










RESEARCH ARTICLE

Environmental drivers of body size in North American bats

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Abstract

1. Bergmann's rule—which posits that larger animals live in colder areas—is thought to influence variation in body size within species across space and time, but evidence for this claim is mixed.
2. We used Bayesian hierarchical models to test four competing hypotheses for spatiotemporal variation in body size within 20 bat species across North America: (1) the heat conservation hypothesis, which posits that increased body size facilitates body heat conservation (and which is the traditional explanation for the mechanism underlying Bergmann's rule); (2) the heat mortality hypothesis, which posits that increased body size increases susceptibility to acute heat stress; (3) the resource availability hypothesis, which posits that increased body size is enabled in areas with more abundant food; and (4) the starvation resistance hypothesis, which posits that increased body size reduces susceptibility to starvation during acute food shortages.
3. Spatial variation in body mass was most consistently (and negatively) correlated with mean annual temperature, supporting the heat conservation hypothesis. Across time, variation in body mass was most consistently (and positively) correlated with net primary productivity, supporting the resource availability hypothesis.
4. Climate change could influence body size in animals through both changes in mean annual temperature and resource availability. Rapid reductions in body size associated with increasing temperatures have occurred in short-lived, fecund

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species, but such reductions will be obscured by changes in resource availability in longer-lived, less fecund species.

KEYWORDS

Bayesian hierarchical modelling, Bergmann's rule, body size clines, Chiroptera, climate change, geographic information systems, primary productivity

1 | INTRODUCTION

Body size influences every aspect of organismal biology, including lifespan (Lindstedt & Calder, 1981; Speakman, 2005), metabolism (Brown et al., 2004; Clarke et al., 2010), movement (Carbone et al., 2005; Noonan et al., 2020), reproductive biology (Blueweiss et al., 1978; Fenchel, 1974) and extinction risk (Brown, 1995; Ripple et al., 2017). Understanding the factors that drive variation in body size is thus among the most important goals in ecology (Kaspari, 2005). Bergmann's rule (Bergmann, 1847; Salewski & Watt, 2017), which states that animals residing in colder climates are larger than those residing in warmer climates, is a widely known macroecological pattern. Although originally and primarily applied to differences in body size among closely related species, Bergmann's rule is often believed to extend to differences in body size within species as well (Ashton, 2002; Blackburn & Hawkins, 2004; Meiri & Dayan, 2003; Riemer et al., 2018; Watt et al., 2010).

The mechanism traditionally hypothesized to underlie Bergmann's rule is that increased size facilitates body heat conservation (hereafter, the 'heat conservation hypothesis'; Ashton, 2002; Bergmann, 1847; Mayr, 1956; Watt et al., 2010). Homeotherms maintain stable, elevated body temperatures, resulting in substantial metabolic heat loss to the environment when environmental temperatures are much colder than body temperatures (Fristoe et al., 2015; McCafferty et al., 2011) but often also in difficulty dissipating excess body heat during periods of high temperatures (Cunningham et al., 2021). The ratio between surface area and volume decreases with increasing body size, so while absolute heat loss increases with increasing body size, smaller animals dissipate relatively more heat across their relatively larger surface areas (Withers et al., 2016). Larger body size could, therefore, be an adaptation to climates with cooler average temperatures, while smaller body size could be an adaptation to climates with relatively warmer temperatures.

Despite its intuitive appeal, empirical support for the heat conservation hypothesis within species is mixed. Although ecologists have accumulated substantial evidence that individuals within species tend to be larger in colder climates (e.g. Ashton, 2002; McQueen et al., 2022; Meiri & Dayan, 2003; Smith et al., 1995), some recent tests have failed to find consistent relationships between temperature and the body sizes of individuals within species (Freeman, 2017; Riemer et al., 2018). Additionally, physiologists

have questioned the validity of the heat conservation hypothesis on physiological grounds, arguing that mass-specific metabolic heat loss is far less important to animals than total heat loss and that other physical traits (e.g. hair length, insulative fat) are far more effective and adaptable means of reducing metabolic requirements (Geist, 1987; McNab, 2010; Scholander, 1955). In sum, and despite the widespread acceptance of the heat conservation hypothesis in the ecological literature, the extent to which variation in average temperature translates to variation in body size within species remains an open question.

Because of scepticism surrounding the primary mechanism assumed to underlie Bergmann's rule, biologists have proposed other hypotheses for geographical clines in body size within species that are consistent with Bergmann's rule (Kelly et al., 2018; Meiri et al., 2007; Watt et al., 2010). For example, larger individuals exhibit acute heat stress at lower temperatures than smaller individuals, and thus experience greater risk of mortality from heat stress than smaller individuals (hereafter the 'heat mortality hypothesis'; Peralta-Maraver & Rezende, 2021; Smith et al., 1995; but see McKechnie et al., 2021; Taylor, 1998). This idea posits an additional (or alternative) mechanism by which animals from warmer climates are smaller than their counterparts from colder climates and is supported in the genus *Neotoma* (i.e. woodrats; Brown & Lee, 1969; Smith et al., 1995). A second alternative is the 'resource availability hypothesis', through which increased resource availability—often correlated with temperature across the globe (Chu et al., 2016; Gillman et al., 2015)—results in larger individuals (e.g. Huston & Wolverton, 2011; McNab, 2010; Rosenzweig, 1968; Yom-Tov & Geffen, 2011). If the resource availability hypothesis is true, clinal variation in body size consistent with Bergmann's rule may arise over limited geographic extents (e.g. a local elevational gradient where increased precipitation increases productivity as temperature decreases), but body sizes should *decrease* as temperatures decrease at larger spatial scales (which would contradict Bergmann's rule). Finally, a third hypothesis proposed to explain Bergmann's rule is the 'starvation resistance' (or 'seasonality') hypothesis. According to this hypothesis, large body size buffers against resource scarcity driven by seasonality (Boyce, 1979). Because seasonality increases at higher latitudes and fasting endurance decreases at colder temperatures (Lindstedt & Boyce, 1985), this dynamic may produce a size cline consistent with Bergmann's rule. The starvation resistance hypothesis has received support from studies on songbirds (Jones

et al., 2005), muskrats (*Ondatra zibethicus*; Boyce, 1978) and bobcats (*Lynx rufus*; Wigginton & Dobson, 1999).

