

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47

No general relationship between mass and temperature in endotherm species

Kristina Riemer^{1*}, Robert P Guralnick², 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.

¹Department of Wildlife Ecology and Conservation, 110 Newins-Ziegler Hall, PO Box 110430, University of Florida, Gainesville, FL 32611-0430, USA

²Department of Natural History, University of Florida, Gainesville, FL 32611

³Informatics 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)

48 Bergmann's rule describes a negative relationship between body mass and temperature
49 across space that is believed to be common in endothermic species¹⁻⁵. Many hypotheses have
50 been proposed to explain this pattern⁶⁻⁸ including the heat loss hypothesis, which argues that the
51 higher surface area to volume ratio of smaller individuals results in improved heat dissipation in
52 hot environments¹. Though originally described for closely-related species⁶, the majority of
53 studies have focused on the intraspecific form of Bergmann's rule^{9,10} by assessing trends in
54 individual size within a species¹¹⁻¹³. Bergmann's rule has been questioned both empirically and
55 mechanistically¹⁴⁻¹⁷ but the common consensus from recent reviews is that the pattern is
56 general^{7,8,18,19}.

57 It has recently been suggested that this negative relationship between mass and
58 temperature could result in decreasing individual size across species in response to climate
59 change²⁰ and that this may be a “third universal response to warming”²¹. The resulting shifts in
60 size distributions could significantly alter ecological communities²², especially if the rate of size
61 decrease varies among species²⁰. While there is limited empirical research on body size
62 responses to changes in temperature through time (but see refs 17, 23, 24), the apparent
63 generality of Bergmann's rule across space indicates the likelihood of a similar relationship in
64 response to temperature dynamics.

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

72 27). The reviews tabulate the results of these individual studies and assess patterns in the
73 direction and significance of relationships across species. Such aggregation of published results
74 allows for a more general understanding of the pattern but, in addition to limitations of the
75 underlying studies, the conclusions may be influenced by publication bias and selective reporting
76 where studies or individual analyses that do not support Bergmann's rule are published less
77 frequently²⁹.

78 A data-intensive approach to analyzing Bergmann's rule, evaluating the pattern using
79 large amounts of broad scale data, has the potential to overcome existing limitations in the
80 literature and provides a new perspective on the generality of Bergmann's rule. Understanding
81 the generality of the temperature-mass relationship has important implications for how size will
82 respond to climate change. We use data from Vertnet³⁰, a large compilation of digitized museum
83 records that contains over 700,000 globally distributed individual-level size measures, to
84 evaluate the intraspecific relationship between temperature and mass for 960 mammal and bird
85 species. The usable data include about 275,000 individuals with an average of about 300
86 individuals per species, and the individuals of each species analyzed span at least 20 years and
87 five latitudinal degrees. This approach reduces or removes many of the limitations to previous
88 approaches and the results suggest that Bergmann's rule is not a strong or general pattern.

89

90 **RESULTS**

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

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

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

115

116 **DISCUSSION**

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

120 mammal species there was no significant change in mass across a temperature gradient and
121 temperature explained minimal intraspecific variation in mass (Fig. 2A). This was true regardless
122 of taxonomic group (Fig. 2 and 3), temporal lag in temperature (Fig. 4), species' size, location, or
123 sampling intensity or extent (Fig. 5). These results are consistent with two previous studies that
124 examined museum specimen size measurements across latitude. The first study showed that 22
125 out of 47 North American mammal species studied had no relationship between latitude and
126 length, and 10 of the 25 significant relationships were opposite the expected direction¹⁴. The
127 second found a similar proportion of non-significant results (42/87), but a lower proportion of
128 significant relationships that opposed the rule (9/45) for carnivorous mammals³². While a greater
129 proportion of species had significant negative relationships than positive in both our study and
130 the two previous studies, the fraction of significant negative relationships tended to be small. In
131 combination with these two smaller studies, our results suggest that there is little evidence for a
132 strong or general Bergmann's rule when analyzing raw data instead of summarizing published
133 results.

