bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

No general relationship between mass and temperature in endotherm species

Kristina Riemer[1*], Robert P Guralnick[2], Ethan White[1,3]

Bergmann's rule is a widely accepted biogeographic rule that individuals within a species are smaller in warmer environments. While there are many single-species studies and integrative reviews documenting this pattern, a data-intensive approach has not been used to determine the generality of this pattern. We assessed the strength and direction of the relationship between temperature and individual mass for almost 1,000 bird and mammal species. The majority of species did not have a strong relationship between temperature and mass. Most species had non-significant correlations with coefficients near zero. These results suggest that Bergmann's rule is not general and temperature is not a dominant driver of biogeographic variation in mass. Further understanding size variation will require integrating multiple processes that influence size. The lack of dominant temperature forcing weakens the justification for the hypothesis that global warming could result in widespread decreases in body size.

[1]Department of Wildlife Ecology and Conservation, 110 Newins-Ziegler Hall, PO Box 110430, University of Florida, Gainesville, FL 32611-0430, USA
[2]Department of Natural History, University of Florida, Gainesville, FL 32611
[3]Informatics Institute, 432 Newell Drive, PO Box 115585, University of Florida, Gainesville, FL 32611-8545

Correspondence and requests for materials should be addressed to K.R. (email: kristina.riemer@weecology.org)

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Bergmann's rule describes a negative relationship between body mass and temperature across space that is believed to be common in endothermic species[1–5]. Many hypotheses have been proposed to explain this pattern[6–8] including the heat loss hypothesis, which argues that the higher surface area to volume ratio of smaller individuals results in improved heat dissipation in hot environments[1]. Though originally described for closely-related species[6], the majority of studies have focused on the intraspecific form of Bergmann's rule[9,10] by assessing trends in individual size within a species[11–13]. Bergmann's rule has been questioned both empirically and mechanistically[14–17] but the common consensus from recent reviews is that the pattern is general[7,8,18,19].

It has recently been suggested that this negative relationship between mass and temperature could result in decreasing individual size across species in response to climate change[20] and that this may be a “third universal response to warming”[21]. The resulting shifts in size distributions could significantly alter ecological communities[22], especially if the rate of size decrease varies among species[20]. While there is limited empirical research on body size responses to changes in temperature through time (but see refs 17, 23, 24), the apparent generality of Bergmann's rule across space indicates the likelihood of a similar relationship in response to temperature dynamics.

The generality of Bergmann's rule is based on many individual studies that analyze empirical data on body size across an environmental gradient (e.g., refs 11, 25-28) and reviews that compile and evaluate the results from these studies[7,8,19]. Most individual studies of Bergmann's rule are limited by: 1) analyzing only one or a few species (e.g., ref 11); 2) using small numbers of observations (e.g., ref 26); 3) only including data at the small scales typical of ecological studies (e.g., ref 28); 4) using latitude instead of directly assessing temperature (e.g., ref); and 5) focusing on statistical significance instead of the strength of the relationship (e.g., ref

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

27). The reviews tabulate the results of these individual studies and assess patterns in the direction and significance of relationships across species. Such aggregation of published results allows for a more general understanding of the pattern but, in addition to limitations of the underlying studies, the conclusions may be influenced by publication bias and selective reporting where studies or individual analyses that do not support Bergmann's rule are published less frequently[29].

A data-intensive approach to analyzing Bergmann's rule, evaluating the pattern using large amounts of broad scale data, has the potential to overcome existing limitations in the literature and provides a new perspective on the generality of Bergmann's rule. Understanding the generality of the temperature-mass relationship has important implications for how size will respond to climate change. We use data from Vertnet[30], a large compilation of digitized museum records that contains over 700,000 globally distributed individual-level size measures, to evaluate the intraspecific relationship between temperature and mass for 960 mammal and bird species. The usable data include about 275,000 individuals with an average of about 300 individuals per species, and the individuals of each species analyzed span at least 20 years and five latitudinal degrees. This approach reduces or removes many of the limitations to previous approaches and the results suggest that Bergmann's rule is not a strong or general pattern.

RESULTS

Most of the species in this study showed weak non-significant relationships between temperature and mass (Fig. 1 and 2). The distribution of correlation coefficients was centered near zero with a mean correlation coefficient of -0.05 across species (Fig. 2A). Relationships for most species (78%) were not significantly different from zero, while 15% of species' relationships were significant and negative and 7% were significant and positive (Fig. 2A).

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Temperature explained less than 10% of variation in mass (i.e., $-0.316 < r < 0.316$) for 87% of species, and less than 25% of variation in mass in nearly all species (97%; i.e., $-0.5 < r < 0.5$), indicating that temperature explained very little of the observed variation in mass for most species (Fig. 2A).

The weak, non-directional relationships indicated by the distribution of correlation coefficients are consistent across taxonomic groups and temporal lags. Correlation coefficient distributions for both endotherm classes, mammals and birds, (Fig. 2B) are similar to the distribution for all species (Fig. 2A). Similarly, there are no unusually strong or directional correlation coefficient distributions among any of the 30 orders analyzed (Fig. 3). Correlation coefficient distributions for temperature-mass relationships using lagged temperatures were similar to those using temperature from the collection year (Fig. 4; Supplementary Fig. 1), indicating that there was not a meaningful temporal lag effect on the response of species' masses to temperature. Correlation coefficients were not generally influenced by sample size (Fig. 5A), extent of variation in temperature or mass (Fig. 5B-C), species' average mass (Fig. 5D), or species' average latitude (Fig. 5E). While temperature is considered the actual driver, some studies use latitude as a proxy when evaluating variation in size[1,31]; results did not differ qualitatively when latitude was used instead of temperature (Supplementary Fig. 2). Results were robust to a variety of decisions and stringencies about how to filter the size data (Supplementary Fig. 3 and 4).

DISCUSSION

In contrast to conventional wisdom and several recent review papers, our analysis of nearly 1,000 species shows little to no support for a negative temperature-mass relationship that is sufficiently strong or common to be considered a biogeographic rule. For most bird and

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

mammal species there was no significant change in mass across a temperature gradient and temperature explained minimal intraspecific variation in mass (Fig. 2A). This was true regardless of taxonomic group (Fig. 2 and 3), temporal lag in temperature (Fig. 4), species' size, location, or sampling intensity or extent (Fig. 5). These results are consistent with two previous studies that examined museum specimen size measurements across latitude. The first study showed that 22 out of 47 North American mammal species studied had no relationship between latitude and length, and 10 of the 25 significant relationships were opposite the expected direction[14]. The second found a similar proportion of non-significant results (42/87), but a lower proportion of significant relationships that opposed the rule (9/45) for carnivorous mammals[32]. While a greater proportion of species had significant negative relationships than positive in both our study and the two previous studies, the fraction of significant negative relationships tended to be small. In combination with these two smaller studies, our results suggest that there is little evidence for a strong or general Bergmann's rule when analyzing raw data instead of summarizing published results.