Some ecologists and evolutionary biologists have suggested that Bergmann's rule should apply over time as well as space (e.g. Gardner et al., 2011; Merckx et al., 2018; Smith et al., 1995; Van Buskirk et al., 2010; Weeks et al., 2020). In other words, as temperatures fluctuate over time, the average size of individuals within a species should decrease as temperatures rise and increase as temperatures fall. Although early studies of this temporal equivalent to Bergmann's rule focused on time scales of thousands of years (Smith et al., 1995), more recent studies have found that changes in body size can occur over decades or even years (Ballinger & Nachman, 2022; Van Buskirk et al., 2010; Weeks et al., 2020). However, and similar to the original (spatial) conceptualization of Bergmann's rule, empirical evidence for this temporal equivalent is mixed (Sheridan & Bickford, 2011; Teplitsky & Millien, 2014; Yom-Tov & Geffen, 2011). This may be because mechanisms distinct from the heat conservation hypothesis—such as the heat mortality, resource availability and starvation resistance hypotheses detailed above—additionally (or alternatively) influence shifts in body size over time. For example, extreme climatic events can trigger rapid evolution of traits (Campbell-Staton et al., 2017; Donihue et al., 2018), which is consistent with the heat mortality and starvation resistance hypotheses. As another example, positive effects of periods of high resource availability on fat reserves and growth have been documented in many taxa (e.g. Altmann & Alberts, 2005; Boutin & Larsen, 1993; Brett, 1971; Monteith et al., 2014), which would support the resource availability hypothesis. Testing these alternative hypotheses across both space and time provides a lens through which to anticipate how changes in climate may affect body size in the future, as well as the pace at which changes in body size may occur. The heat conservation hypothesis posits a gradual evolutionary mechanism for changes in body size, the heat mortality and starvation resistance hypotheses posit sudden evolutionary changes from acute events, and the resource availability hypothesis posits an ecological mechanism that may alter body size most rapidly of all.

To evaluate the mechanistic underpinnings of Bergman's rule, we tested whether spatial and temporal (interannual) variation in body mass of North American bats is best supported by the heat conservation, heat mortality, resource availability or starvation resistance hypotheses (summarized in Table 1). As with many taxa, the intra-specific formulation of Bergmann's rule is exhibited by some species of bats (e.g. Bogdanowicz, 1990; Burnett, 1983; Lausen et al., 2008, 2019), but does not appear to be the norm among the clade as a whole (Riemer et al., 2018). Critically, extensive records of bat captures permit a rare opportunity to test for Bergmann's rule and evaluate its associated hypotheses while accounting for other factors (e.g. sex, age, reproductive condition and time of year) that influence body size. We compiled 17 such data sets and used Bayesian hierarchical models to weigh evidence for each hypothesis across both space and time for 20 species of North American bats. Because the existence of the temporal formulation of Bergmann's rule is largely built upon an assumption that the spatial rule arises from an

TABLE 1 Descriptions of the hypotheses tested in this paper, including the name, spatial version of the hypothesis, proxy data used to test the spatial hypothesis, temporal version of the hypothesis, and proxy data used to test the temporal hypothesis.

Hypothesis name	Spatial hypothesis	Spatial proxy data	Temporal hypothesis	Temporal proxy data
Heat conservation	Because larger body size increases an individual's ability to conserve body heat, individuals will be larger in areas where average temperatures are lower	Mean annual temperature (1970–2000; WorldClim; Fick & Hijmans, 2017)	Because larger body size increases an individual's ability to conserve body heat, individuals will be larger after years in which average temperatures are lower	Mean temperature in the preceding 365 days (DAYMET; Thornton et al., 2020)
Heat mortality	Because larger individuals tend to have lower critical thermal maxima, individuals will be smaller in areas where maximum temperatures are higher	Mean annual maximum temperature (1980–2010; DAYMET; Thornton et al., 2020)	Because larger individuals tend to have lower critical thermal maxima, individuals will be smaller after years in which maximum temperatures are higher	Maximum temperature in the preceding 365 days (DAYMET; Thornton et al., 2020)
Resource availability	Because individuals living in more productive environments tend to be larger, individuals will be larger in areas where primary productivity is higher	Net primary productivity during April–October (2000–2016; MODIS; Stockli, 2020)	Because individuals living in more productive environments tend to be larger, individuals will be larger after years in which primary productivity is higher	Net primary productivity in months preceding capture, inclusive of month of capture (MODIS; Stockli, 2020)
Starvation resistance	Because larger body size increases an individual's ability to survive periods of resource scarcity, individuals will be larger in areas where periods of resource scarcity (e.g. winters) are most severe	Average minimum temperature in April, May, September, and October (1970–2000; WorldClim; Fick & Hijmans, 2017)	Because larger body size increases an individual's ability to survive periods of resource scarcity, individuals will be larger after years in which periods of resource scarcity (e.g. winters) are most severe	Average minimum temperature in the April, May, September, and October preceding capture (DAYMET; Thornton et al., 2020)

evolutionary process that manifests across time, we expected observed patterns of variation in body mass to be driven by the same process or processes across both time and space. In other words, if variation in body mass across space was best explained by one of our four hypotheses, we also expected variation in body mass across time to be best explained by the same hypothesis. A consistent correlation across both space and time would provide strong evidence for a consistent evolutionary force driving variation in body size.

