2011; Sheridan and Bickford 2011; Teplitsky and Millien 2014). Therefore, body size is expected to increase with latitude in Northern Hemisphere species due to cooler temperatures and decrease through time due to warming temperatures (Millien et al. 2006). However, we found no clear evidence for such a congruence between spatial and temporal size variation. As in Teplitsky and Millien (2014), latitudinal patterns were more often detected and stronger—by an order of magnitude—than temporal patterns. Overall, size patterns in space and time were more often detected for BW and HBL than for craniodental measurements, especially for temporal changes. When species changed in size over the past 120 years, most of them decreased in size, although responses were heterogeneous, similar to findings from previous studies (Gardner et al. 2011; Sheridan and Bickford 2011; Teplitsky and Millien 2014).

Trait variability.—Intraspecific trait variability was much lower for craniodental than external measurements, as in Stephens et al. (2015). Larger variability in BW may be due to seasonal fluctuations, reproductive condition, time of measurement (pre- or post-mortem), health status of an individual, measurement error (see below), and—for the smallest mammals with high metabolic rates (e.g., shrews)—time since last meal (Meiri and Dayan 2003; Meiri and Thomas 2007; Yom-Tov and Geffen 2011; Stephens et al. 2015). Conversely, HBL and craniodental measurements are minimally affected by pregnancy and lactation (Meiri and Dayan 2003; Stephens et al. 2015; Villar and Naya 2018). The main weaknesses associated with using BW and HBL for studies on size variation include their non-replicability, the imprecision and variance of the measuring devices (e.g., traditional spring scales versus digital balances), and potentially high levels of intra- and inter-observer bias (Stephens et al. 2015; reviewed in Theriot et al. 2022). Therefore, the variability associated with BW and HBL may not provide a clear signal in species-level studies on size variation.

Size patterns and associated changes in morphological variability.—In general, we did not detect any increase in size variability with latitude, whereas over time, size variability increased in several of our study species. This discrepancy may arise from different rates of change in selective pressures driving size changes, or from differences in the strength and nature of this selection.

Unique phylogeographic histories related to distinct recolonization routes from refugia in North America during the Last Glacial Maximum may also affect species size variability, independent of latitude or the environment (Hayes and Harrison 1992; Brant and Ortí 2003; Rowe et al. 2006; Bhagwat and Willis 2008; Garcia-Elfring et al. 2017). With post-glacial recolonization, populations at high latitudes may possess decreased trait variability due to a genetic bottleneck (Excoffier et al. 2009; Garcia-Elfring et al. 2017; Nadeau and Urban 2019), affecting the ability of a species to adapt to climate warming (Excoffier et al. 2009; Garcia-Elfring et al. 2017; Nadeau and Urban 2019). The observed amount of trait variability of a species may be a proxy for its adaptability to local environmental changes across its distribution range (Blois et al. 2013). A species displaying no latitudinal size trend or limited trait variability within its range may be less constrained by its environment and have a greater tolerance of variation in its environmental conditions. Such species may therefore be more likely to change in size through plasticity or local adaptation (Reed and Frankham 2001; Hampe and Petit 2005). However, the ability of a species to rely on these mechanisms depends on the amount of variability existing across space or through time, as well as the rate of environmental change or its phylogeographic history.

Limitations of our study.—We did not account for the regional variation in climate change in our study, which is asymmetrical and spatially heterogeneous (Walther et al. 2002). Thermal patterns across altitudinal and latitudinal gradients can greatly differ (La Sorte et al. 2014; Verheyen et al. 2019). Although altitudinal gradients are more geographically restricted, greater temperature shifts may occur across small changes in elevation compared to much larger latitudinal distances (La Sorte et al. 2014; Verheyen et al. 2019). Therefore, species may demonstrate heterogeneous, non-linear variation in their morphology due to variable clinal differences in abiotic factors across their latitudinal and/or altitudinal ranges (Tingley et al. 2012; Pinsky et al. 2013; Verheyen et al. 2019). Changes in morphology may also be related to changes in vegetation and dietary shifts due to climate warming over time rather than a direct response to climate change (Caumul and Polly 2005; Millien et al. 2017; Gigliotti et al. 2020). In mammals, the selective pressures acting on cranial morphology (e.g., zygomatic arch and maxillary toothrow) and masticatory musculature have been linked to different chewing performances depending on the type of food processed (Cox et al. 2012; Millien et al. 2017; Grossnickle 2020).

Morphological changes may also be driven by interspecific competition between sympatric species sharing similar food resources (Millien 2004; Dayan and Simberloff 2005; Grant and Grant 2006; Bolnick et al. 2011; Stuart et al. 2014; Millien et al. 2017; Villar and Naya 2018) and their degree of specialization for these resources (e.g., Martinez et al. 2014). Phenotypically similar species are expected to experience increased levels of competition compared to those that are more dissimilar (Brown and Wilson 1956; MacArthur and Levins 1964; Pergams and Lawler 2009; Stuart and Losos 2013; Millien et al. 2017). One exception is mammal populations that may not experience similar levels of competition due to increased access to anthropogenic food resources or cyclically high abundances of prey (Frafjord and Stevy 1998; Yom-Tov 2003; Bateman and Fleming 2012).

Better knowledge of the current range-wide patterns of size variability in a given species may inform us on the nature of its response to climate warming, potentially affecting conservation efforts for vulnerable populations (Blois et al. 2013; Coristine and Kerr 2015; Razgour et al. 2019). However, the mechanisms driving size variation and variability in mammals are multiple (e.g., Juman et al. 2022). Here, we focused directly on latitude (and indirectly on those drivers associated with latitude), but the observed heterogeneity in patterns of size variation points to other mechanisms operating at a local scale and idiosyncratically across species. At this scale, size variation may be the result of phenotypic plasticity, local adaptation, or a combination of both (Pergams and Lacy 2008; Pergams and Lawler 2009). Not only are these mechanisms expected to act on size differently across species, but also across the morphological traits of an individual, making it even more challenging to disentangle these key components for species persistence with climate warming (de Villemereuil et al. 2018; Razgour et al. 2019; Chardon et al. 2020). Our study demonstrates that heterogeneity in size variation and variability across space and through time should be considered when assessing the sensitivity and future response of species to climate warming.

