

1 **Conformity to Bergmann's rule in birds depends on nest design**  
2 **and migration**

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13 Running title: Bergmann's rule depends on nest design and migration

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16 Word count: 7085

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18

## 19 **Abstract**

20

21 Species' geographic ranges and range limits are thought to be determined by climate, and across climatic  
22 gradients the morphology of populations varies non-randomly. Ecogeographic rules seek to characterise  
23 such variation, with Bergmann's rule positing that organisms inhabiting colder environments are typically  
24 larger-bodied than those inhabiting warmer environments. While Bergmann's rule has been supported  
25 across a range of taxonomic groups, how organisms' behaviour may moderate its effect remains unclear.  
26 Here we investigate whether conformity to Bergmann's rule among birds of the Western Palearctic varies  
27 in relation to nest design and migratory behaviour, using phylogenetic comparative analyses. We test  
28 predictions using data on nest structure and location, migration, body mass, latitudinal distribution,  
29 annual mean temperature and phylogenetic relatedness for a sample of >500 species. We find that  
30 conformity to Bergmann's rule depends strongly on migratory behaviour: non-migratory species breeding  
31 at colder, more northerly latitudes are larger-bodied, while body mass is unaffected by climate in short-  
32 and long-distance migrants. Among non-migratory species, conformity to Bergmann's rule depends,  
33 further, on nest design: species with more open nests, who are thus most exposed to adverse climatic  
34 conditions while breeding, conform most strongly to Bergmann's rule. Our findings suggest that enclosed  
35 nesting and migration allow smaller bodied species to breed in colder environments than their body size  
36 would otherwise allow. Therefore, we conclude that organisms' behaviour can strongly affect exposure to  
37 environmental selection pressures.

38

39 **Keywords:** body size, Bergmann's rule, geographic range, latitude, niche construction, nest building,  
40 migration, phylogenetic comparative methods, temperature

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42

## 43 **Introduction**

44

45 Species' geographic ranges and range limits are influenced by abiotic factors such as environmental  
46 conditions and physical barriers to dispersal, and by biotic factors such as competition for resources and  
47 the risk of predation (Gaston 2003, 2009). Whilst the relative importance of these factors varies between  
48 species and geographic regions, the availability of ambient and productive energy primarily determines  
49 species' geographic ranges and range limits (Currie et al. 2004). This is because species' range edges  
50 occur at climatic thresholds and vary predictably with changes in climatic conditions (Gaston 2003,  
51 2009), because organisms have a unique set of environmental conditions in which they can survive and  
52 reproduce (Blackburn and Gaston 1996). The morphology of individuals also varies non-randomly across  
53 geographic clines. Ecogeographic principles seek to characterise such variation, with Bergmann's rule  
54 being one of the most widely known and enduring examples (James, 1970). Bergmann's rule posits that  
55 species inhabiting colder environments are larger than species inhabiting warmer environments, because  
56 larger bodied organisms have a lower surface area to volume ratio and thus a greater ability to conserve  
57 heat (Bergmann 1847).

58 However, evidence that body size and morphology correlate in accordance with Bergmann's rule  
59 remains variable, and its general validity across diverse animal taxa has been questioned (Blackburn et al.  
60 1999, Meiri and Dayan 2003). At the intraspecific level, a substantial minority (~25-30%) of bird species  
61 fail to conform to Bergmann's rule (Ashton 2002, Meiri and Dayan 2003). While Bergmann's rule is  
62 broadly supported across bird species globally, the magnitude and direction of relationships between body  
63 size and climate varies widely among geographic regions and taxonomic groups (Olson et al. 2009).  
64 Further, within taxonomic subsets, Bergmann's rule is not supported in the majority of bird genera,  
65 families and orders (Olson et al. 2009). Taken together, these results suggest that while broadly valid,  
66 conformity to Bergmann's rule is mediated by other factors.