Our results are inconsistent with recent reviews, which have reported that the majority of species conform to Bergmann's rule[7,8,19]. While these reviews had meaningful proportions of results that were either non-significant or opposite of Bergmann's rule, the proportion of significant results in support of Bergmann's rule was higher and therefore resulted in conclusions that supported the generality of the temperature-mass relationship. Generalizing from results in the published literature involves the common challenges of publication bias and selective reporting[29]. In addition, because the underlying Bergmann's rule studies typically report minimal statistical information, often providing only relationship significance or direction instead of p-values or correlation coefficients[19], proper meta-analyses and associated assessments of biological significance are not possible. While several reviews found no evidence for publication

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

bias using limited analyses[7,32], the notable differences between the conclusions of our data-intensive approach and those from reviews suggests that publication bias in papers about Bergmann's rule warrants further investigation. These differences also demonstrate the value of data-intensive approaches in ecology for overcoming potential weaknesses and biases in the published literature. Directly analyzing large quantities of data from hundreds of species allows us to assess the generality of patterns originally reported in smaller studies while avoiding the risk of publication bias. This approach also makes it easier to integrate other factors that potentially influence size into future analyses. The new insight gained from this data-intensive approach demonstrates the value of investing in large compilations of ecologically-relevant data[33] and the proper training required to work with these datasets[34].

The original formulation of Bergmann's rule, and the scope of our conclusions, apply only to endotherms. However, negative temperature-mass relationships have also been documented in ectotherms, with the pattern referred to as the size-temperature rule[35–37]. In contrast to the hypotheses for Bergmann's rule, which are based primarily on homeostasis[21], the size-temperature rule in ectotherms is thought to result from differences between growth and development rates[38]. The current version of Vertnet did not have sufficient amounts of ectotherm size data to support strong conclusions about the ectotherm size-temperature rule. However, the seven amphibian and reptile species with sufficient data showed weak relationships similar to endotherms (Supplementary Fig. 5). Future work exploring the ectotherm size-temperature rule in natural systems using data-intensive approaches is necessary for understanding the generality of this pattern.

A number of processes have been suggested to produce negative temperature-mass relationships, including heat loss, starvation, resource availability, migratory ability, and phylogenetic constraints[6]. Most of the proposed hypotheses have not been tested sufficiently to

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

allow for strong conclusions to be drawn about their potential to produce Bergmann's rule[6,8,17] and the widely studied heat loss hypothesis has been questioned for a variety of reasons[6,8,14,39,40]. While no existing hypotheses have been confirmed to be operating, it is possible that some processes are producing negative relationships between size and temperature. The lack of a strong relationship does not preclude processes that result in a negative temperature-mass relationship, but it does suggest that these processes are weak relative to other factors that influence intraspecific size.

The relative importance of the many factors that can influence size within a species is as yet unknown. Size is affected by abiotic factors such as humidity and resource availability[17], characteristics of individuals like clutch size[41], and community context, including if and what kinds of gaps there are in size-related niches[42] and the trophic effects of primary productivity on consumer size[20]. Temperature itself can have indirect effects on size, such as via habitat changes in water flow or food availability, that result in size responses opposite of Bergmann's rule[21]. Anthropogenic influences have been shown to influence the effect of temperature on size[43], and similar impacts of dispersal, extinctions, and the varying scales of climate change have been proposed[44]. While our work provides some weak support for temperature having a negative effect on animal body size, given that more species have negative significant relationships than positive, it appears that some combination of other factors more strongly drives intraspecific size variation for most taxa.

The lack of evidence for temperature as a primary determinant of size variation in endotherm species calls into question the hypothesis that decreases in organism size may represent a third universal response to global warming. The potentially general decline in size with warming was addressed by assessments that evaluated dynamic body size responses to temperature using similar approaches to the Bergmann's rule reviews discussed above[17,20,21].

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

These temporal reviews had similar results to those for spatial relationships, but the conclusions of these studies clearly noted the variability in body size responses and the need for future data-intensive work[20,21] using broader temperature ranges[17] to fully assess the temperature-size relationship.

Our results in combination with those from other studies suggest that much of the observed variation in size is not explained simply by temperature. While there is still potential for the size of endotherms, and other aspects of organismal physiology and morphology, to respond to both geographic gradients in temperature and climate change, these responses may not be as easily explained solely by temperature as has been suggested. This requires that future attempts to explain variation in the size of individuals across space or time use an integrative approach to include the influence of multiple factors, and their potential interactions, on organism size. This will be facilitated by analyzing spatiotemporal data similar to that used in this study, which includes wide ranges of time, space, and environmental conditions for large numbers of species and individuals. This data-intensive approach provides a unique perspective on the general responses of bird and mammal species to temperature, and has potential to assist in further investigation of the complex combinations of factors that determine biogeographic patterns of endotherm size and how species respond to changes in climate.

METHODS

Data

Organismal data were obtained from Vertnet, a publicly available data platform for digitized specimen records from museum collections primarily in North America but that provide global data[30]. Body mass is routinely measured when organisms are collected, with relatively high precision and consistent methods, by most field biologists, whose intent is to use those

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

organisms for research and preservation in natural history collections[45,46]. These measurements are included on written labels and ledgers associated with specimens, which are digitized and mobilized in standard formats, e.g., Darwin Core[47]. In addition to other trait information, mass has recently been extracted from Darwin Core formatted records published in Vertnet and converted to a more usable form[48]. This crucial step reduces variation in how these measurements are reported by standardizing the naming conventions and harmonizing all measurement values to the same units[48]. We downloaded the entire September 2016 dataset snapshots for Mammalia, Aves, Amphibia, and Reptilia[49–52] using the Data Retriever[53] and filtered for those records that had mass measurements available. Fossil specimen records with mass measurements were removed.

We only analyzed species with at least 30 georeferenced individuals whose collection dates spanned at least 20 years and collection locations at least five degrees latitude, in order to ensure sufficient sample size and spatiotemporal extent to accurately represent each species' temperature-mass relationship. We selected individual records with geographic coordinates for collection location, collection dates between 1900 and 2010, and species-level taxonomic identification, which were evaluated to assure no issues with synonymy or clear taxon concept issues. To minimize inclusion of records of non-adult specimens, we identified the smallest mass associated with an identified adult life stage category for each species and removed all records with mass values below this minimum adult size. Results were not qualitatively different due to either additional filtering based on specimen lifestage (Supplementary Fig. 3) or removal of outliers (Supplementary Fig. 4). Temperatures were obtained from the Udel_AirT_Precip global terrestrial raster provided by NOAA from their website at http://www.esrl.noaa.gov/psd/, a 0.5 by 0.5 decimal degree grid of monthly mean temperatures from 1900 to 2010[54]. For each specimen, the mean annual temperature at its collection location was extracted for the year of

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

collection.