134 Our results are inconsistent with recent reviews, which have reported that the majority of
135 species conform to Bergmann's rule^{7,8,19}. While these reviews had meaningful proportions of
136 results that were either non-significant or opposite of Bergmann's rule, the proportion of
137 significant results in support of Bergmann's rule was higher and therefore resulted in conclusions
138 that supported the generality of the temperature-mass relationship. Generalizing from results in
139 the published literature involves the common challenges of publication bias and selective
140 reporting²⁹. In addition, because the underlying Bergmann's rule studies typically report minimal
141 statistical information, often providing only relationship significance or direction instead of p-
142 values or correlation coefficients¹⁹, proper meta-analyses and associated assessments of
143 biological significance are not possible. While several reviews found no evidence for publication

144 bias using limited analyses^{7,32}, the notable differences between the conclusions of our data-
145 intensive approach and those from reviews suggests that publication bias in papers about
146 Bergmann's rule warrants further investigation. These differences also demonstrate the value of
147 data-intensive approaches in ecology for overcoming potential weaknesses and biases in the
148 published literature. Directly analyzing large quantities of data from hundreds of species allows
149 us to assess the generality of patterns originally reported in smaller studies while avoiding the
150 risk of publication bias. This approach also makes it easier to integrate other factors that
151 potentially influence size into future analyses. The new insight gained from this data-intensive
152 approach demonstrates the value of investing in large compilations of ecologically-relevant
153 data³³ and the proper training required to work with these datasets³⁴.

154 The original formulation of Bergmann's rule, and the scope of our conclusions, apply
155 only to endotherms. However, negative temperature-mass relationships have also been
156 documented in ectotherms, with the pattern referred to as the size-temperature rule^{35–37}. In
157 contrast to the hypotheses for Bergmann's rule, which are based primarily on homeostasis²¹, the
158 size-temperature rule in ectotherms is thought to result from differences between growth and
159 development rates³⁸. The current version of Vertnet did not have sufficient amounts of ectotherm
160 size data to support strong conclusions about the ectotherm size-temperature rule. However, the
161 seven amphibian and reptile species with sufficient data showed weak relationships similar to
162 endotherms (Supplementary Fig. 5). Future work exploring the ectotherm size-temperature rule
163 in natural systems using data-intensive approaches is necessary for understanding the generality
164 of this pattern.

165 A number of processes have been suggested to produce negative temperature-mass
166 relationships, including heat loss, starvation, resource availability, migratory ability, and
167 phylogenetic constraints⁶. Most of the proposed hypotheses have not been tested sufficiently to

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

175 The relative importance of the many factors that can influence size within a species is as
176 yet unknown. Size is affected by abiotic factors such as humidity and resource availability¹⁷,
177 characteristics of individuals like clutch size⁴¹, and community context, including if and what
178 kinds of gaps there are in size-related niches⁴² and the trophic effects of primary productivity on
179 consumer size²⁰. Temperature itself can have indirect effects on size, such as via habitat changes
180 in water flow or food availability, that result in size responses opposite of Bergmann's rule²¹.
181 Anthropogenic influences have been shown to influence the effect of temperature on size⁴³, and
182 similar impacts of dispersal, extinctions, and the varying scales of climate change have been
183 proposed⁴⁴. While our work provides some weak support for temperature having a negative
184 effect on animal body size, given that more species have negative significant relationships than
185 positive, it appears that some combination of other factors more strongly drives intraspecific size
186 variation for most taxa.

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

192 These temporal reviews had similar results to those for spatial relationships, but the conclusions
193 of these studies clearly noted the variability in body size responses and the need for future data-
194 intensive work^{20,21} using broader temperature ranges¹⁷ to fully assess the temperature-size
195 relationship.

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

209

210 **METHODS**

211 **Data**

212 Organismal data were obtained from Vertnet, a publicly available data platform for
213 digitized specimen records from museum collections primarily in North America but that provide
214 global data³⁰. Body mass is routinely measured when organisms are collected, with relatively
215 high precision and consistent methods, by most field biologists, whose intent is to use those

216 organisms for research and preservation in natural history collections^{45,46}. These measurements
217 are included on written labels and ledgers associated with specimens, which are digitized and
218 mobilized in standard formats, e.g., Darwin Core⁴⁷. In addition to other trait information, mass
219 has recently been extracted from Darwin Core formatted records published in Vertnet and
220 converted to a more usable form⁴⁸. This crucial step reduces variation in how these
221 measurements are reported by standardizing the naming conventions and harmonizing all
222 measurement values to the same units⁴⁸. We downloaded the entire September 2016 dataset
223 snapshots for Mammalia, Aves, Amphibia, and Reptilia⁴⁹⁻⁵² using the Data Retriever⁵³ and
224 filtered for those records that had mass measurements available. Fossil specimen records with
225 mass measurements were removed.