2 | METHODS AND MATERIALS

2.1 | Data collection

We compiled biometric data on bats captured throughout North America using mist nets between 2000 and 2016 (Figure 1). All bats were captured with permission from state, provincial and federal management authorities and according to protocols approved by institutional animal care and use review boards. All biometric data contained information on capture location, date of capture, species, sex, age class, reproductive state (pregnant/lactating/post-lactating/scrotal/non-reproductive) and mass. Because body mass varies with species, sex, age class, reproductive state and time of year, we accounted for potential variation related to these factors by calculating the mean mass for each species/sex/reproductive state combination in each month, subtracting the corresponding mean value from the mass of each individual in the data set and dividing this by the standard deviation of body mass values for that species to ensure that effect sizes are comparable across species of different sizes. The final data set included only data from adult bats captured between April and October, for species represented by ≥ 150 individuals and that were captured across $\geq 2.5^\circ$ of latitude.

To test hypotheses for clinal variation in body mass, we extracted environmental variables from remotely sensed raster data sets. To test the heat conservation hypothesis across space, we extracted data for each capture location from the 30-s (~1 km) resolution version of the WorldClim 2.1 mean temperature data set (mean annual temperature, 1970–2000; Fick & Hijmans, 2017). We centered mean annual temperatures in our data set at zero by subtracting the mean annual temperature across all capture locations. To test the heat conservation hypothesis across time, we extracted data for each capture location from the DAYMET daily climate summaries 1-km resolution data set (Thornton et al., 2020) using the DAYMETR package (version 1.4; Hufkens et al., 2018). We used those data to calculate the midpoint of low and high temperatures in the 365 days before each bat was captured and then subtracted the average of this value at the capture location during our study period (2000–2016) to obtain a final centered metric of year-to-year differences in mean temperatures.

To test the heat mortality hypothesis across space, we extracted data for each capture location from the DAYMET daily climate summaries 1-km resolution data set (Thornton et al., 2020) and used those data to calculate the maximum temperature at each capture location in each year between 1980 and 2010 (the time period in which DAYMET data is available that most closely matches the WorldClim 2.1 time frame). We then calculated the mean annual maximum temperature across this 30-year period at each site and subtracted the mean annual maximum temperature across all sites to obtain a final centered metric of long-term maximum annual temperatures. To test the heat mortality hypothesis across time, we extracted data for each capture location from the DAYMET daily climate summaries 1-km resolution data set (Thornton et al., 2020). We calculated the maximum temperature in the prior 365 days for each capture event, then subtracted the long-term average for this value

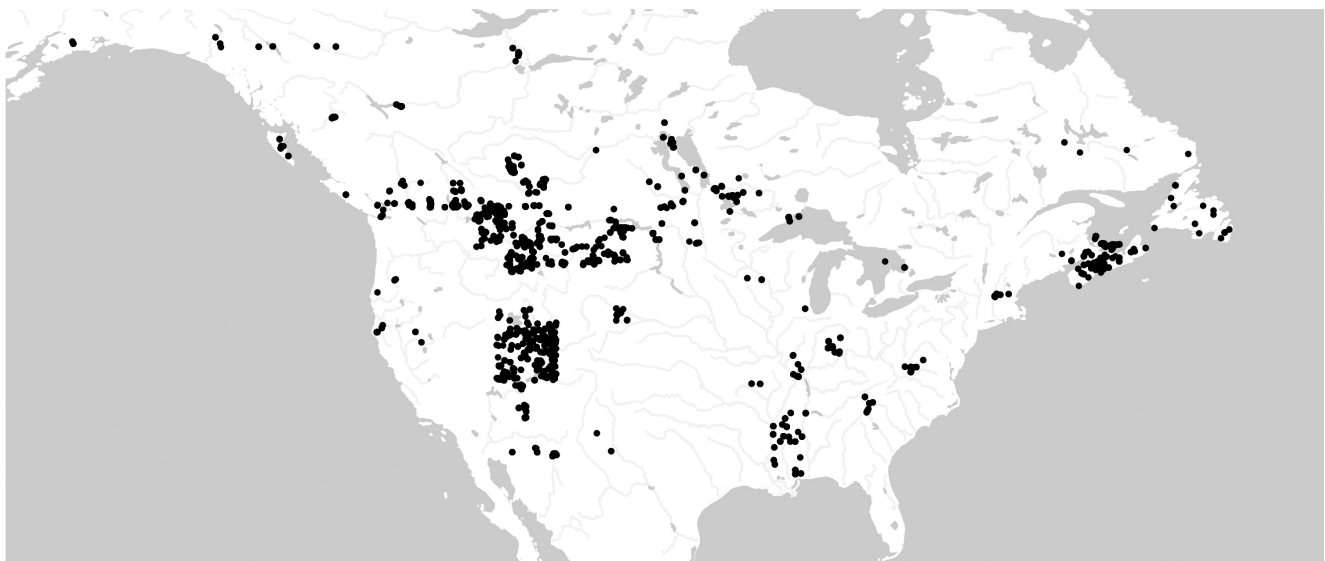


FIGURE 1 Map of capture locations for bats included in our analyses. Our final data set included 31,303 bats sampled from 1190 sites along a $>30^\circ$ gradient in latitude.

at the site of capture to calculate a final centered metric of year-to-year differences in maximum temperatures.

To test the resource availability hypothesis across space, we extracted data for each capture location from the 0.1-degree (~10 km) resolution version of the MODIS monthly net primary productivity data set (Stockli, 2020). Primary productivity is positively correlated with insect biomass across both space (Borer et al., 2012; Lind et al., 2017) and time (Bell, 1985; Frith & Frith, 1985), and summer precipitation—another common proxy for resource availability—is positively correlated with annual survival in little brown bats (*Myotis lucifugus*; Frick et al., 2010). We averaged monthly net primary productivity across months during the active season for bats (April–October) for all available years (2000–2016), then divided by the mean value across all sites to obtain a final metric centered at one. To test the resource availability hypothesis across time, we extracted data from the same rasters and averaged net primary productivity for months preceding the date a bat was captured (in the year of capture, inclusive of the month of capture, starting in April), then divided by the average of this value at the site of capture for the entire time period.