This resulted in a final dataset containing records for 274,652 individuals from 960 bird and mammal species[55-104]. The average number of individuals per species was 286, ranging from 30 to 15,415 individuals. The species in the dataset were diverse, including volant, non-volant, placental, and marsupial mammals, and both migratory and non-migratory birds. There were species from all continents except Antarctica, though the majority of the data were concentrated in North America (Fig. 1A). The distribution of the species' mean masses was strongly right-skewed, as expected for broad scale size distributions[105], with 74% of species having average masses less than 100 g. Size ranged from very small (3.7 g desert shrew *Notiosorex crawfordi* and 2.6 g calliope hummingbird *Stellula calliope*) to very large (78 kg California sea lion *Zalophus californianus* and 5.8 kg wild turkey *Meleagris gallopavo*). These specimen data and code have been deposited online in the Dryad Data Repository (http://datadryad.org/).

Analysis

We fit the intraspecific relationship between mean annual temperature and mass for each species with ordinary least squares linear regression (e.g., Fig. 1B-D; Supplementary Fig. 6) using the statsmodels.formula.api module in Python[106]. The strength of the relationship was evaluated using the correlation coefficient and its significance. For significance testing, we controlled for the large number of tests with false discovery rate control[107] implemented in the stats package in R[108], and used the standard alpha cut-off of 0.05. False discovery rate control maintains the Type I error rate (proportion of false positives) across all tests at the chosen value of alpha and therefore gives an accurate estimate of the number of significant relationships[107].

We investigated various potential correlates of the strength of Bergmann's rule. Because it has been argued that Bergmann's rule is exhibited more strongly by some groups than others[14],

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

we examined correlation coefficient distributions within each class and order. As a temporal lag in size response to temperature is likely, we assessed species' temperature-mass relationships using temperatures from 1 to 50 years prior to collection year. We also examined the relationship between species' correlation coefficients and five variables to understand potential statistical and biological influences on the results. We did so with the number of individuals, temperature range, and mass range to determine if the relationship was stronger when more data points or more widely varying values were available. Because it has been argued that Bergmann's rule is stronger in larger species[109] and at higher latitudes[4,43], we examined variability with both mean mass and mean latitude for each species. We also conducted all analyses using latitude instead of mean annual temperature.

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

FIGURES

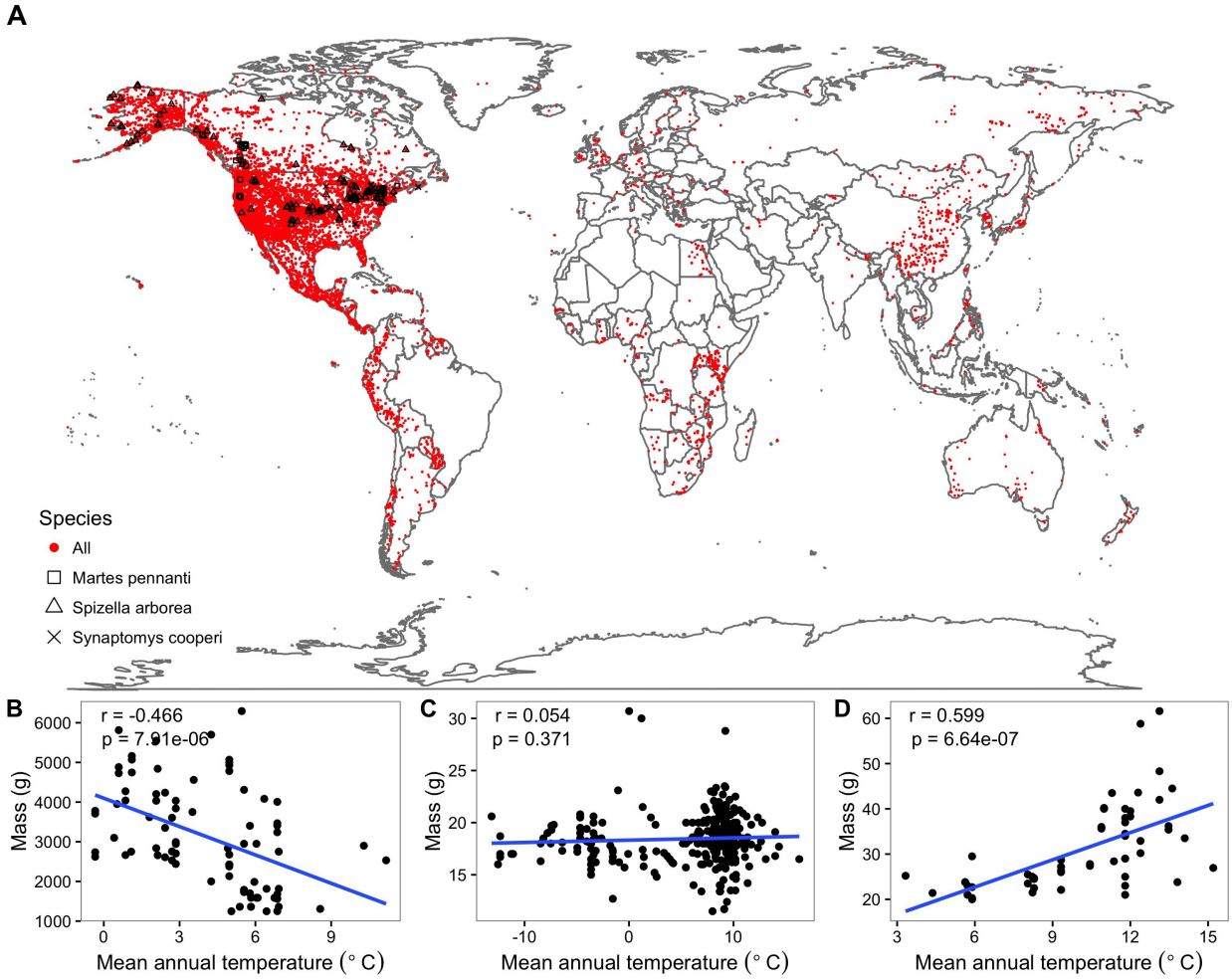

Figure 1. (A) Spatial collection locations of all individual specimens. All species shown with red circles except three species, whose relationships between mean annual temperature and mass are shown at bottom (B-D), are marked with black symbols. These species were chosen as representative of the variability in relationship strength and direction exhibited by the 978 species from the study: *Martes pennanti* had a negative relationship with temperature explaining a substantial amount of variation in mass (B; black square); *Spizella arborea* had no directional relationship between temperature and mass with temperature having little explanatory power (C; black triangle); *Synaptomys cooperi* had a strong positive temperature-mass relationship with a correlation coefficient (r) in the 99th percentile of all species' values (D; black X). Intraspecific temperature-mass relationships are shown with black circles for all individuals and ordinary least squares regression trends as blue lines. Linear regression correlation coefficients and p-values in upper left hand corner of figure for each species.