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CONFLICTS OF INTEREST

The authors declare they have no conflicts of interest.

AUTHOR CONTRIBUTIONS

KEC: Conceptualization (equal); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); visualization (lead); writing – original draft (lead); writing – review and editing (equal). LEO: Conceptualization (equal); supervision (supporting); writing – review and editing (equal). VM: Conceptualization (equal); formal analysis (supporting); methodology (supporting); supervision (lead); writing – review and editing (equal).

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DATA AVAILABILITY

Raw data measurements and accession numbers of the museum specimens are found in Supplementary Data SD1.

SUPPLEMENTARY DATA

Supplementary Data SD1.— List of specimens used in analyses on body size variation with accession numbers and raw data measurements. FMNH – Field Museum of Natural History; RM – Redpath Museum; MS – Musée de la nature et des sciences de Sherbrooke; CMN – Canadian Museum of Nature.

Supplementary Data SD2.— An example of the six landmarks recorded on the skull specimens of a (A) shrew species (*Sorex cinereus*, FMNH 172482) and a (B) rodent species (*Tamiasciurus hudsonicus*, CMN 19361). From these landmarks, three craniodental measurements were calculated: (1) the condylobasal length of the skull (CBL) as the distance between landmarks 1 and 2; (2) the skull width (SW) between landmarks 4 and 5; and (3) the maxillary toothrow length (MTR) between landmarks 5 and 6.

Supplementary Data SD3.— Summary statistics (mean, range, standard deviation, CV, and sample size) of all 5 morphological traits (CBL, SW, MTR, HBL, BW) for each study species. CBL = condylobasal length, SW = skull width, MTR = maxillary toothrow length, HBL = head-and-body length, and BW = body weight.

Supplementary Data SD4.— Phylogeny used to test for a phylogenetic signal. Using the TimeTree database, the topology and branch lengths in millions of years were obtained from estimates of the date of divergence from one species to its closest relative among those being studied (Kumar et al. 2017). Highlighted groups are of the different orders of the studied species (Rodentia, Carnivora, and Eulipotyphla).

Supplementary Data SD5.— Post-hoc Tukey pairwise mean comparisons with single-step *P*-value adjustments for sexual size dimorphism for each trait within species. Sexual dimorphism was only detected in 13 cases for head-and-body length (HBL), condylobasal length (CBL), skull width (SW), and maxillary toothrow length (MTR), but not for body weight (BW); * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

Supplementary Data SD6.— Main effect and interaction terms of the linear models for each species with Size as a response variable and Latitude, Year, Trait, and Sex as dependent variables; * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

Supplementary Data SD7. **—** Linear regressions of the latitudinal size trends (Latitude) of each species for each log-transformed morphological trait including condylobasal length (CBL), skull width (SW), maxillary toothrow length (MTR), head-and-body length (HBL), and body weight (BW). A total of 17 latitudinal size trends were significant; * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

Supplementary Data SD8.— Post-hoc Tukey pairwise mean comparisons with multiplicity adjustment comparing the slopes of the size-latitude relations between different pairs of morphological traits for each species; * $P \leq 0.05$, ** $P \leq 0.01$, and *** $P \leq 0.001$. CBL = condylobasal length, SW = skull width, MTR = maxillary toothrow length, HBL = head-and-body length, and BW = body weight.

Supplementary Data SD9. **—** Linear regressions of the temporal size trends (Year) of each species for each log-transformed morphological trait including condylobasal length (CBL), skull width (SW), maxillary toothrow length (MTR), head-and-body length (HBL), and body weight (BW). A total of 15 temporal size trends were significant; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Supplementary Data SD10.— Post-hoc Tukey pairwise mean comparisons with multiplicity adjustment comparing the slopes of the size-time relations between different pairs of morphological traits for each species; * $P \leq 0.05$, ** $P \leq 0.01$, and *** $P \leq 0.001$. CBL = condylobasal length, SW = skull width, MTR = maxillary toothrow length, HBL = head-and-body length, and BW = body weight.

Supplementary Data SD11.— Latitudinal trend in morphological variability estimated by the absolute residual values from the size-latitude linear models; * $P \leq 0.05$, ** $P \leq 0.01$, and *** $P \leq 0.001$. CBL = condylobasal length, SW = skull width, MTR = maxillary toothrow length, HBL = head-and-body length, and BW = body weight.

Supplementary Data SD12.— Temporal trend in morphological variability estimated by the absolute residual values from the size-time linear models; * $P \leq 0.05$, ** $P \leq 0.01$, and *** $P \leq 0.001$. CBL = condylobasal length, SW = skull width, MTR = maxillary toothrow length, HBL = head-and-body length, and BW = body weight.

LITERATURE CITED

Adams D., Collyer M., Kaliontzopoulou A., Sherratt E. 2017. Geomorph: software for geometric morphometric analyses. https://cran.r-project.org/package=geomorph.

Aguilar-Kirigin Á.J., Naya D.E. 2013. Latitudinal patterns in phenotypic plasticity: the case of seasonal flexibility in lizards' fat body size. Oecologia 173:745–752.

Allen J. 1901. A preliminary study of the North American opossums of the genus *Didelphis*. American Museum of Natural History, New York.

Ashton K.G., Tracy M.C. 2000. Is Bergmann's rule valid for mammals? The American Naturalist 156:390–415.

Astúa D. 2010. Cranial sexual dimorphism in New World marsupials and a test of Rensch's rule in Didelphidae. Journal of Mammalogy 91:1011–1024.

Bateman P.W., Fleming P.A. 2012. Big city life: carnivores in urban environments. Journal of Zoology 287:1–23.

Bergmann C. 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Göttinger Studien 3:595–708

Bhagwat S.A., Willis K.J. 2008. Species persistence in northerly glacial refugia of Europe: a matter of chance or biogeographical traits? Journal of Biogeography 35:464–482.

Björklund M. 2019. Be careful with your principal components. Evolution 73:2151–2158.

Blackburn T.M., Gaston, K.J., Loder N. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. Diversity and Distributions 5:165–174.

Blois J.L., Williams J.W., Fitzpatrick M.C., Jackson S.T., Ferrier S. 2013. Space can substitute for time in predicting climate-change effects on biodiversity. Proceedings of the National Academy of Sciences 110:9374–9379.