To test the starvation resistance hypothesis across space, we extracted data for each capture location from the 30-second (~1 km) resolution version of the WorldClim 2.1 minimum temperature data set (mean minimum temperature, 1970–2000; Fick & Hijmans, 2017). To estimate the severity of resource limitation in the period in which bats are most resource-limited, we averaged minimum temperatures across September, October, April and May, which roughly represent night-time temperatures during the times of the year when bats tend to be most energetically vulnerable. Regardless of whether they hibernate or migrate for the winter, bats at temperate latitudes must gain a substantial amount of weight in the autumn (Cheng et al., 2019; Guglielmo, 2018; Kunz et al., 1998; Lacki et al., 2015; Sommers et al., 2019), and they tend to be energetically stressed in the early spring before insects become abundant (Arlettaz et al., 2001; Encarnação et al., 2004; Jonasson & Guglielmo, 2019). Daily minimum temperatures during autumn and spring thus represent a biologically informed proxy for resource limitation. We centered mean minimum spring and autumn temperatures in our data set at zero by subtracting the mean minimum spring and autumn temperatures across all capture locations. To test the starvation resistance hypothesis across time, we extracted data from the DAYMET daily climate summaries 1-km resolution data set (Thornton et al., 2020). We averaged the minimum daily temperatures for the spring (April and May) and autumn (September and October) preceding the date on which a bat was caught and subtracted the average value at the site of capture during our study period.

2.2 | Statistical analysis

We used the R statistical software environment (version 4.0.2; R Core Team, 2020) to quantify the influence of our environmental variables on bat body mass across both space and time. We used the

modelling software 'Stan' (Carpenter et al., 2017) via the R package BRMS (version 2.13.3; Bürkner, 2017) to build a single Gaussian-family Bayesian model for each species (i.e. 20 models in total; Figure A1) to quantify the effects on body mass of the environmental predictors detailed above. Each model included three chains that were run for 12,000 iterations (2000 iterations of warm-up and 10,000 iterations of sampling). We assessed chain convergence using the Gelman-Rubin diagnostic (\hat{R}) and precision of parameter estimation using effective sample size. $\hat{R} < 1.01$ and effective sample sizes $> 10,000$ represent acceptable convergence and parameter precision (Gelman et al., 2013; Kruschke, 2015). We used leave-one-out cross-validation to check model fit using the R packages LOO (version 2.3.1; Vehtari et al., 2017) and BAYESPLOT (version 1.7.2; Gabry et al., 2019) to visually assess the cross-validated probability integral transform.

3 | RESULTS

The final data set contained 31,422 individuals of 20 species captured at 1190 locations (Figure 1; Table A1). Most species were larger at higher latitudes, but body size remained relatively constant over our study period (Figure A2). Significant spatial and interannual variation existed among all predictor variables, enabling detection of meaningful relationships between body mass and predictor variables (Figure A3).

3.1 | Spatial variation in body mass

Spatial variation in body mass most consistently supported the heat conservation hypothesis, with most species exhibiting greater body mass in areas with colder mean annual temperatures (Figure 2a, Figure A4). For 15 of 20 species, body mass declined with increasing mean annual temperature (i.e. $\beta < 0$), and the probability that the coefficient was less than zero was $> 95\%$ for 6 of these species (*Eptesicus fuscus*, *Lasionycteris noctivagans*, *Myotis lucifugus*, *M. ciliolabrum*, *M. evotis* and *Parastrellus hesperus*). Most species exhibited minimal variation in body mass with respect to maximum temperature (Figure 2b), primary productivity (Figure 2c) and spring/autumn temperatures (Figure 2d), suggesting a lack of support for heat mortality, resource availability and starvation resistance hypotheses, respectively. For these three hypotheses, coefficients were relatively evenly distributed around 0; 90% credible intervals overlapped 0 in most cases, and credible intervals that did not overlap zero were distributed relatively evenly around zero.

3.2 | Temporal (interannual) variation in body mass

Temporal variation in body mass most consistently supported the resource availability hypothesis, with most species exhibiting greater body mass during years in which net primary productivity was higher (Figure 3c, Figure A4). For 14 of 20 species, body mass increased with