226 We only analyzed species with at least 30 georeferenced individuals whose collection
227 dates spanned at least 20 years and collection locations at least five degrees latitude, in order to
228 ensure sufficient sample size and spatiotemporal extent to accurately represent each species'
229 temperature-mass relationship. We selected individual records with geographic coordinates for
230 collection location, collection dates between 1900 and 2010, and species-level taxonomic
231 identification, which were evaluated to assure no issues with synonymy or clear taxon concept
232 issues. To minimize inclusion of records of non-adult specimens, we identified the smallest mass
233 associated with an identified adult life stage category for each species and removed all records
234 with mass values below this minimum adult size. Results were not qualitatively different due to
235 either additional filtering based on specimen lifestage (Supplementary Fig. 3) or removal of
236 outliers (Supplementary Fig. 4). Temperatures were obtained from the Udel_AirT_Precip global
237 terrestrial raster provided by NOAA from their website at <http://www.esrl.noaa.gov/psd/>, a 0.5
238 by 0.5 decimal degree grid of monthly mean temperatures from 1900 to 2010⁵⁴. For each
239 specimen, the mean annual temperature at its collection location was extracted for the year of

240 collection.

241 This resulted in a final dataset containing records for 274,652 individuals from 960 bird
242 and mammal species⁵⁵⁻¹⁰⁴. The average number of individuals per species was 286, ranging from
243 30 to 15,415 individuals. The species in the dataset were diverse, including volant, non-volant,
244 placental, and marsupial mammals, and both migratory and non-migratory birds. There were
245 species from all continents except Antarctica, though the majority of the data were concentrated
246 in North America (Fig. 1A). The distribution of the species' mean masses was strongly right-
247 skewed, as expected for broad scale size distributions¹⁰⁵, with 74% of species having average
248 masses less than 100 g. Size ranged from very small (3.7 g desert shrew *Notiosorex crawfordi*
249 and 2.6 g calliope hummingbird *Stellula calliope*) to very large (78 kg California sea lion
250 *Zalophus californianus* and 5.8 kg wild turkey *Meleagris gallopavo*). These specimen data and
251 code have been deposited online in the Dryad Data Repository (<http://datadryad.org/>).

252

253 **Analysis**

254 We fit the intraspecific relationship between mean annual temperature and mass for each
255 species with ordinary least squares linear regression (e.g., Fig. 1B-D; Supplementary Fig. 6)
256 using the statsmodels.formula.api module in Python¹⁰⁶. The strength of the relationship was
257 evaluated using the correlation coefficient and its significance. For significance testing, we
258 controlled for the large number of tests with false discovery rate control¹⁰⁷ implemented in the
259 stats package in R¹⁰⁸, and used the standard alpha cut-off of 0.05. False discovery rate control
260 maintains the Type I error rate (proportion of false positives) across all tests at the chosen value
261 of alpha and therefore gives an accurate estimate of the number of significant relationships¹⁰⁷.

262 We investigated various potential correlates of the strength of Bergmann's rule. Because
263 it has been argued that Bergmann's rule is exhibited more strongly by some groups than others¹⁴,

264 we examined correlation coefficient distributions within each class and order. As a temporal lag
265 in size response to temperature is likely, we assessed species' temperature-mass relationships
266 using temperatures from 1 to 50 years prior to collection year. We also examined the relationship
267 between species' correlation coefficients and five variables to understand potential statistical and
268 biological influences on the results. We did so with the number of individuals, temperature
269 range, and mass range to determine if the relationship was stronger when more data points or
270 more widely varying values were available. Because it has been argued that Bergmann's rule is
271 stronger in larger species¹⁰⁹ and at higher latitudes^{4,43}, we examined variability with both mean
272 mass and mean latitude for each species. We also conducted all analyses using latitude instead of
273 mean annual temperature.