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

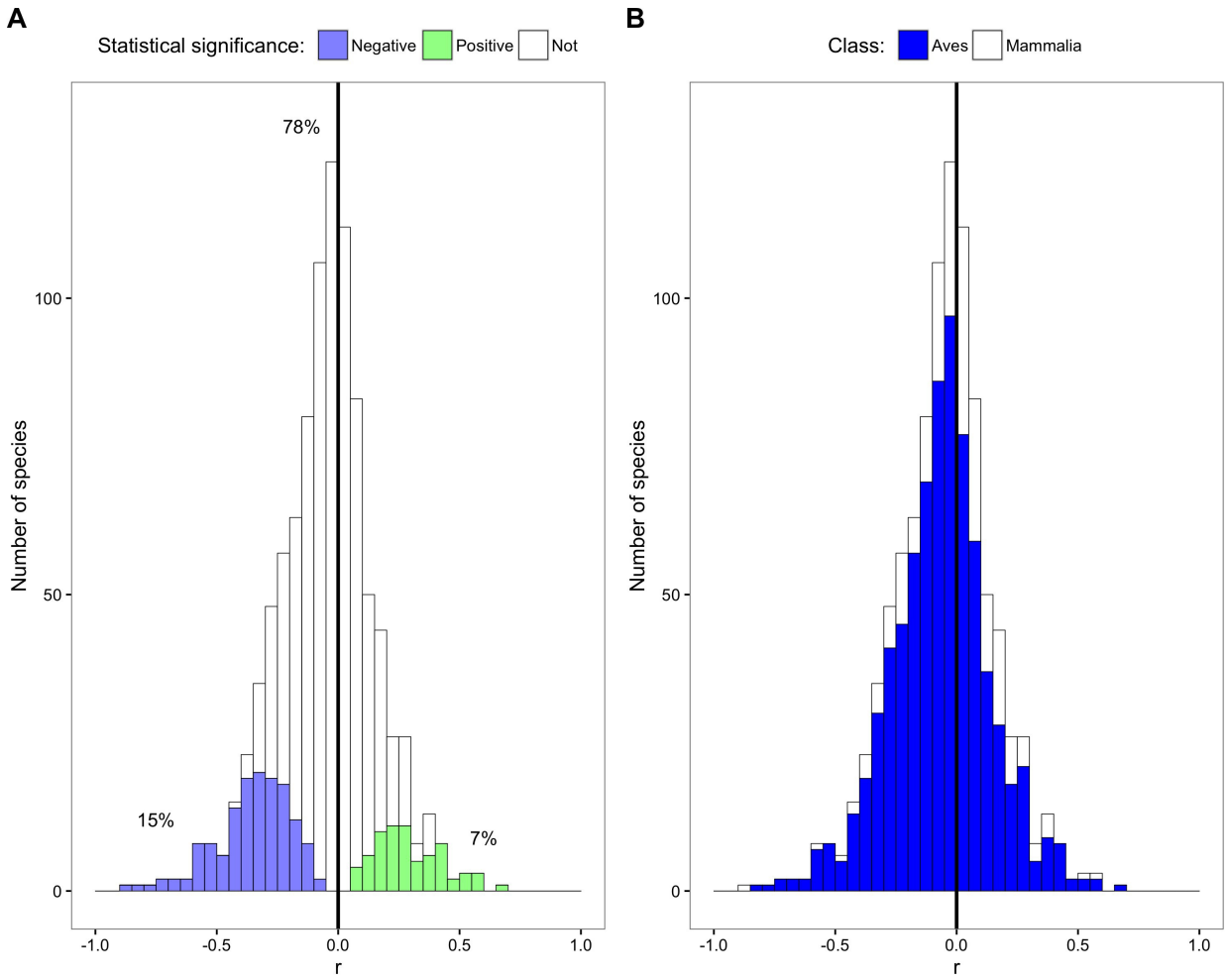

Figure 2. (A) Stacked histogram of correlation coefficients (r) for all species' intraspecific temperature-mass relationships. Colored bars are proportion of species with statistically significant relationships, both negative (purple) and positive (green), while white bars indicate proportion of species with relationship slopes that are not significantly different from zero. Percentages correspond to proportion of species in each group. (B) Stacked histogram of all species' correlation coefficients with bar color corresponding to taxonomic class. Dark vertical lines are correlation coefficients of zero.