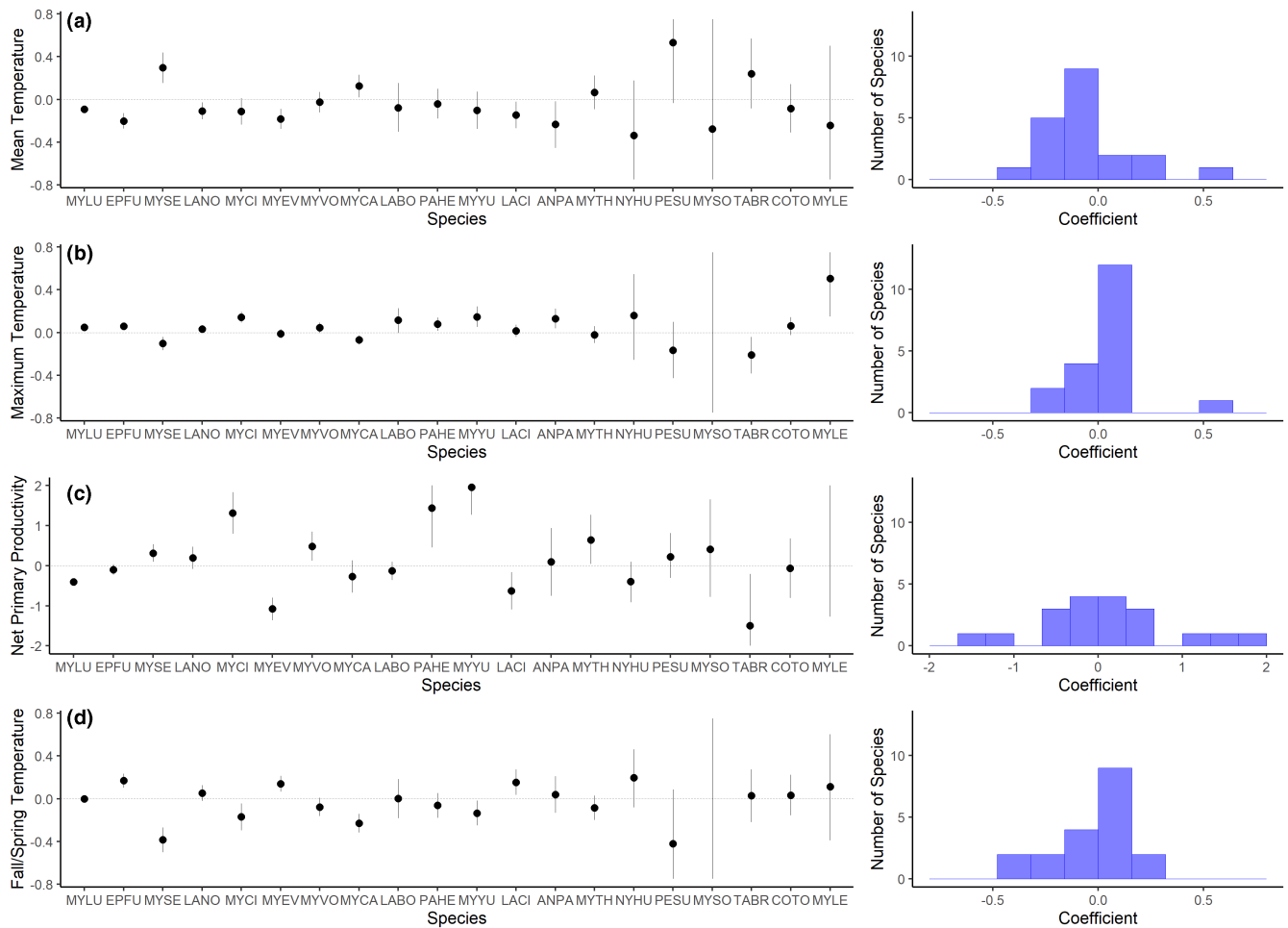


FIGURE 2 Intraspecific patterns in body mass across space in 20 species of North American bats, which most strongly support the heat conservation hypothesis. In the left column, we plotted the regression coefficient (slope) for each species' relationship between body mass and the predictor variable of interest (points) and 90% credible intervals (lines). Points above the dotted line at 0 indicate species in which individual body mass increased as the variable of interest (a. Mean annual temperature; b. Maximum annual temperature; c. Net primary productivity; d. Autumn/spring temperature) increased. Species are ordered from largest (left) to smallest (right) sample sizes. In the right column, we plotted histograms of the coefficients. Row (a) represents tests of the heat conservation hypothesis, Row (b) represents tests of the heat mortality hypothesis, Row (c) represents tests of the resource availability hypothesis, and Row (d) represents tests of the starvation resistance hypothesis. Distributions centered on zero indicate no consistent effect of the variable of interest on body mass, while distributions centered asymmetrically around zero indicate directional effects. Credible intervals were truncated at the limit of the y-axis for ease of interpretation. The mean estimate of the coefficient for the effect of net primary productivity on body mass for *Myotis leibii* (MYLE; 4.29) was excluded from the y-axis of that graph to improve interpretability of coefficient estimates for the other species, but the 90% credible interval for that estimate crosses zero as shown in the graph. Species codes are listed in [Table A1](#).

increasing net primary productivity (i.e. $\beta > 0$), and the probability that the coefficient was above zero was $>95\%$ for 8 of these species (*Eptesicus fuscus*, *Myotis lucifugus*, *M. ciliolabrum*, *M. californicus*, *M. sodalis*, *M. leibii*, *Nycticeius humeralis*, *Perimyotis subflavans*). Most species exhibited little variation in body mass with respect to year-to-year differences in mean annual temperatures ([Figure 3a](#)), maximum temperatures ([Figure 3b](#)), or spring/autumn temperatures ([Figure 3d](#)), suggesting a lack of support for heat conservation, heat mortality and starvation resistance hypotheses, respectively. For these hypotheses, coefficients were relatively evenly distributed around 0, 90% credible intervals overlapped 0 in most cases, and credible intervals that did not overlap zero were relatively evenly distributed around zero or were distributed in the direction opposite most coefficients.

4 | DISCUSSION

Bergmann's rule may not be as conspicuous in nature as it was historically believed to be, but most bat species in our study followed a latitudinal gradient in body size consistent with the rule ([Figure A2](#)), indicating that Bergmann's rule is a common (if not ubiquitous) pattern. When we tested four competing hypotheses for the mechanism underlying the pattern, spatial variation in body mass of bats was most consistently correlated with mean annual temperature (supporting the heat conservation hypothesis, historically assumed to underlie Bergmann's rule; [Figure 2](#); [Figures A4 and A5](#)), and interannual temporal variation in body mass was most consistently correlated with net primary productivity (supporting