274

275

276

277

278

279

280

281

282

283

284

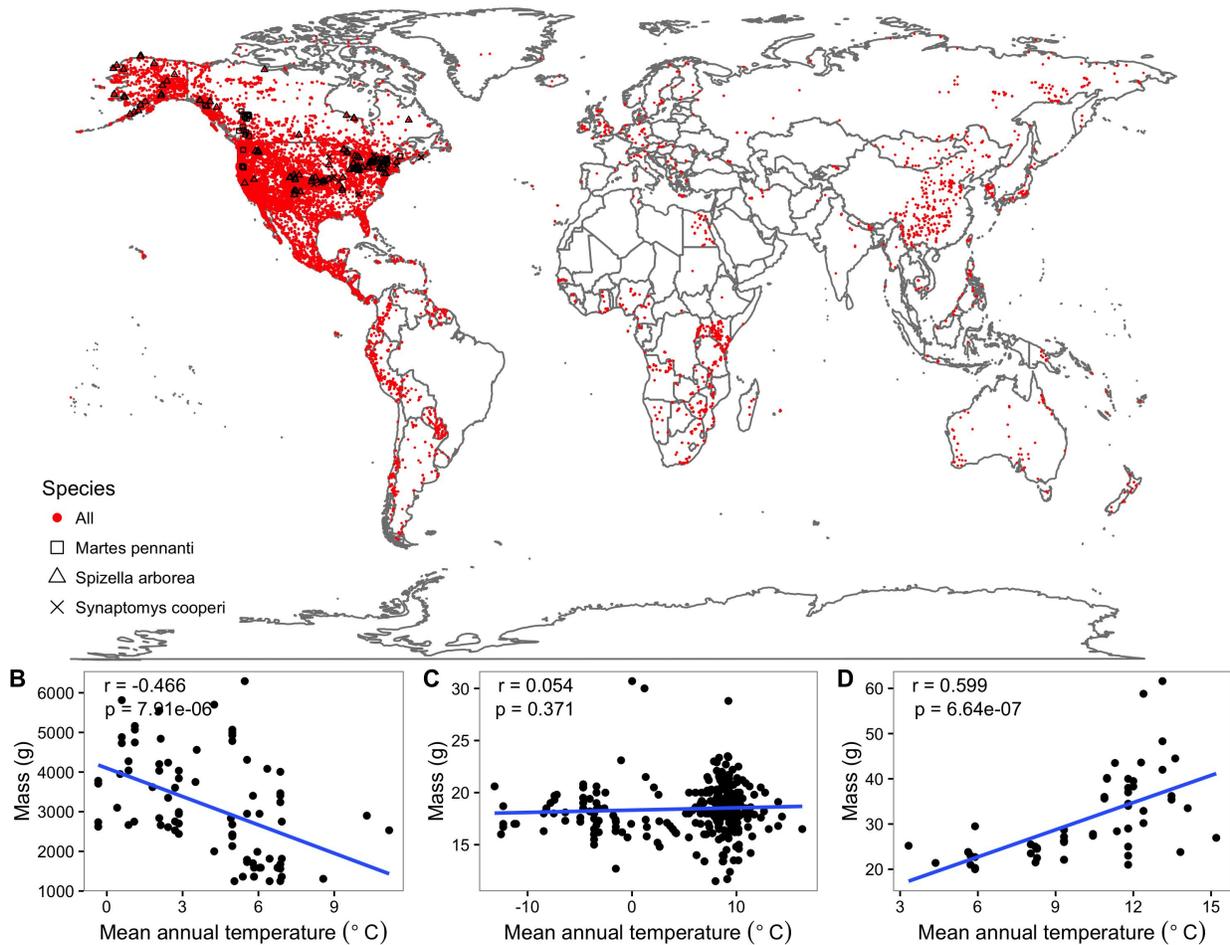
285

286

287

288 FIGURES
289

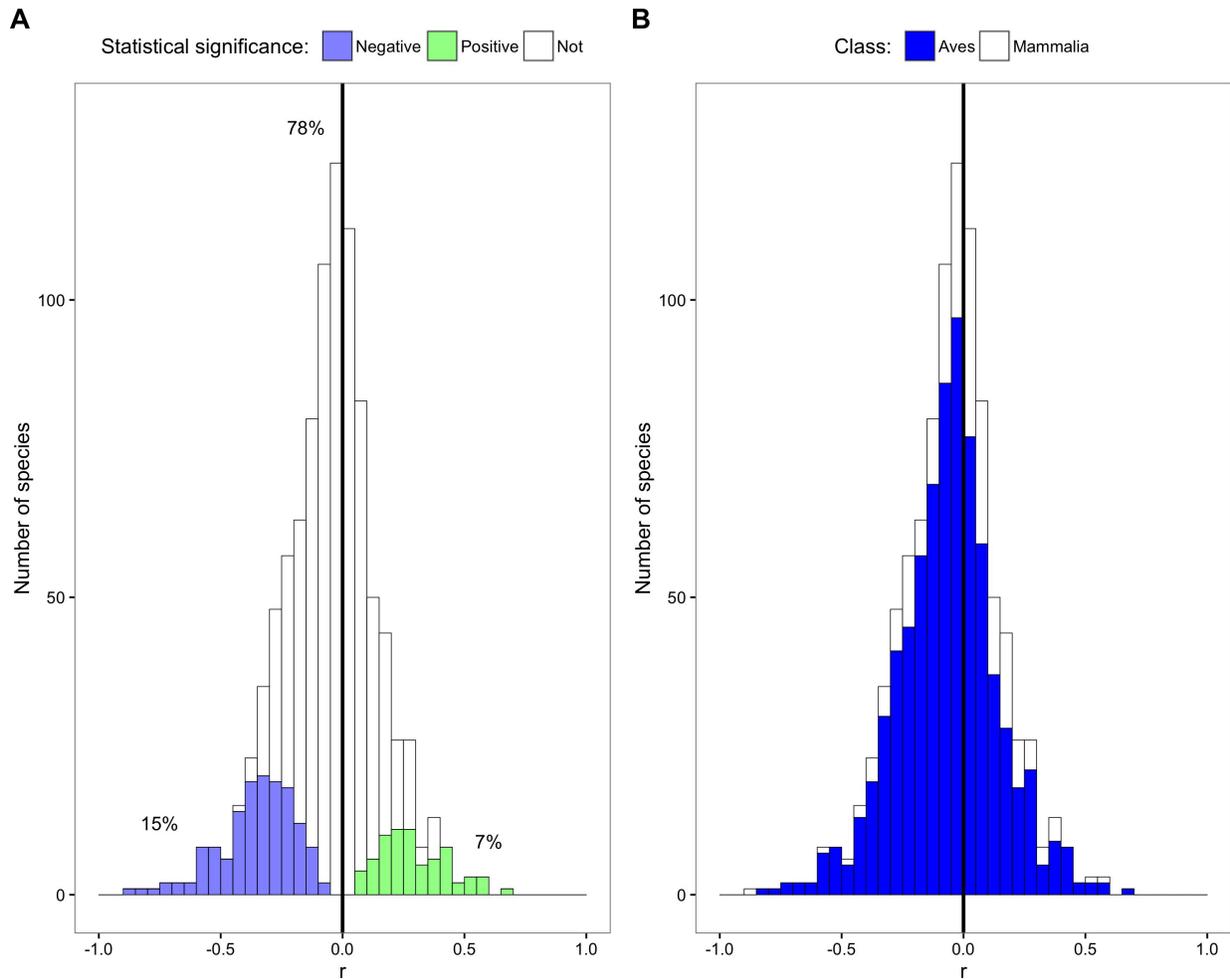
A



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

303
304
305
306
307

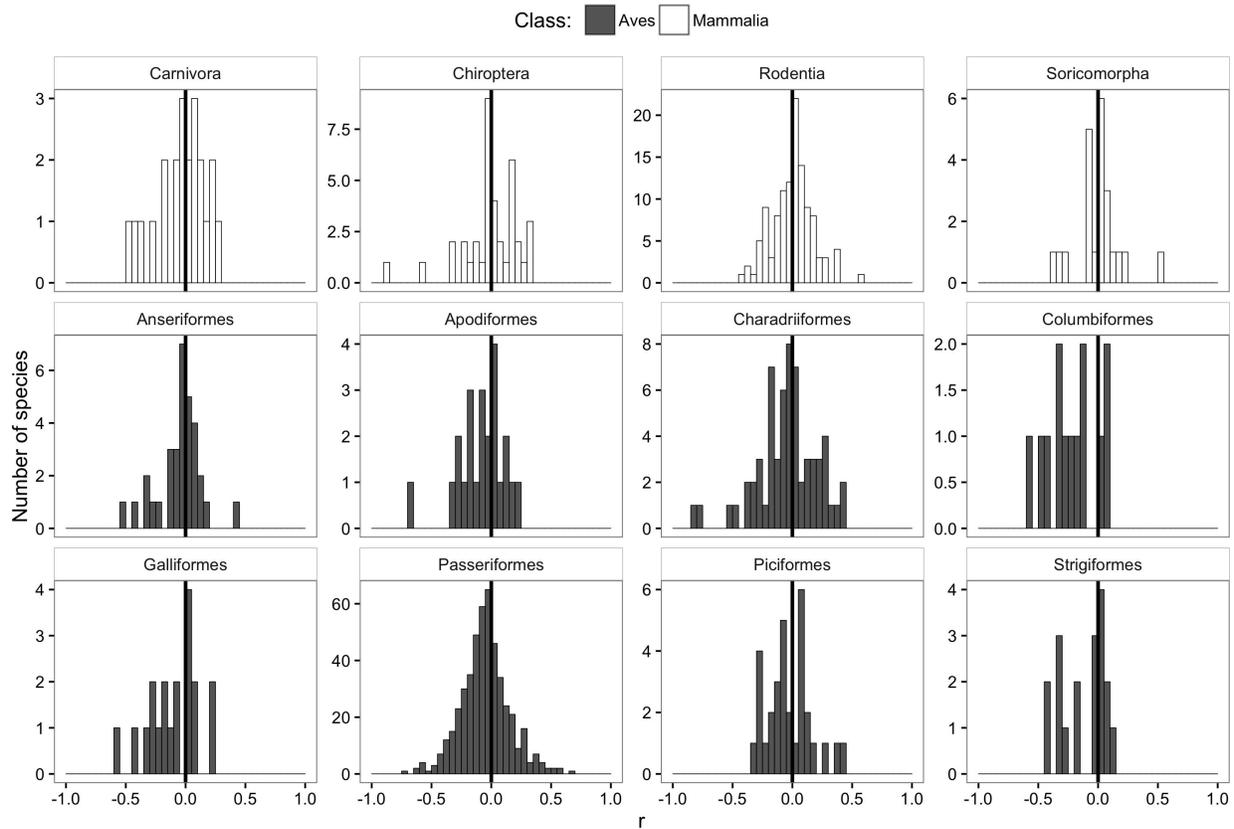