Blomberg S.P., Garland Jr T., Ives A.R. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57:717–745.

Bolnick D.I., Amarasekare P., Araújo M.S., Bürger R., Levine J.M., Novak M., Rudolf V.H.W., Schreiber S.J., Urban M.C., Vasseur D.A. 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology & Evolution 26:183–192.

Brant S.V., Ortí G. 2003. Phylogeography of the Northern short-tailed shrew, *Blarina brevicauda* (Insectivora: Soricidae): past fragmentation and postglacial recolonization. Molecular Ecology 12:1435–1449.

Brown W.L., Wilson E.O. 1956. Character displacement. Systematic Zoology 5:49–64.

Caumul R., Polly P.D. 2005. Phylogenetic and environmental components of morphological variation: skull, mandible, and molar shape in marmots (*Marmota*, Rodentia). Evolution 59:2460–2472.

Chardon N.I., Pironon S., Peterson M.L., Doak D.F. 2020. Incorporating intraspecific variation into species distribution models improves distribution predictions, but cannot predict species traits for a wide-spread plant species. Ecography 43:60–74.

Chen I.-C., Hill K., Ohlemüller R., Roy D.B., Thomas C.D. 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026.

Choate J.R. 1972. Variation within and among populations of the short-tailed shrew in Connecticut. Journal of Mammalogy 53:116–128.

Coristine L., Kerr J. 2015. Temperature-related geographical shifts among passerines: contrasting processes along poleward and equatorward range margins. Ecology and Evolution 5:5162–5176.

Cox P.G., Rayfield E.J., Fagan M.J., Herrel A., Pataky T.C., Jeffery N. 2012. Functional evolution of the feeding system in rodents. PLoS One 7:e36299.

Creighton G.K. 1980. Static allometry of mammalian teeth and the correlation of tooth size and body size in contemporary mammals. Journal of Zoology 191:435–443.

Cuozzo F.P. 2001. Craniodental body mass estimators in the dwarf bushbaby (*Galagoides*). American Journal of Physical Anthropology 115:187–190.

Damuth J., MacFadden B.J. 1990. Body size in mammalian paleobiology: estimation and biological implications. Cambridge University Press, Cambridge.

Dayan T., Simberloff D. 2005. Ecological and community-wide character displacement: the next generation. Ecology Letters 8:875–894.

Dayan T., Tchernov E., Yom-Tov Y., Simberloff D. 1989. Ecological character displacement in Saharo-Arabian *Vulpes*: outfoxing Bergmann's rule. Oikos 55:263–272.

de Villemereuil P., Mouterde M., Gaggiotti O.E., Till-Bottraud I. 2018. Patterns of phenotypic plasticity and local adaptation in the wide elevation range of the alpine plant *Arabis alpina*. Journal of Ecology 106:1952–1971.

Dehnel A. 1949. Studies on the genus *Sorex* L. Annales Universitatis Mariae Curie-Sklowdowska, Section C 4:18–102.

Dewsbury D.A., Baumgardner D.J., Evans R.L., Webster D.G. 1980. Sexual dimorphism for body mass in 13 taxa of muroid rodents under laboratory conditions. Journal of Mammalogy 61:146–149.

Drickamer L.C., Bernstein J. 1972. Growth in two subspecies of *Peromyscus maniculatus*. Journal of Mammalogy 53:228–231.

Excoffier L., Foll M., Petit R. 2009. Genetic consequences of range expansions. Annual Review of Ecology, Evolution, and Systematics 40:481–501.

Fenn A.M., Zervanos, S.M., Florant G.L. 2009. Energetic relationships between field and laboratory woodchucks (*Marmota monax*) along a latitudinal gradient. Ethology Ecology & Evolution 21:299–315.

Forsman A., Betzholtz P.-E., Franzén M. 2016. Faster poleward range shifts in moths with more variable colour patterns. Scientific Reports 6:36265.

Frafjord K., Stevy I. 1998. The red fox in Norway: morphological adaptation or random. Zeitschrift fur Saugetierkunde 63:16–25.

Garcia-Elfring A., Barrett R.D.H., Combs M., Davies T.J., Munshi-South J., Millien V. 2017. Admixture on the northern front: population genomics of range expansion in the white-footed mouse (*Peromyscus leucopus*) and secondary contact with the deer mouse (*Peromyscus maniculatus*). Heredity 119:447–458.

Gardner A. 1973. The systematics of the genus *Didelphis* (Marsupialia: Didelphidae) in North and Middle America. Special Publication fo the Museum Texas Tech University 4:1–81.

Gardner J.L., Peter A., Kearney M.R., Joseph L., Heinsohn R. 2011. Declining body size: a third universal response to warming? Trends in Ecology & Evolution 26:285–291.

Gigliotti L.C., Berg N.D., Boonstra R., Cleveland S.M., Diefenbach D.R. Gese E.M., Ivan J.S., Kielland K., Krebs C.J., Kumar A.V. et al. 2020. Latitudinal variation in snowshoe hare (*Lepus americanus*) body mass: a test of Bergmann's rule. Canadian Journal of Zoology 98:88–95.

Gingerich P.D., Winkler D.A. 1979. Patterns of variation and correlation in the dentition of the red fox, *Vulpes vulpes*. Journal of Mammalogy 60:691–704.

Gomes A.C., Valente A. 2016. Cranial and body size variation in the Iberian red fox (*Vulpes vulpes silacea*). Mammalian Biology 81:638–643.

Google LCC. 2022. Google Earth Pro V 7.3.6.934.

Grant P.R., Grant B.R. 2006. Evolution of character displacement in Darwin's finches. Science 313:224–226.

Grossnickle D.M. 2020. Feeding ecology has a stronger evolutionary influence on functional morphology than on body mass in mammals. Evolution 74:610–628.

Guilday J. 1957. Individual and geographic variation in *Blarina brevicauda* from Pennsylvania. Annals of the Carnegie Museum 35:41–68.

Hampe A., Petit R.J. 2005. Conserving biodiversity under climate change: the rear edge matters. Ecology Letters 8:461–467.

Hayes J.P., Harrison R.G. 1992. Variation in mitochondrial DNA and the biogeographic history of woodrats (*Neotoma*) of the Eastern United States. Systematic Biology 41:331–344.