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

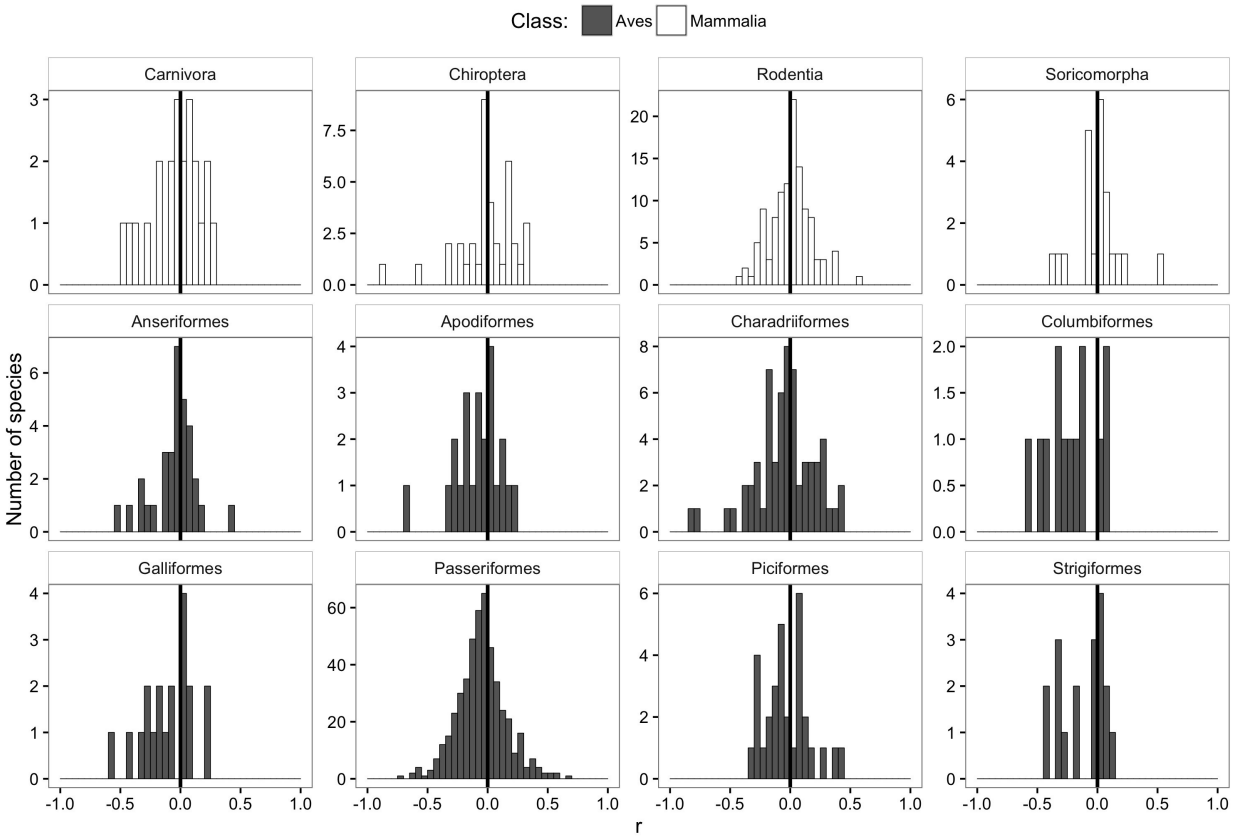

Figure 3. Stacked histograms of correlation coefficients (r) from intraspecific temperature-mass relationships for each taxonomic order represented by more than ten species, with order shown above histogram. Height of y-axis varies depending on number of species. Bar color indicates taxonomic class. Dark vertical lines are correlation coefficients of zero. Trends for the remaining 22 orders are similar.

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

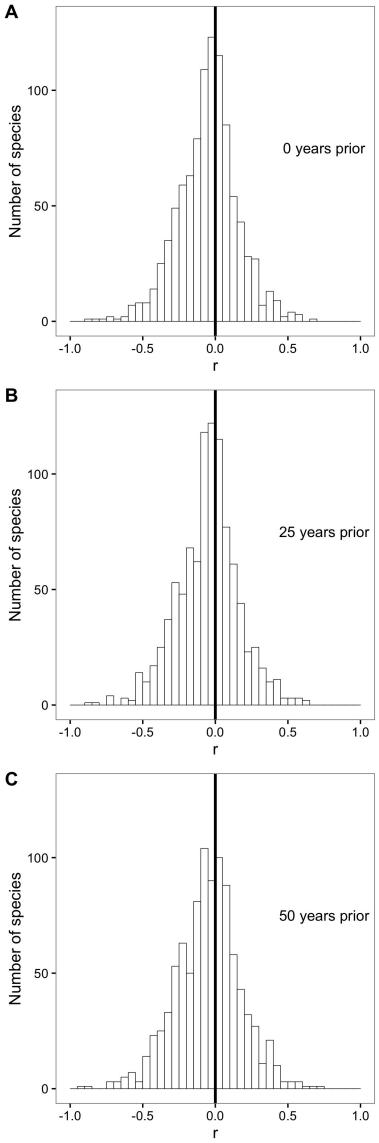

Figure 4. Histograms of correlation coefficients (r) for all species' intraspecific temperature-mass relationships with mean annual temperature from (A) the year in which individuals were collected, (B) 25 years prior to collection year, and (C) 50 years prior to collection year. Dark vertical lines are correlation coefficients of zero.

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

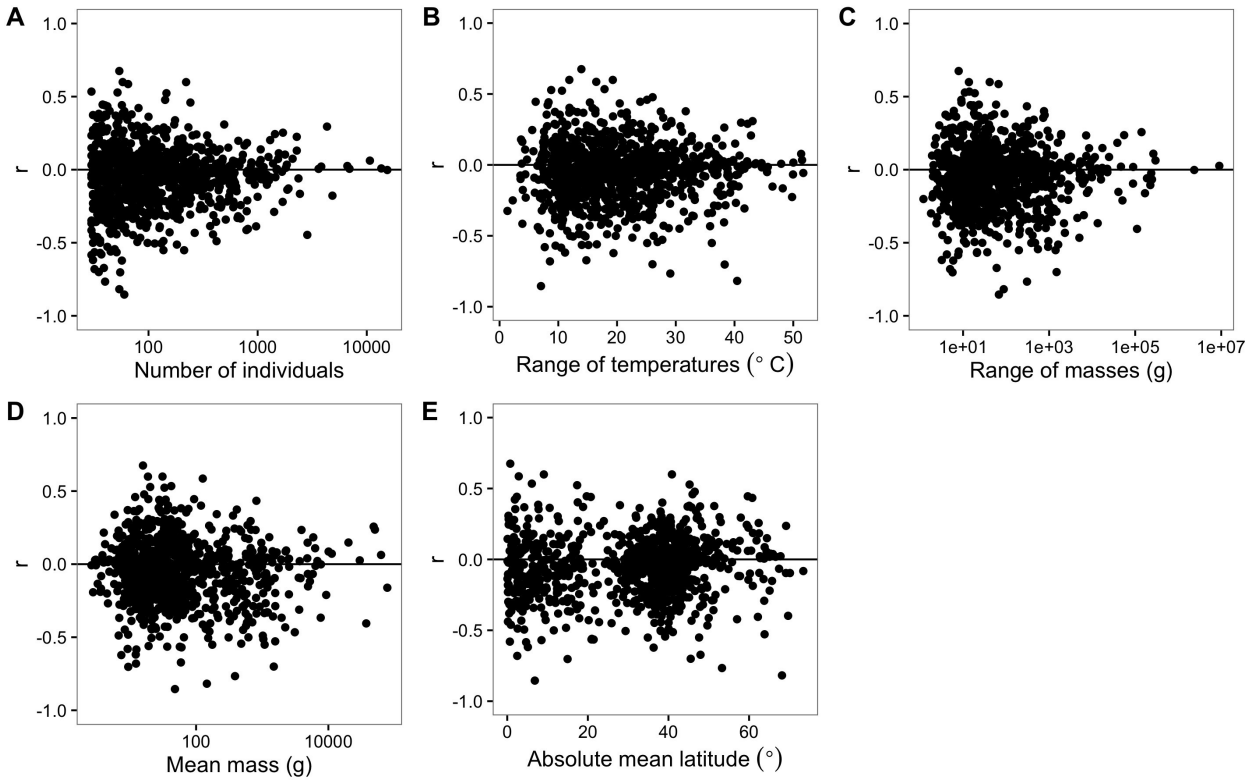

Figure 5. Variation in all species' correlation coefficients (r) across the following variables for each species: (A) number of individuals, (B) collection year temperature range, (C) mass range, (D) mean mass, and (E) absolute mean latitude. Horizontal lines are correlation coefficients of zero. The x-axes of some plots (A, C, D) are on a log scale to better show spread of values.