308



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

317
318
319
320
321
322
323
324
325
326
327

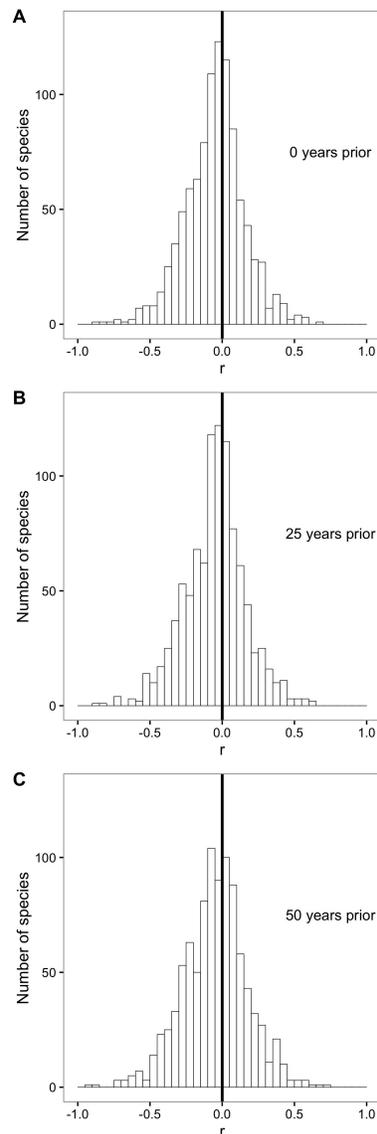
328



330 **Figure 3.** Stacked histograms of correlation coefficients (r) from intraspecific temperature-mass
331 relationships for each taxonomic order represented by more than ten species, with order shown
332 above histogram. Height of y-axis varies depending on number of species. Bar color indicates
333 taxonomic class. Dark vertical lines are correlation coefficients of zero. Trends for the remaining
334 22 orders are similar.