Heldstab S.A. 2021. Latitude, life history and sexual size dimorphism correlate with reproductive seasonality in rodents. Mammal Review 51:256–271.

Hell P., Paule L., Sevcenko S., Danko S., Panigaj L., Vitaz V. 1989. Craniometrical investigation of the red fox (*Vulpes vulpes*) from the Slovak Carpathians and adjacent lowlands. Folia Zoologica 38:139–155.

Hickling R., Roy D.B., Hill J.K., Thomas C.D. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biology 12:450–455.

Hijmans R. 2017. Raster: geographic data analysis and modeling. https://cran.r-project.org/package=raster.

Holmes M.W., Boykins G.K.R., Bowie R.C.K., Lacey E.A. 2016. Cranial morphological variation in *Peromyscus maniculatus* over nearly a century of environmental change in three areas of California. Journal of Morphology 277:96–106.

Hothorn T., Bretz F., Westfall P. 2008. Simultaneous inference in general parametric models. Biometrical Journal 50:346–363.

Huggins J.A., Kennedy M.L. 1989. Morphologic variation in the masked shrew (*Sorex cinereus*) and the smoky shrew (*S. fumeus*). The American Midland Naturalist 122:11–25.

Huson L.W., Page R.J.C. 1979. A comparison of fox skulls from Wales and South-East England. Journal of Zoology 187:465–470.

Innes D.G.L., Bendell J.F., Naylor B.J., Smith B.A. 1990. High densities of the masked shrew, *Sorex cinereus,* in Jack Pine Plantations in Northern Ontario. The American Midland Naturalist 124:330–341.

Jones J.K., Findley J.S. 1954. Geographic distribution of the short-tailed shrew, *Blarina brevicauda*, in the Great Plains. Transactions of the Kansas Academy of Science (1903-) 57:208–211.

Jones J.K., Glass B.P. 1960. The short-tailed shrew, *Blarina brevicauda*, in Oklahoma. The Southwestern Naturalist 5:136–142.

Juman M., Millien V., Olson L.E.O., Sargis E.J. 2022. Recent and rapid ecogeographical rule reversals in Northern Treeshrews. Scientific Reports 12: 19689.

Kennedy M.L., Lindsay S.L. 1984. Morphological variation in the raccoon, *Procyon lotor*, and its relationship to genic and environmental variation. Journal of Mammalogy 65:195–205.

Kirkland G. 1978. The short-tailed shrew, *Blarina brevicauda* (Say), in the Central mountains of West Virginia. Proceedings of the Pennsylvania Academy of Science 52:126–130.

Kirkland G., Hench J. 1980. Notes on the small mammals of the Carbaugh Run Natural Area Adams County, Pennsylvania. Proceedings of the Pennsylvania Academy of Science 54:31–35.

Kumar S., Stecher G., Suleski M., Hedges S.B. 2017. TimeTree: a resource for timelines, timetrees, and divergence times. Molecular Biology and Evolution 34:1812–1819.

Kurtén B. 1967. Some quantitative approaches to dental microevolution. Journal of Dental Research 46:817–828.

La Sorte F.A., Butchart S.H.M., Jetz W., Böhning-Gaese K. 2014. Range-wide latitudinal and elevational temperature gradients for the world's terrestrial birds: implication under global climate change. PLoS One 9:e98361.

Law C.J., Young C., Mehta R.S. 2016. Ontogenetic scaling of theoretical bite force in Southern sea otters (*Enhydra lutris nereis*). Physiological and Biochemical Zoology: Ecological and Evolutionary Approaches 89:347–363.

Lázaro J., Dechmann D.K.N. 2021. Dehnel's phenomenon. Current Biology 31:R463-465.

Lázaro, J., Dechmann, D. K., LaPoint, S., Wikelski, M., Hertel, M. (2017). Profound reversible seasonal changes of individual skull size in a mammal. *Current Biology*, *27*(20), R1106-R1107.

Lázaro J., Hertel M., Muturi M., Dechmann D.K.N. 2019. Seasonal reversible size changes in the braincase and mass of common shrews are flexibly modified by environmental conditions. Scientific Reports 9:2489.

Lenth R.V. 2016. Least-squares means: The R package lsmeans. Journal of Statistical Software 69: 1-33.

MacArthur R., Levins R. 1964. Competition, habitat selection, and character displacement in a patchy environment. Proceedings of the National Academy of Sciences 51:1207–1210.

Martin R.E., Pine R.H., DeBlase A.F. 2000. A manual of mammalogy: with keys to families of the world. 3rd ed. McGraw Hill, Boston.

Martinez J.J., Millien V., Simone I., Priotto J.W. 2014. Ecological preference between generalist and specialist rodents: spatial and environmental correlates of phenotypic variation. Biological Journal of the Linnean Society 112: 180-203.

Mayr E. 1956. Geographic character gradients and climatic adaptation. Evolution 10:105–108.

McCain C.M., King S.R.B. 2014. Body size and activity times mediate mammalian responses to climate change. Global Change Biology 20:1760–1769.

McCoy K.D., Boulinier T., Tirard C., Michalakis Y. 2003. Host-dependent genetic structure of parasite populations: differential dispersal of seabird tick host races. Evolution 57:288–296.

McNab B.K. 1971. On the ecological significance of Bergmann's rule. Ecology 52:845–854.

Meiri S., Dayan T. 2003. On the validity of Bergmann's rule. Journal of Biogeography 30:331–351.

Meiri S., Dayan T., Simberloff D., Grenyer R. 2009a. Life on the edge: carnivore body size variation is all over the place. Proceedings of the Royal Society B: Biological Sciences 276:1469–1476.

Meiri S., Guy D., Dayan T., Simberloff D. 2009b. Global change and carnivore body size: data are stasis. Global Ecology and Biogeography 18:240–247.

Meiri S., Thomas G.H. 2007. The geography of body size – challenges of the interspecific approach. Global Ecology and Biogeography 16:689–693.

Mezhzherin V.A. 1964. Dehnel's phenomenon and its possible explanation. Acta Theriologica 8:95–114.

Millien V. 2004. Relative effects of climate change, isolation and competition on body size evolution in the Japanese field mouse *Apodemus argenteus*. Journal of Biogeography 31:1267-1276.

Millien V., Lyons S.K., 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 9:853–869.