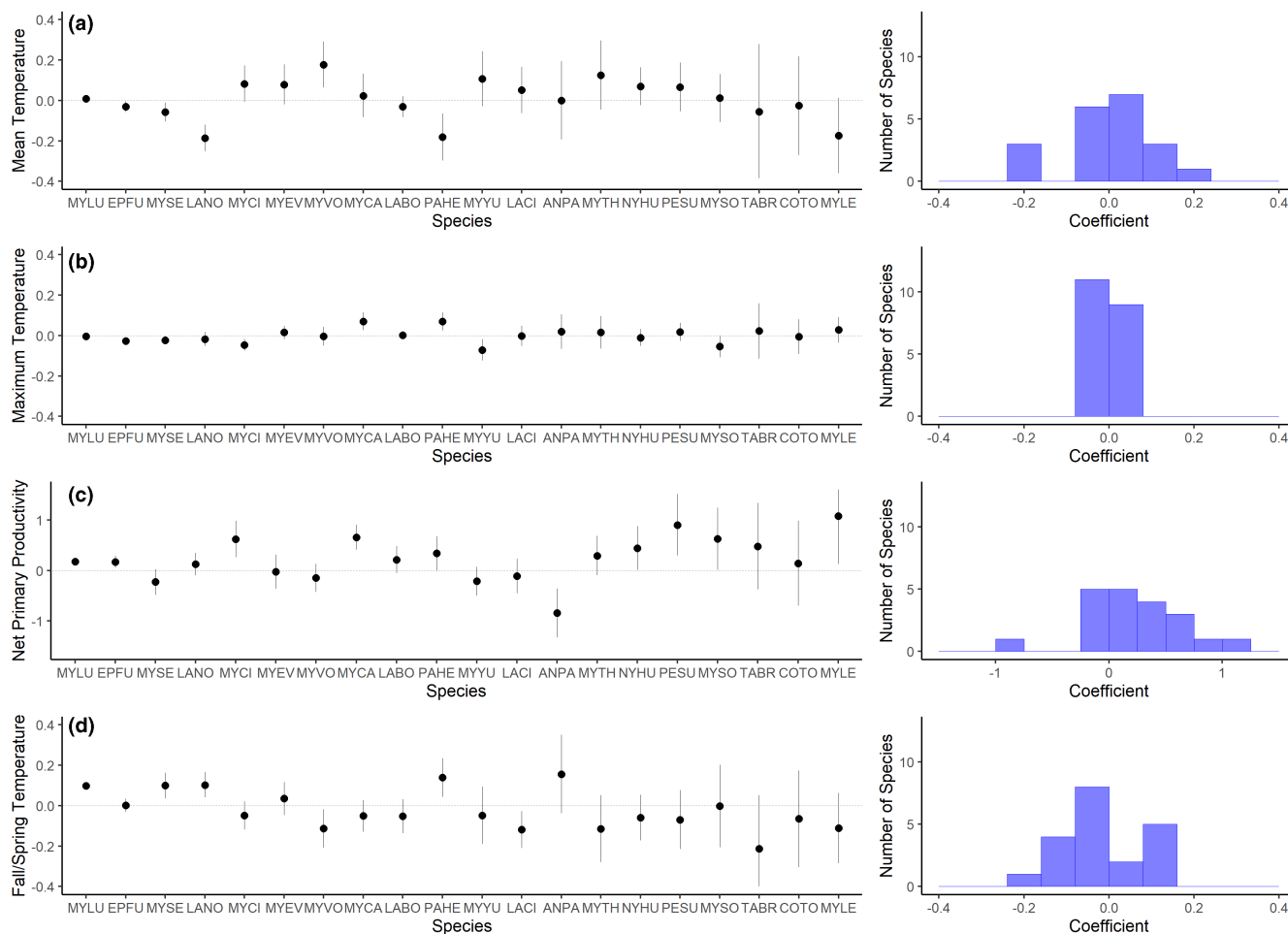


FIGURE 3 Intraspecific patterns in body mass across time in 20 species of North American bats, which most strongly support the resource availability hypothesis. In the left column, we plotted the regression coefficient (slope) for each species' relationship between body mass and the predictor variable of interest (points) and 90% credible intervals (lines). Points above the dotted line at 0 indicate species with larger masses as the variable of interest (a. Mean annual temperature; b. Maximum annual temperature; c. Net primary productivity; d. Autumn/spring temperature) increased. Species are ordered from largest (left) to smallest (right) sample sizes. In the right column, we plotted histograms of the coefficients. Row (a) represents tests of the heat conservation hypothesis, Row (b) represents tests of the heat mortality hypothesis, Row (c) represents tests of the resource availability hypothesis, and Row (d) represents tests of the starvation resistance hypothesis. Distributions centered on zero indicate no consistent effect of the variable of interest on body mass, while distributions centered asymmetrically around zero indicate consistent effects. Credible intervals were truncated at the limit of the y-axis for ease of interpretation. Species codes are listed in [Table A1](#).

the resource availability hypothesis; [Figure 2](#); [Figures A4 and A5](#)). These results highlight that both spatial and temporal patterns of variation in body size can have an energetic basis, but via two distinct pathways: even if spatial variation in body size is driven by energy loss to the environment in the form of heat, temporal variation in body size can be driven by energy gain from food availability.

Across North America, body mass of bats was most consistently correlated with mean annual temperature, matching the traditional hypothesis—the heat conservation hypothesis—for Bergmann's rule (Bergmann, 1847; Mayr, 1956). However, this mechanism had little influence on temporal variation in body size, perhaps because selective pressure via size-dependent differences in energy expenditure could take considerable time to manifest. Compared with the heat mortality and starvation resistance hypotheses—which assume

punctuated bouts of high mortality driven by extreme heat or resource scarcity, respectively—the heat conservation hypothesis posits more gradual selection on body size. Differences in survival and reproduction between small individuals and large individuals may, therefore, fail to manifest in measurable population-level variation in body size from year to year, even when it is unusually warm or cold. If the heat conservation hypothesis drives Bergmann's rule, population-level changes in body size should occur only after the climate departs from historical norms over many generations.

Although recent research has cast doubt on the idea that the heat conservation hypothesis underlies Bergmann's rule (Riener et al., 2018), our results provide modest support for the heat conservation hypothesis, perhaps because we were able to account for several important confounding sources of variation in body mass (e.g. sex, reproductive status, time of year, resource availability). A

diverse array of factors contributes to variation in body mass, and their cumulative influence often swamps variation driven by mean annual temperature (Ballinger & Nachman, 2022; Jones et al., 2005; Meiri et al., 2007; Nunes et al., 2017). Given this challenge, carefully accounting for potential confounds is necessary for clarifying the extent to which mean annual temperature drives variation in body size within species. Additionally, our threshold for minimum sample sizes was higher than the threshold used by Riemer et al. ($n = 150$ vs. $n = 30$), and our ability to detect strong evidence for our best-supported hypotheses was positively correlated with sample size. Of the coefficients with >95% probability of supporting the best-supported hypotheses, five of six coefficients that supported the heat conservation hypothesis across space and four of eight coefficients that supported the resource availability process across time were located in species with $n > 1000$ individuals. Given the degree of confounding variation in body size inherent in such broadly collected data, compiling very large data sets ($n > 1000$) may be necessary to detect Bergmann's rule within species in wild populations.