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

REFERENCES

1. Bergmann, C. Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Gottinger Stud.* **1,** 595–708 (1847).
2. Brown, J. H. & Lee, A. K. Bergmann's Rule and Climatic Adaptation in Woodrats (Neotoma). *Evolution* **23,** 329–338 (1969).
3. Kendeigh, S. C. Tolerance of cold and Bergmann's rule. *The Auk* **86,** 13–25 (1969).
4. Freckleton, R., Harvey, P. & Pagel, M. Bergmann's rule and body size in mammals. *Am. Nat.* **161,** 821–825 (2003).
5. Carotenuto, F., Diniz-Filho, J. A. F. & Raia, P. Space and time: The two dimensions of Artiodactyla body mass evolution. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **437,** 18–25 (2015).
6. Blackburn, T., Gaston, K. & Loder, N. Geographic gradients in body size: a clarification of Bergmann's rule. *Divers. Distrib.* 165–174 (1999).
7. Ashton, K. Patterns of within- species body size variation of birds: strong evidence for Bergmann's rule. *Glob. Ecol. Biogeogr.* **11,** 505–523 (2002).
8. Watt, C., Mitchell, S. & Salewski, V. Bergmann's rule; a concept cluster? *Oikos* **119,** 89–100 (2010).
9. Rensch, B. Some problems of geographical variation and species-formation. *Proc. Linn. Soc. Lond.* **150,** 275–278 (1938).
10. Meiri, S. Bergmann's rule-what's in a name? *Glob. Ecol. Biogeogr.* **20,** 203–207 (2011).
11. Langvatn, R. & Albon, S. D. Geographic Clines in Body-Weight of Norwegian Red Deer - A Novel Explanation of Bergmann Rule. *Holarct. Ecol.* **9,** 285–293 (1986).
12. Gardner, J. L., Heinsohn, R. & Joseph, L. Shifting latitudinal clines in avian body size correlate with global warming in Australian passerines. *Proc. Biol. Sci.* **276,** 3845–3852 (2009).
13. Yom-Tov, Y. & Geffen, E. Geographic variation in body size: The effects of ambient

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

temperature and precipitation. *Oecologia* **148,** 213–218 (2006).

14. McNab, B. K. On the ecological significance of Bergmann's rule. *Ecology* **52,** 845-854 (1971).
15. Geist, V. Bergmann's rule is invalid. *Can. J. Zool.* **65,** 1035-1038 (1987).
16. Huston, M. A. & Wolverton, S. Regulation of animal size by eNPP, Bergmann's rule, and related phenomena. *Ecol. Monogr.* **81,** 349–405 (2011).
17. Teplitsky, C. & Millien, V. Climate warming and Bergmann's rule through time: is there any evidence? *Evol. Appl.* **7,** 156–68 (2014).
18. Ashton, K., Tracy, M. & Queiroz, A. D. Is Bergmann's rule valid for mammals? *Am. Nat.* **156,** 390–415 (2000).
19. Meiri, S. & Dayan, T. On the validity of Bergmann's rule. *J. Biogeogr.* 331–351 (2003).
20. Sheridan, J. A. & Bickford, D. Shrinking body size as an ecological response to climate change. *Nat. Clim. Change* **1,** 401–406 (2011).
21. Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L. & Heinsohn, R. Declining body size: a third universal response to warming? *Trends Ecol. Evol.* **26,** 285–91 (2011).
22. Brose, U. *et al.* Climate change in size-structured ecosystems. *Philos. Trans. R. Soc. B Biol. Sci.* **367,** 2903–2912 (2012).
23. Smith, F., Betancourt, J. & Brown, J. Evolution of body size in the woodrat over the past 25,000 years of climate change. *Science* **270,** 2012-2014 (1995).
24. Caruso, N. M., Sears, M. W., Adams, D. C. & Lips, K. R. Widespread rapid reductions in body size of adult salamanders in response to climate change. *Glob. Change Biol.* **20,** 1751–1759 (2014).
25. Barnett, R. J. Bergmann â s Rule and Variation in Structures Related to Feeding in the Gray Squirrel. *Evolution* **31,** 538–545 (1977).
26. Fuentes, E. R. & Jaksić, F. M. Latitudinal Size Variation of Chilean Foxes: Tests of Alternative Hypotheses. *Ecology* **60,** 43–47 (1979).
27. Dayan, T., Tchernov, E., Yom-tov, Y. & Simberloff, D. Ecological Character Displacement

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

in Saharo-Arabian Vulpes : Outfoxing Bergmann â s Rule. *Oikos* **55,** 263–272 (1989).

28. Sand, H., Cederlund, G. & Danell, K. Geographical and latitudinal variation in growth patterns and adult body size of Swedish moose (Alces alces). *Oecologia* **102,** 433–442 (1995).
29. Koricheva, J., Gurevitch, J. & Mengersen, K. *Handbook of meta-analysis in ecology and evolution*. (2013). doi:10.2307/j.ctt24hq6n
30. Constable, H. *et al.* VertNet: A new model for biodiversity data sharing. *PLoS Biol.* **8,** 1–4 (2010).
31. Stillwell, R. C. Are latitudinal clines in body size adaptive? *Oikos* **119,** 1387–1390 (2010).
32. Meiri, S., Dayan, T. & Simberloff, D. Carnivores, biases and Bergmann's rule. *Biol. J. Linn. Soc.* **81,** 579–588 (2004).
33. Hampton, S. E. *et al.* Big data and the future of ecology. *Front. Ecol. Environ.* **11,** 156–162 (2013).
34. Hampton, S. E. *et al.* Skills and knowledge for data-intensive environmental research. *Bioscience* (in press).
35. Ray, C. The application of Bergmann's and Allen's rules to the poikilotherms. *J. Morphol.* **106,** 85–108 (1960).
36. Angilletta, M. J. & Dunham, A. E. The temperature-size rule in ectotherms: Simple evolutionary explanations may not be general. *Am. Nat.* **162,** 332–342 (2003).
37. Adams, D. C. & Church, J. O. Amphibians do not follow Bergmann's rule. *Evolution* **62,** 413–420 (2008).
38. Forster, J., Hirst, A. G. & Woodward, G. Growth and development rates have different thermal responses. *Am. Nat.* **178,** 668–78 (2011).
39. James, F. C. Geographic Size Variation in Birds and Its Relationship to Climate. *Ecology* **51,** 365–390 (1970).
40. McNamara, J. M., Higginson, A. D. & Verhulst, S. The influence of the starvation-predation trade-off on the relationship between ambient temperature and body size among endotherms. *J. Biogeogr.* **43,** 809–819 (2016).

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

41. Boyer, A. G., Cartron, J.-L. E. & Brown, J. H. Interspecific pairwise relationships among body size, clutch size and latitude: deconstructing a macroecological triangle in birds. *J. Biogeogr.* **37,** 47–56 (2009).