Millien V., Ledevin R., Boué C., Gonzalez A. 2017. Rapid morphological divergence in two closely related and co-occurring species over the last 50 years. Evolutionary Ecology 31:847–864.

Moncrief N., Choate J., Genoways H. 1982. Morphometric and geographic relationships of short-tailed shrews (genus *Blarina*) in Kansas, Iowa, and Missouri. Annals of Carnegie Museum 51:157–180.

Montana State University - Yellowstone National Park Research Coordination Network. 2014. Lat/Lon and UTM conversion. http://rcn.montana.edu/resources/Converter.aspx.

Nadeau C.P., Urban M.C. 2019. Eco-evolution on the edge during climate change. Ecography 42:ecog.04404.

Naya D.E., Bozinovic F., Karasov W.H. 2008. Latitudinal trends in digestive flexibility: testing the climatic variability hypothesis with data on the intestinal length of rodents. The American Naturalist 172:E122–E134.

Naya D.E., Naya H., Cook J. 2017. Climate change and body size trends in aquatic and terrestrial endotherms: does habitat matter? PLoS One 12:e0183051.

Ochocińska D., Taylor J.R.E. 2003. Bergmann's rule in shrews: geographical variation of body size in Palearctic *Sorex* species. Biological Journal of the Linnean Society 78:365–381.

Pacifici M., Visconti P., Butchart S.H.M., Watson J.E.M., Cassola F.M., Rondinini C. 2017. Species' traits influenced their response to recent climate change. Nature Climate Change 7:205–208.

Pagel M. 1999. Inferring the historical patterns of biological evolution. Nature 401:877–884.

Pergams O.R.W., Ashley M.V. 1999. Rapid morphological change in Channel Island deer mice. Evolution 53:1573–1581.

Pergams O.R.W., Lacy R.C. 2008. Rapid morphological and genetic change in Chicago-area *Peromyscus*. Molecular Ecology 17:450–463.

Pergams O.R.W., Lawler J.J. 2009. Recent and widespread rapid morphological change in rodents. PLoS One 4:e6452.

Pinsky M.L., Worm B., Fogarty M.J., Sarmiento J.L., Levin S.A. 2013. Marine taxa track local climate velocities. Science 341:1239–1242.

Quintero I., Wiens J.J. 2013. Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. Ecology Letters 16:1095–1103.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Radchuk V., Reed T., Teplitsky C., van de Pol M., Charmantier A., Hassall C., Adamík P., Adriaensen F., Ahola M.P., Arcese P., et al. 2019. Adaptive responses of animals to climate change are most likely insufficient. Nature Communications 10:3109.

Razgour O., Forester B., Taggart J.B., Bekaert M., Juste J., Ibánez C., Puechmaille S.J., Novella-Fernandez R., Alberdi A., Manel S. 2019. Considering adaptive genetic variation in climate change vulnerability assessment reduces species range loss projections. Proceedings of the National Academy of Sciences 116:10418–10423.

Reed D.H., Frankham R. 2001. How closely correlated are molecular and quantitative measures of genetic variation? A meta-analysis. Evolution 55:1095–1103.

Rensch B. 1938. Some problems of geographical variation and species-formation. Proceedings of the Linnean Society of London 150:275–285.

Revell LJ. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3:217–223.

Rowe K.C., Heske E.J., Paige K.N. 2006. Comparative phylogeography of eastern chipmunks and white-footed mice in relation to the individualistic nature of species. Molecular Ecology 15:4003–4020.

Roy-Dufresne E., Logan T., Simon J.A., Chmura G.L., Millien V. 2013. Poleward expansion of the white-footed mouse (*Peromyscus leucopus*) under climate change: implications for the spread of Lyme disease. PLoS One 8:e80724.

Sargis E.J., Millien V., Woodman N., Olson L.E. 2018. Rule reversal: ecogeographical patterns of body size variation in the common treeshrew (Mammalia, Scandentia). Ecology and Evolution 8:1634–1645.

Schloerke B., Crowley J., Cook D., Briatte F., Marbach M., Thoen E., Elberg A., Larmarange J. 2020. GGally: extension to "ggplot2." https://CRAN.R-project.org/package=GGally.

Schmidt E., Fauteux D., Therrien J.-F., Gauthier G., Seyer Y. 2020. Improving diet assessment of Arctic terrestrial predators with the size of rodent mandibles. Journal of Zoology 311:23–32.

Schulte-Hostedde A. 2008. Sexual size dimorphism in rodents. In: J. Wolff & P. Sherman, editors. Rodent Societies: An Ecological and Evolutionary Perspective. University of Chicago Press, Chicago, Illinois; p. 115-128.

Shelomi M., Zeuss D. 2017. Bergmann's and Allen's rules in native European and Mediterranean Phasmatodea. Frontiers in Ecology and Evolution 5:25.

Shen B., Song S., Zhang L., Wang Z., Ren C., Li Y. 2022. Temperature trends in some major countries from the 1980s to 2019. Journal of Geographical Sciences 32:79–100.

Sheridan J.A., Bickford D. 2011. Shrinking body size as an ecological response to climate change. Nature Climate Change 1:401–406.

Souto-Lima R.B., Millien V. 2014. The influence of environmental factors on the morphology of red-backed voles *Myodes gapperi* (Rodentia, Arvicolinae) in Quebec and Western Labrador. Biological Journal of the Linnean Society 112: 204-218.

Stephens R.B., Karau K.H. Yahnke C.J., Wendt S.R., Rowe R.J. 2015. Dead mice can grow – variation of standard external mammal measurements from live and three postmortem body states. Journal of Mammalogy 96:185–193.

Stuart Y.E., Campbell T.S., Hohenlohe P.A., Reynolds R.G., Revell L.J., Losos J.B. 2014. Rapid evolution of a native species following invasion by a congener. Science 346:463–466.

Stuart Y.E., Losos J.B. 2013. Ecological character displacement: glass half full or half empty? Trends in Ecology & Evolution 28:402–408.

Taylor J.R.E., Rychlik L., Churchfield S. 2013. Winter reduction in body mass in a very small, nonhibernating mammal: consequences for heat loss and metabolic rates. Physiological and Biochemical Zoology 86:9–18.

Teplitsky C., Millien V. 2014. Climate warming and Bergmann's rule through time: is there any evidence? Evolutionary Applications 7:156–168.