That resource availability might drive body mass variation temporally but not spatially is consistent with predictions of the ideal free distribution model of resource selection (Fretwell & Lucas, 1969; Royama, 1970) and the 'more-individual hypothesis' for species-energy relationships (Srivastava & Lawton, 1998; Storch et al., 2018; Wright, 1983). If individuals within a species are distributed in an ideal free manner, populations should be denser in areas with greater resource availability, such that per capita resource availability is roughly equivalent over the species' geographic range. In this scenario, individuals should not necessarily be appreciably larger or heavier in resource-rich areas than in resource-poor areas, but populations should be denser or sparser, respectively. In other words, additional energy is converted into additional individuals, rather than larger individuals. However, if resource availability changes from year to year, this equilibrium can be disrupted, leading to temporary situations in which per capita resource availability is higher in some areas than others until population densities reach a steady state of resource availability. In this scenario, individuals would likely be larger or heavier in (temporarily) resource-rich areas than in (temporarily) resource-poor areas, and this temporal variation in body mass would be driven more by changes in nutritional condition (i.e. fat reserves and muscle mass) than by differences in body size arising from directional selection. This dynamic is likely to be particularly pronounced in long-lived species that produce few offspring (such as bats; Wilkinson & South, 2002), because population density cannot rapidly track changes in resource availability via increases in recruitment.

Our analyses indicate that the evolutionary processes that drive spatial patterns in body size might not produce equivalent temporal patterns over short time scales. Variation in body size occurs both temporally and spatially, but the processes that generate each can be distinct and should thus be observable over markedly different timescales. Motivated by patterns of spatial variation in body size, many biologists have searched for analogous patterns through time,

typically over the course of years or decades (e.g. Caruso et al., 2014; Sheridan & Bickford, 2011; Teplitsky & Millien, 2014). However, the evolutionary processes that give rise to spatial patterns could take centuries or millennia to manifest, even when they are straightforward (and spatial patterns in body size are rarely so). Biologists searching for such evolutionary processes may detect signatures from unrelated ecological processes that occur over much shorter timescales, which could easily confound or contradict studies that do not test multiple mechanisms simultaneously. This is especially true for long-lived species, for which the pace of evolutionary change is likely to be slower than for short-lived, more fecund species.

Climate change may induce changes in body size in animals, but any such changes are likely to be more complex than has been appreciated. Over the nearly two decades that we collected data, the primary driver of interannual variation in body size was resource availability. Increases in mean annual temperatures could make many ecosystems more productive for a longer portion of the year, but changes in precipitation can both accentuate and dampen such shifts in productivity (Chu et al., 2016; La Pierre et al., 2016). Any changes in body size driven by climate change will, therefore, depend on the extent to which mean annual temperature, amount of precipitation and timing of precipitation are altered for a given area. Moreover, and because net primary productivity does not meaningfully influence body size across space, any such changes are likely to be transient, renormalizing over time if humans eventually curb greenhouse gas emissions.

Life history traits should mediate the influence of climate change on body size. The most compelling evidence of rapid changes in body size due to climate change comes from songbirds (e.g. Van Buskirk et al., 2010; Weeks et al., 2020), which are shorter lived and more fecund than bats. Controlling for size, bats live on average 3.5 times longer than other placental mammals (Wilkinson & South, 2002). Individuals with lifespans >30 years have been documented in several species, and bats typically produce only 1–2 offspring per year (Barclay & Harder, 2003; Wilkinson & South, 2002). Because the pace of life is positively correlated with the pace of evolution (i.e. smaller, more fecund species tend to evolve more rapidly; Martin & Palumbi, 1993; Gillooly et al., 2005; Nabholz et al., 2008), the processes that lead to spatial variation in body size should arise faster over time in short-lived species than in long-lived species. Short-lived species may also exhibit temporal changes in body size from developmental pathways (i.e. cohorts of individuals who developed in warm or resource-rich periods of time; Ballinger & Nachman, 2022; Teplitsky & Millien, 2014). Additional studies that enable direct comparisons of the pace of body size change across taxa with different life history strategies will increase ecologists' understanding of the extent and pace of, and mechanisms underlying, changes in body size caused by climate change.

Differences in natural history between species are likely to influence the extent to which any given species conforms to biogeographic rules (Meiri et al., 2007; Yom-Tov & Yom-Tov, 2005). We examined our results for evidence that wintering strategy (hibernation vs. migration), phylogeny (*Myotis* spp. vs. species in other

genera), and geography (species resident to eastern vs. western North America) are correlated with adherence to or deviation from the broad patterns we describe above; we found no clear evidence that these factors alter our general results. It is also tempting to ascribe deviation from the broader patterns to idiosyncratic characteristics of an individual species' natural history. For example, pallid bats (*Antrozous pallidus*) are commonly regarded as the only ground-foraging species of bat in North America (Lenhart et al., 2010), and they are the only species in our analyses that exhibited strong evidence for lower body mass in years of higher primary productivity (Figure 3c). One could hypothesize that increased productivity is correlated with denser or taller ground vegetation, making hunting more difficult for this species. However, some of our individual results are undoubtedly statistical noise—with 20 independent tests of each hypothesis, on average one test should be 'significant' in each direction even if the null hypothesis is true overall. For this reason, caution is warranted in using our results to speculate about why any single species adheres to or diverges from the broader patterns we found.