335
336
337
338
339
340
341
342
343
344
345
346
347
348
349
350

351



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

357

358

359

360

361

362

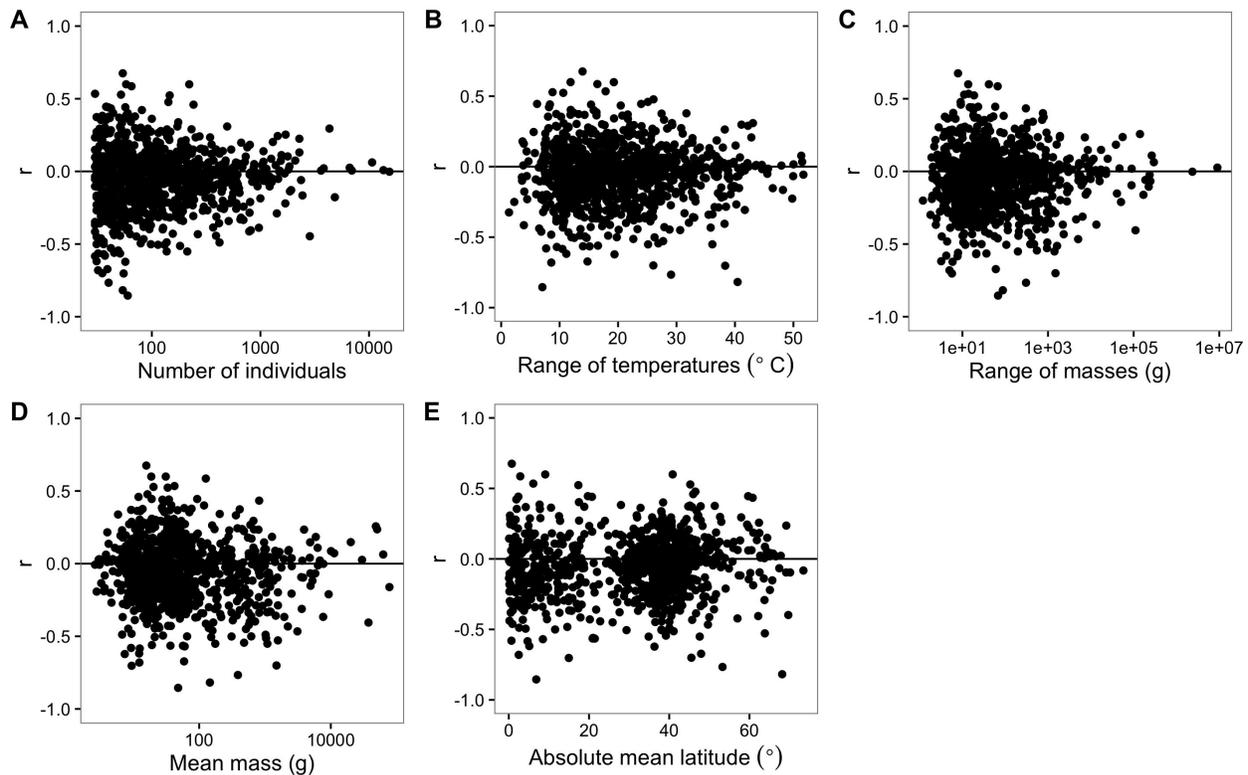
363

364

365

366

367



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

373
374
375
376
377
378
379
380
381
382
383
384
385
386
387
388
389
390
391
392

393
394
395

REFERENCES

1. Bergmann, C. Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger 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

- 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's Rule and Variation in Structures Related to Feeding in the Gray Squirrel. *Evolution* **31**, 538–545 (1977).
 26. Fuentes, E. R. & Jaksic, 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

- in Saharo-Arabian Vulpes : Outfoxing Bergmann'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., Higinson, 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).

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.

- 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,

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,

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:

- <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,

- 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:

- 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

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. Benjamini, 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).

396

397

398

399

400

401

402

403

404

405

406

407

408

409 **Author contributions**

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

412

413 **Acknowledgements**

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

420

421 **Competing financial interests**

422 No competing financial interests

423

424