Theriot M.K., Lanier H.C., Olson L.E. 2022. Harnessing natural history collections to detect trends in body-size change as a response to warming: A critique and review of best practices. Methods in Ecology and Evolution 00:1–13.

Tingley M.W., Koo M.S., Moritz C., Rush A.C., Beissinger S.R. 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. Global Change Biology 18:3279–3290.

Townsend M. 1935. Studies on some of the small mammals of Central New York. Wildlife Annals 4:6–120.

Villar C.H., Naya D.E. 2018. Climate change and temporal trends in body size: the case of rodents. Oikos 127:1186–1194.

Walther G.-R., Post E., Convey P., Menzel A., Parmesan C., Beebee T.J.C., Fromentin J.-M., Hoegh-Guldberg O., Bairlein F. 2002. Ecological responses to recent climate change. Nature 416:389–395.

West Virginia Department of Environmental Protection. 2011. Coordinate conversion and identification. http://tagis.dep.wv.gov/convert/.

Yom-Tov Y. 2003. Body sizes of carnivores commensal with humans have increased over the past 50 years. Functional Ecology 17:323–327.

Yom-Tov Y., Geffen E. 2011. Recent spatial and temporal changes in body size of terrestrial vertebrates: probable causes and pitfalls. Biological Reviews 86:531–541.

Yom-Tov Y., Yom-Tov J. 2005. Global warming, Bergmann’s rule and body size in the masked shrew *Sorex cinereus* Kerr in Alaska. Journal of Animal Ecology 74:803–808.

Zervanos S.M., Maher C.R., Florant G.L. 2014. Effects of body mass on hibernation strategies of woodchucks (*Marmota monax*). Integrative and Comparative Biology 54:443–451.

Zervanos S.M., Maher C.R., Waldvogel J.A., Florant G.L. 2010. Latitudinal differences in the hibernation characteristics of woodchucks (*Marmota monax*). Physiological and Biochemical Zoology 83:135–141.

van Zyll de Jong C. 1976. A comparison between woodland and tundra forms of the common shrew (*Sorex cinereus*). Canadian Journal of Zoology 54:963–973.

van Zyll de Jong C., Kirkland G.L. 1989. A morphometric analysis of the *Sorex cinereus* group in Central and Eastern North America. Journal of Mammalogy 70:110–122.

Verheyen J., Tüzün N., Stoks R. 2019. Using natural laboratories to study evolution to global warming: contrasting altitudinal, latitudinal, and urbanization gradients. Current Opinion in Insect Science 35:10-19.

FIGURE LEGENDS

Fig. 1.—Slope coefficients of the latitudinal size trends of each species for each log-transformed morphological trait including condylobasal length, skull width, maxillary toothrow length, head-and-body length, and body weight. A total of 17 size trends were significant, with nine positive trends and eight negative trends (* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$).

Fig. 2.—Slope coefficients of the temporal size trends of each species for each log-transformed morphological trait including condylobasal length, skull width, maxillary toothrow length, head-and-body length, and body weight. A total of 15 size trends were significant, with four positive trends and 11 negative trends (* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$).

TABLES

Table 1. — Coefficient values for the linear models with Size as a response variable and Latitude, Year, Trait, and Sex as factors; * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, ns $P > 0.05$.

Species	Latitude	Year	Trait	Sex
Blarina brevicauda	96.39***	246.88***	50278.08***	7.40**
Sorex cinereus	21.59***	468.73***	15433.90***	2.47$^{\text{ns}}$
Sylvilagus floridanus	180.99***	0.20$^{\text{ns}}$	7967.39***	0.18$^{\text{ns}}$
Marmota monax	116.91***	156.68***	7324.77***	0.00$^{\text{ns}}$
Tamias striatus	1508.15***	31.25***	34370.31***	1.05$^{\text{ns}}$
Tamiasciurus hudsonicus	24.56***	2178.21***	42795.09***	0.96$^{\text{ns}}$
Napaeozapus insignis	3.91*	1.57$^{\text{ns}}$	25411.41***	0.76$^{\text{ns}}$
Zapus hudsonius	179.34***	69.91***	10840.85***	0.10$^{\text{ns}}$
Microtus pennsylvanicus	41.47***	210.20***	15853.00***	0.04$^{\text{ns}}$
Myodes gapperi	126.43***	30.44***	16633.59***	2.72$^{\text{ns}}$
Peromyscus gossypinus	0.22$^{\text{ns}}$	57.12***	17660.36***	0.03$^{\text{ns}}$
Peromyscus leucopus	0.11$^{\text{ns}}$	76.05***	46756.33***	0.24$^{\text{ns}}$
Peromyscus maniculatus	79.54***	95.40***	33683.10***	1.14$^{\text{ns}}$
Didelphis virginiana	285.98***	144.48***	5019.71***	46.61***
Mephitis mephitis	244.46***	159.77***	8361.40***	0.01$^{\text{ns}}$
Procyon lotor	39.65***	33.41***	13763.16***	5.50*
Vulpes vulpes	0.63$^{\text{ns}}$	94.48***	7863.26***	24.21***

Table 2. —Mean comparisons test and Pearson correlations between the latitudinal and temporal size trends (slope values) for each morphological trait and overall; * $P \leq 0.05$, ** $P \leq 0.01$, ns $P > 0.05$. CBL = condylobasal length, SW = skull width, MTR = maxillary toothrow length, HBL = head-and-body length, and BW = body weight.