42. Smith, F. a *et al.* The evolution of maximum body size of terrestrial mammals. *Science* **330,** 1216–1219 (2010).

43. Faurby, S. & Araújo, M. B. Anthropogenic impacts weaken Bergmann's rule. *Ecography* 1–2 (2016). doi:10.1111/ecog.02287

44. Clauss, M., Dittmann, M. T., Müller, D. W. H., Meloro, C. & Codron, D. Bergmann′s rule in mammals: A cross-species interspecific pattern. *Oikos* **122,** 1465–1472 (2013).

45. Winker, K. Obtaining, Preserving, and Preparing Bird Specimens. *J. Field Ornithol.* **71,** 250–297 (2000).

46. Hoffmann, A. *et al.* Field Methods and Techniques for Monitoring Mammals. *Man. Field Rec. Tech. Protoc. Taxa Biodivers. Invent. Monit.* **8,** 482–529 (2010).

47. Wieczorek, J. *et al.* Darwin Core: An Evolving Community-Developed Biodiversity Data Standard. *PLoS ONE* **7,** e29715–e29715 (2012).

48. Guralnick, R. P. *et al.* The importance of digitized biocollections as a source of trait data and a new VertNet resource. *Database J. Biol. Databases Curation* 1–13 (2016). doi:10.1093/database/baw158

49. Bloom, D., Wieczorek, J. & Russell, L. Vertnet_Amphibia_Sep2016. CyVerse Data Commons. http://datacommons.cyverse.org/browse/iplant/home/shared/commons_repo/curated/Vertnet_Amphibia_Sep2016. 19 October 2016, date last accessed. (2016).

50. Bloom, D., Wieczorek, J. & Russell, L. Vertnet_Aves_Sep2016. CyVerse Data Commons. http://datacommons.cyverse.org/browse/iplant/home/shared/commons_repo/curated/Vertnet_Aves_Sep2016. 19 October 2016, date last accessed. (2016).

51. Bloom, D., Wieczorek, J. & Russell, L. Vertnet_Mammalia_Sep2016. CyVerse Data Commons.

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

http://datacommons.cyverse.org/browse/iplant/home/shared/commons_repo/curated/Vertnet_Mammalia_Sep2016. 19 October 2016, date last accessed. (2016).

52. Bloom, D., Wieczorek, J. & Russell, L. Vertnet_Reptilia_Sep2016. CyVerse Data Commons. http://datacommons.cyverse.org/browse/iplant/home/shared/commons_repo/curated/Vertnet_Reptilia_Sep2016. 19 October 2016, date last accessed. (2016).

53. Morris, B. D. & White, E. P. The EcoData Retriever: Improving Access to Existing Ecological Data. *PLoS ONE* **8,** 1–7 (2013).

54. Willmott, C. J. & Matsuura, K. Terrestrial Air Temperature and Precipitation: Monthly and Annual Time Series (1950-1999). http://climate.geog.udel.edu/~climate/html_pages/README.ghcn_ts2.html (2001).

55. MSB Mammal Collection (Arctos). Museum of Southwestern Biology. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=msb_mamm (source published on 2015-10-27, accessed on 2017-10-19)

56. Ornithology Collection Passeriformes - Royal Ontario Museum. Royal Ontario Museum. Source: http://gbif.rom.on.ca:8180/ipt/resource.do?r=birdspass (source published on 2015-09-11, accessed on 2017-10-19)

57. MVZ Mammal Collection (Arctos). Museum of Vertebrate Zoology, UC Berkeley. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=mvz_mammal (source published on 2015-10-27, accessed on 2017-10-19)

58. MVZ Bird Collection (Arctos). Museum of Vertebrate Zoology, UC Berkeley. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=mvz_bird (source published on 2015-10-27, accessed on 2017-10-19)

59. KUBI Mammalogy Collection. KU Biodiversity Institute. Source: http://ipt.nhm.ku.edu/ipt/resource.do?r=kubi_mammals (source published on 2016-02-03, accessed on 2017-10-19)

60. CAS Ornithology (ORN). California Academy of Sciences. Source: http://ipt.calacademy.org:8080/ipt/resource.do?r=orn (source published on 2015-10-05,

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

accessed on 2017-10-19)

61. DMNS Bird Collection (Arctos). Denver Museum of Nature & Science. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=dmns_bird (source published on 2015-10-26, accessed on 2017-10-19)
62. UCLA Donald R. University of California, Los Angeles. Dickey Bird and Mammal Collection. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=ucla_birds_mammals (source published on 2015-03-02, accessed on 2017-10-19)
63. DMNS Mammal Collection (Arctos). Denver Museum of Nature & Science. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=dmns_mamm (source published on 2015-10-26, accessed on 2017-10-19)
64. UAM Mammal Collection (Arctos). University of Alaska Museum. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=uam_mamm (source published on 2015-10-27, accessed on 2017-10-19)
65. UWBM Mammalogy Collection. University of Washington Burke Museum. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=uwbm_mammals (source published on 2015-02-23, accessed on 2017-10-19)
66. UAM Bird Collection (Arctos). University of Alaska Museum. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=uam_bird (source published on 2015-10-27, accessed on 2017-10-19)
67. UMMZ Birds Collection. University of Michigan Museum of Zoology. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=ummz_birds (source published on 2015-10-28, accessed on 2017-10-19)
68. CUMV Bird Collection (Arctos). Cornell University Museum of Vertebrates. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=cumv_bird (source published on 2015-10-26, accessed on 2017-10-19)
69. CUMV Mammal Collection (Arctos). Cornell University Museum of Vertebrates. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=cumv_mamm (source published on 2015-10-26,

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

accessed on 2017-10-19)

70. MLZ Bird Collection (Arctos). Moore Laboratory of Zoology. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=mlz_bird (source published on 2015-10-26, accessed on 2017-10-19)

71. LACM Vertebrate Collection. Natural History Museum of Los Angeles County. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=lacm_verts (source published on 2015-04-17, accessed on 2017-10-19)

72. CHAS Mammalogy Collection (Arctos). Chicago Academy of Sciences. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=chas_mammals (source published on 2016-06-23, accessed on 2017-10-19)

73. Ornithology Collection Non Passeriformes - Royal Ontario Museum. Royal Ontario Museum. Source: http://gbif.rom.on.ca:8180/ipt/resource.do?r=birdsnonpass (source published on 2015-06-02, accessed on 2017-10-19)

74. KUBI Ornithology Collection. KU Biodiversity Institute. Source: http://ipt.nhm.ku.edu/ipt/resource.do?r=kubi_ornithology (source published on 2014-12-17, accessed on 2017-10-19)

75. MSB Bird Collection (Arctos). Museum of Southwestern Biology. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=msb_bird (source published on 2015-10-27, accessed on 2017-10-19)

76. Biodiversity Research and Teaching Collections - TCWC Vertebrates. Texas A&M University Biodiversity Research and Teaching Collections. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=tcwc_verts (source published on 2015-09-05, accessed on 2017-10-19)