While recent evidence indicates that higher temperatures caused by climate change are inducing rapid evolution in body size in some species (Gardner et al., 2011; Van Buskirk et al., 2010; Weeks et al., 2020), we found no evidence that this is occurring in bats. Spatial variation in body mass of North American bats most consistently supported the heat conservation hypothesis for Bergmann's rule, but the heat conservation hypothesis does not explain variation in body size over time. Instead, interannual variation in body mass in the past two decades was most consistently correlated with changes in resource availability. For bats and other long-lived species, temperature-induced reductions in body size could take substantially longer to manifest than for short-lived, more fecund species like songbirds and temperature-driven changes in body size will be obscured by variation in resource availability.

AUTHOR CONTRIBUTIONS

JA conceived the study, analysed the data and led the writing of the manuscript. JG and DK supervised the analysis and writing of the manuscript. All authors collected and prepared data, reviewed drafts and approved the manuscript for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

All data and code required to reproduce analyses are archived on Zenodo: <https://doi.org/10.5281/zenodo.7577279> (Alston et al., 2023). Because much of the bat location data underlying our analyses are subject to legal restrictions on use and/or may reveal the location of sensitive sites (e.g. hibernacula, maternity roosts), longitudes have been offset by 5–10 km.

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SUPPORTING INFORMATION

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

Table A1. Table detailing species-specific information, including species code (used in figures), the number of individuals included in each species' model, the latitudinal range covered by individuals of

each species (in degrees) and the number of distinct sites at which each species was captured, the mean number of times each site was sampled (and range of times each site was sampled).

Table A2. Table detailing site-specific capture data, including site ID, latitude, longitude, first year sampled, last year sampled, total number of years sampled, number of species sampled and number of individuals sampled.

Figure A1. Graphical representation of an individual model. The same model was used for each species (for a total of 20 models). In each model, standardized body mass is a function of the four proxies for the spatial hypotheses, the four proxies for the temporal hypotheses, and random intercepts for each data provider (to account for known differences in protocols for weighing bats). This approach allows tests for the relative contribution of each hypothesis in shaping body size while accounting for the others. In the event that multiple factors interact to influence body size, this approach also allows detection of contributions to body size from multiple hypotheses simultaneously.

Figure A2. Intraspecific patterns in body mass across latitude and year in 20 species of North American bats. In the left column, we plotted each species' regression coefficient (points) and 90% credible interval (lines). Points above the dotted line at 0 indicate species with larger masses as the variable of interest (A. Latitude; B. Year) increased. Species are ordered from largest (left) to smallest (right) sample sizes. In the right column, we plotted histograms of the coefficients. Distributions centered on zero indicate no consistent effect of a predictor on body mass, while distributions centered asymmetrically around zero indicate consistent effects. Species tend to be larger at higher latitudes but show no clear pattern of changes in body size over time during our study period.

Figure A3. Scatterplots depicting relationships between latitude and variables of interest (left column), and year and variables of interest (right column). Each point represents one capture location, trend lines represent a linear regression of the trend across space or time, and the color of the points represents the number of bats captured at a location (darker points denote more captures). Confidence intervals (95%) are represented by gray ribbons (which are very narrow in all regressions due to large sample sizes). Contrary to expectations, net primary productivity at capture sites increased at higher latitudes (due in part to a large number of bats captured in the arid southwestern United States where primary productivity is low, and the exclusion of winter months when primary productivity is much lower at more northern sites). Following expectations, mean annual temperatures, maximum temperatures, and spring and autumn temperatures decreased as latitude increased. If body size is driven by any of these predictor variables, geographic variation in each of these predictor variables (or some combination thereof) could create a spatial pattern of body mass consistent with Bergmann's Rule. Across time during our study period, spring and autumn temperatures and net primary productivity increased, while mean annual temperatures and maximum temperatures were relatively constant. Consequently, only spring and autumn temperatures and net primary productivity could lead to an observed trend of shrinking body mass over the

total duration of our study. Nevertheless, interannual variation in each of these variables was substantial, so if any of these predictor variables are initiating rapid evolutionary change in body size, our analyses are likely to detect it.

Figure A4. Because statistical noise introduced by unimportant predictors may lead to spurious results, and because meaningful latitudinal gradients in body size appeared to be more common than mean-temperature-driven gradients in body size, we tested for the influence of our best-supported variables if other predictors were excluded from the model. In the left column, we plotted the regression coefficient (slope) for each species' relationship between body mass and the predictor variable of interest (points) and 90% credible intervals (lines). Points above the dotted line at 0 indicate species in which individual body mass increased as the variable of interest (A. Mean annual temperature at each capture location (1970-2000) B. Net primary productivity at each capture location in the year of capture) increased. Species are ordered from largest (left) to smallest (right) sample sizes. In the right column, we plotted histograms of the coefficients. Row A represents tests of the heat conservation hypothesis across space, and Row B represents tests of the resource availability hypothesis across time. Species codes are listed in Table A1. Sixteen of 20 coefficients were negative for mean temperature (13 with $p > 0.95$, and another one with $p > 0.90$), and 13 of 20 coefficients were positive for primary productivity (9 with $p > 0.95$, and another 3 with $p > 0.90$), further strengthening the evidence for the heat conservation hypothesis across space and

the resource availability hypothesis through time.

Figure A5. Because bats may lose a substantial amount of heat through the largely unfurred skin of their wings and uropatagia, we conducted a follow-up analysis to check whether accounting for wing size influenced our results (uropatagia are more difficult to quantify). To do this, we divided standardized body mass by forearm length (a proxy for wing size) and re-ran our Bayesian models using our original predictors. Fig. A5 shows coefficients of the original models included in the manuscript (y-axis) plotted against coefficients of the same models if body mass (the response variable) is adjusted/corrected to account for wing size (forearm length). The relationship between coefficients from the initial models and the corrected models fall closely along a 1:1 line, indicating that correcting for wing size has little influence on model coefficients.

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