Trait	*t*-test statistic	Pearson's correlation coefficient (*r*)
CBL	-1.299 ^{ns}	-0.318 ^{ns}
SW	-2.760*	-0.580*
MTR	-1.060 ^{ns}	-0.264 ^{ns}
HBL	-1.935 ^{ns}	-0.447 ^{ns}
BW	-0.761^{ns}	-0.246 ^{ns}
All traits combined	-2.915**	-0.319**

Figure 1

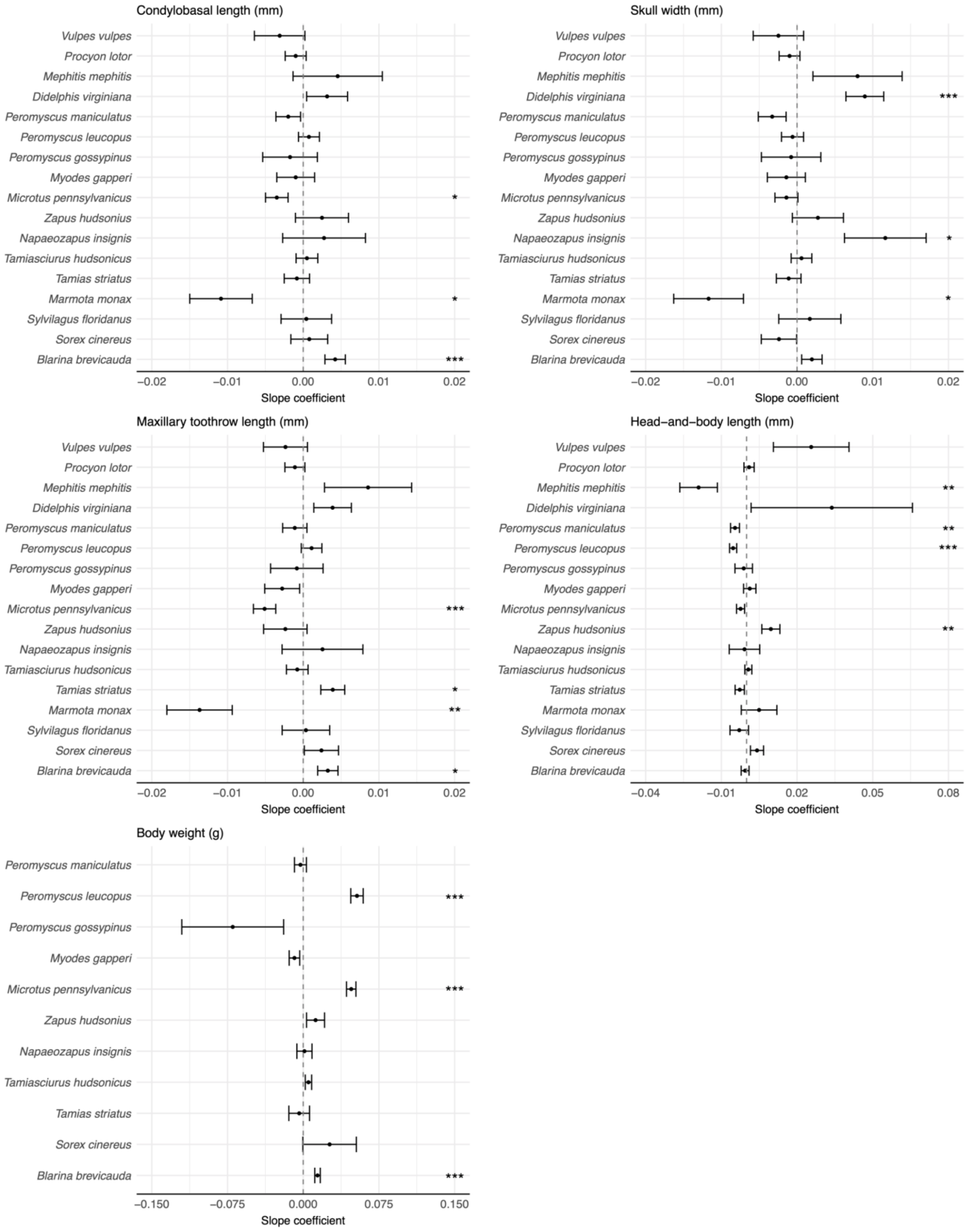
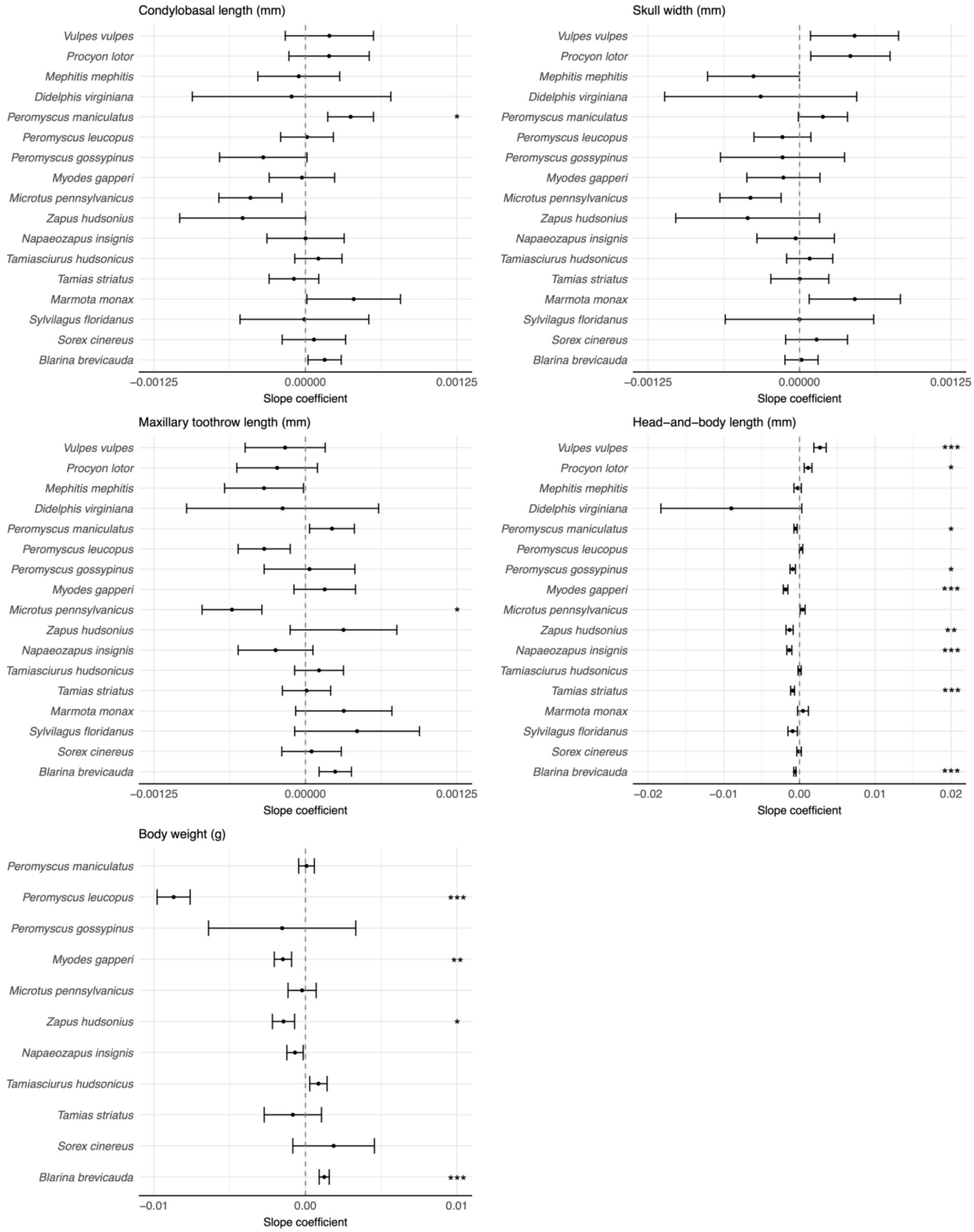