77. TTU Mammals Collection. Museum of Texas Tech University (TTU). Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=ttu_mammals (source published on 2015-02-26, accessed on 2017-10-19)

78. CAS Mammalogy (MAM). California Academy of Sciences. Source:

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

http://ipt.calacademy.org:8080/ipt/resource.do?r=mam (source published on 2015-10-05, accessed on 2017-10-19)

79. Vertebrate Zoology Division - Ornithology, Yale Peabody Museum. Yale Peabody Museum. Source: http://ipt.peabody.yale.edu/ipt/resource.do?r=ipt_vz_orn (source published on 2015-10-09, accessed on 2017-10-19)
80. University of Alberta Mammalogy Collection (UAMZ). University of Alberta Museums. Dataset DOI: doi:10.18165/brxhjf. Source: http://web.macs.ualberta.ca:8088/ipt/resource?r=uamz_mammalogy (source published on 2015-09-20, accessed on 2017-10-19)
81. UAZ Mammal Collection. University of Arizona Museum of Natural History. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=uaz_mammals (source published on 2016-03-29, accessed on 2017-10-19)
82. Conner Museum. Charles R. CRCM Vertebrate Collection. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=crcm_verts (source published on 2015-10-13, accessed on 2017-10-19)
83. SBMNH Vertebrate Zoology. Santa Barbara Museum of Natural History. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=sbmnh_verts (source published on 2015-02-17, accessed on 2017-10-19)
84. Cowan Tetrapod Collection - Birds. University of British Columbia Beaty Biodiversity Museum. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=ubc_bbm_ctc_birds (source published on 2015-04-07, accessed on 2017-10-19)
85. Cowan Tetrapod Collection - Mammals. University of British Columbia Beaty Biodiversity Museum. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=ubc_bbm_ctc_mammals (source published on 2015-04-07, accessed on 2017-10-19)
86. NMMNH Mammal. New Mexico Museum of Natural History and Science. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=nmmnh_mammals (source published on 2015-04-14, accessed on 2017-10-19)
87. Schmidt Museum of Natural History_Mammals. Schmidt Museum of Natural History,

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Emporia State University. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=kstc_schmidt_mammals (source published on 2015-02-12, accessed on 2017-10-19)

88. USAC Mammals Collection. Universidad de San Carlos de Guatemala. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=usac_mammals (source published on 2013-11-04, accessed on 2017-10-19)

89. MLZ Mammal Collection (Arctos). Moore Laboratory of Zoology. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=mlz_mamm (source published on 2015-10-26, accessed on 2017-10-19)

90. Ohio State University Tetrapod Division - Bird Collection (OSUM). Ohio State University. Source: http://hymfiles.biosci.ohio-state.edu:8080/ipt/resource.do?r=osum-birds (source published on 2015-05-22, accessed on 2017-10-19)

91. AMNH Mammal Collections. American Museum of Natural History. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=amnh_mammals (source published on 2015-02-12, accessed on 2017-10-19)

92. DMNH Birds. Delaware Museum of Natural History. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=dmnh_birds (source published on 2015-10-20, accessed on 2017-10-19)

93. CM Birds Collection. Carnegie Museum of Natural History. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=cm_birds (source published on 2015-10-11, accessed on 2017-10-19)

94. WNMU Mammal Collection (Arctos). Western New Mexico University. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=wnmu_mamm (source published on 2015-10-27, accessed on 2017-10-19)

95. UCM Mammals Collection. University of Colorado Museum of Natural History. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=ucm_mammals (source published on 2015-10-27, accessed on 2017-10-19)

96. UWYMV Bird Collection (Arctos). University of Wyoming Museum of Vertebrates. Source:

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

http://ipt.vertnet.org:8080/ipt/resource.do?r=uwymv_bird (source published on 2015-10-27, accessed on 2017-10-19)

97. NCSM Mammals Collection. North Carolina Museum of Natural Sciences. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=ncsm_mammals (source published on 2015-02-20, accessed on 2017-10-19)

98. Vertebrate Zoology Division - Mammalogy, Yale Peabody Museum. Yale Peabody Museum. Source: http://ipt.peabody.yale.edu/ipt/resource.do?r=ipt_vz_mam (source published on 2015-10-09, accessed on 2017-10-19)

99. HSU Wildlife Mammals. Humboldt State University. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=hsu_wildlife_mammals (source published on 2016-03-14, accessed on 2017-10-19)

100. WNMU Bird Collection (Arctos). Western New Mexico University. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=wnmu_bird (source published on 2015-10-27, accessed on 2017-10-19)

101. UWBM Ornithology Collection. University of Washington Burke Museum. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=uwbm_birds (source published on 2015-02-24, accessed on 2017-10-19)

102. UCM Birds. University of Colorado Museum of Natural History. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=ucm_birds (source published on 2015-10-27, accessed on 2017-10-19)

103. University of Alberta Ornithology Collection (UAMZ). University of Alberta Museums. Dataset DOI: doi:10.18165/srgkci. Source: http://web.macs.ualberta.ca:8088/ipt/resource?r=uamz_ornithology (source published on 2015-09-24, accessed on 2017-10-19)

104. SDNHM Birds Collection. San Diego Natural History Museum. Source: http://ipt.vertnet.org:8080/ipt/resource.do?r=sdnhm_birds (source published on 2015-04-06, accessed on 2017-10-19)

105. Brown, J. H. & Nicoletto, P. F. Spatial Scaling of Species Composition: Body Masses of

bioRxiv preprint doi: https://doi.org/10.1101/113753; this version posted March 8, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

North American Land Mammals. *Am. Nat.* **138,** 1478–1512 (1991).

106. Seabold, S. & Perktold, J. Statsmodels: econometric and statistical modeling with Python. *Proc. 9th Python Sci. Conf.* 57–61 (2010).

107. Benajmini, Y. & Hochberg, Y. Controlling the False Discovery Rate : A Practical and Powerful Approach to Multiple Testing. *J R Stat. Soc B* **57,** 289–300 (1995).

108. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria (2016).

109. Steudel, K., Porter, W. P. & Sher, D. The biophysics of Bergmann's rule: a comparison of the effects of pelage and body size variation on metabolic rate. *Can. J. Zool.* **72,** 70–77 (1994).

Author contributions

K.R. and E.P. conceived the study and analyzed the data, K.R. and R.P.G. procured the data, and all authors collaborated in manuscript preparation.

Acknowledgements

This research was supported by the Gordon and Betty Moore Foundation's Data-Driven Discovery Initiative through Grant GBMF4563 and by a CAREER award from the U.S. National Science Foundation (DEB-0953694), both to E.P. White. Vertnet was supported by the U.S. National Science Foundation (NSF DBI 1062148), with additional thanks to all of the data providers. Thanks to Dan McGlinn for assistance with developing this research and Rafael LaFrance for his trait extraction work.

Competing financial interests

No competing financial interests