Condylobasal length (mm)
Vulpes vulpes
Procyon lotor
Mephitis mephitis
Didelphis virginiana
Peromyscus maniculatus
Peromyscus leucopus
Peromyscus gossypinus
Myodes gapperi
Microtus pennsylvanicus
*
Zapus hudsonius
Napaeozapus insignis
Tamiasciurus hudsonicus
Tamias striatus
Marmota monax
*
Sylvilagus floridanus
Sorex cinereus
Blarina brevicauda
***
−0.02
−0.01
0.00
0.01
0.02
Slope coefficient
Skull width (mm)
Vulpes vulpes
Procyon lotor
Mephitis mephitis
Didelphis virginiana
***
Peromyscus maniculatus
Peromyscus leucopus
Peromyscus gossypinus
Myodes gapperi
Microtus pennsylvanicus
Zapus hudsonius
Napaeozapus insignis
*
Tamiasciurus hudsonicus
Tamias striatus
Marmota monax
*
Sylvilagus floridanus
Sorex cinereus
Blarina brevicauda
−0.02
−0.01
0.00
0.01
0.02
Slope coefficient
Maxillary toothrow length (mm)
Vulpes vulpes
Procyon lotor
Mephitis mephitis
Didelphis virginiana
Peromyscus maniculatus
Peromyscus leucopus
Peromyscus gossypinus
Myodes gapperi
Microtus pennsylvanicus
***
Zapus hudsonius
Napaeozapus insignis
Tamiasciurus hudsonicus
Tamias striatus
*
Marmota monax
**
Sylvilagus floridanus
Sorex cinereus
Blarina brevicauda
*
−0.02
−0.01
0.00
0.01
0.02
Slope coefficient
Head−and−body length (mm)
Vulpes vulpes
Procyon lotor
Mephitis mephitis
**
Didelphis virginiana
Peromyscus maniculatus
**
Peromyscus leucopus
***
Peromyscus gossypinus
Myodes gapperi
Microtus pennsylvanicus
Zapus hudsonius
**
Napaeozapus insignis
Tamiasciurus hudsonicus
Tamias striatus
Marmota monax
Sylvilagus floridanus
Sorex cinereus
Blarina brevicauda
−0.04
−0.01
0.02
0.05
0.08
Slope coefficient
Body weight (g)
Peromyscus maniculatus
Peromyscus leucopus
***
Peromyscus gossypinus
Myodes gapperi
Microtus pennsylvanicus
***
Zapus hudsonius
Napaeozapus insignis
Tamiasciurus hudsonicus
Tamias striatus
Sorex cinereus
Blarina brevicauda
***
−0.150
−0.075
0.000
0.075
0.150
Slope coefficient

Figure 2


Condylobasal length (mm)
Vulpes vulpes
Procyon lotor
Mephitis mephitis
Didelphis virginiana
Peromyscus maniculatus *
Peromyscus leucopus
Peromyscus gossypinus
Myodes gapperi
Microtus pennsylvanicus
Zapus hudsonius
Napaeozapus insignis
Tamiasciurus hudsonicus
Tamias striatus
Marmota monax
Sylvilagus floridanus
Sorex cinereus
Blarina brevicauda
−0.00125
0.00000
0.00125
Slope coefficient
Skull width (mm)
Vulpes vulpes
Procyon lotor
Mephitis mephitis
Didelphis virginiana
Peromyscus maniculatus
Peromyscus leucopus
Peromyscus gossypinus
Myodes gapperi
Microtus pennsylvanicus
Zapus hudsonius
Napaeozapus insignis
Tamiasciurus hudsonicus
Tamias striatus
Marmota monax
Sylvilagus floridanus
Sorex cinereus
Blarina brevicauda
−0.00125
0.00000
0.00125
Slope coefficient
Maxillary toothrow length (mm)
Vulpes vulpes
Procyon lotor
Mephitis mephitis
Didelphis virginiana
Peromyscus maniculatus
Peromyscus leucopus
Peromyscus gossypinus
Myodes gapperi
Microtus pennsylvanicus *
Zapus hudsonius
Napaeozapus insignis
Tamiasciurus hudsonicus
Tamias striatus
Marmota monax
Sylvilagus floridanus
Sorex cinereus
Blarina brevicauda
−0.00125
0.00000
0.00125
Slope coefficient
Head−and−body length (mm)
Vulpes vulpes ***
Procyon lotor *
Mephitis mephitis
Didelphis virginiana
Peromyscus maniculatus *
Peromyscus leucopus
Peromyscus gossypinus *
Myodes gapperi ***
Microtus pennsylvanicus
Zapus hudsonius **
Napaeozapus insignis ***
Tamiasciurus hudsonicus
Tamias striatus ***
Marmota monax
Sylvilagus floridanus
Sorex cinereus
Blarina brevicauda ***
−0.02
−0.01
0.00
0.01
0.02
Slope coefficient
Body weight (g)
Peromyscus maniculatus
Peromyscus leucopus ***
Peromyscus gossypinus
Myodes gapperi **
Microtus pennsylvanicus
Zapus hudsonius *
Napaeozapus insignis
Tamiasciurus hudsonicus
Tamias striatus
Sorex cinereus
Blarina brevicauda ***
−0.01
0.00
0.01
Slope coefficient