67 Organisms are able to buffer against environmental selection pressures to some extent via their  
68 behaviour (Odling-Smee et al. 2003). Nesting behaviour may be particularly important in this regard  
69 because nests are structures built to contain and protect offspring and the attending parents during the

70 breeding season (Martin et al. 2017, Hansell 2000). Both aspects of nest structure and location can affect  
71 the exposure of parents and offspring to climatic conditions (Biancucci and Martin 2010). However, the  
72 potential relationship of nests to species' responses to environmental conditions such as those predicted  
73 by Bergmann's rule is currently underexplored. In particular, incubating parents and broods of species  
74 with open nests may be more exposed to the adverse effects of cold weather than those of species with  
75 enclosed nests (Mainwaring et al. 2017). We therefore predict that species with enclosed nests should not  
76 conform as strongly to Bergmann's rule as open nesting species. This prediction has not, so far, found  
77 support at the intraspecific level: body mass is no more likely to increase in colder climates within species  
78 laying in open nests than within those with enclosed nests (including tree cavities, burrows and domed  
79 nests built of vegetation, Meiri and Dayan 2003). Bergmann's rule has been proposed, rather, to depend  
80 on migratory behaviour, as migrating species avoid extreme winter temperatures that may select for large  
81 body size at high latitudes (Ashton 2002, Meiri and Dayan 2003). In support of this idea, some analyses  
82 find that body mass is more likely to increase in colder temperatures within sedentary rather than  
83 migratory bird species, but this pattern is not consistent across studies using different statistical  
84 approaches (Meiri and Dayan 2003, Ashton 2002). As yet, the potential role of nesting and migration in  
85 mediating Bergmann's rule across species, where variation in body mass and geographic range far  
86 exceeds that within species, has not yet been investigated.

87 To investigate the potential role of nest design and migration as mediators of conformity to  
88 Bergmann's rule, we examined the combined effects of nest type, migration and climatic conditions on  
89 body mass among the bird species of the Western Palearctic. We focus on this region due to dramatic  
90 variation in environmental conditions over large-scale latitudinal gradients in the Northern hemisphere, in  
91 which ambient temperatures are considerably colder in northerly than southerly regions. We test  
92 predictions with phylogenetic comparative analyses based on a sample of >500 species with data on nest  
93 design, migratory behaviour, breeding latitude and breeding range temperature. We fit models in which  
94 the slope of body mass on latitude or temperature is allowed to vary between species with differing nest  
95 designs and migratory strategies. We predict that conformity to Bergmann's rule should depend on nest  
96 design as follows: body mass should increase with latitude and decrease with temperature most strongly

97 among species with open nests, followed by those with semi-open nests while those with enclosed nests  
98 conform least to Bergmann's rule. In terms of migration, we predict the strongest conformity to  
99 Bergmann's rule among sedentary (non-migrating) species, followed by short-distance and long-distance  
100 migrants. If nest type and migration have equally important effects on conformity to Bergmann's rule, we  
101 should find the same effects of nest design within each category of migratory behaviour, and vice versa.  
102 Alternatively, if either nest design or migration is a more important mediator of conformity to  
103 Bergmann's rule, one should override the effect of the other.

104

## 105 **Materials and methods**

106

### 107 **Study species**

108

109 We examined relationships between nest design, migration, body mass and breeding climate among bird  
110 species listed as breeding residents in the Birds of the Western Palearctic book series (Cramp and  
111 Simmons 1977, 1980, 1983, Cramp 1985, 1988, 1992, Cramp and Perrins 1993, 1994a, 1994b). Data on  
112 nest structure and location (categorised based on descriptive information), body mass, latitudinal range  
113 and migratory behaviour were collected from the same source for n=857 species, of which n=769 could  
114 be matched with the Jetz et al. (2012) molecular phylogeny. Bioclimatic data (annual mean temperature,  
115 'BIO1') were obtained from the WorldClim global climate database (Fick and Hijmans 2017) and  
116 matched to species' ranges using distribution maps from BirdLife International (BirdLife International &  
117 Handbook of the Birds of the World 2018). Of species included in the phylogeny, data on nest structure  
118 and location were available for n=538 species, body mass for n=518 species, latitudinal range for n=530  
119 species and migratory behaviour for n=538 species. We obtained bioclimatic data only for species that  
120 were included in the phylogeny and which had available body mass, nest design and migration data  
121 (n=518). 3 such species lack temperature data either because the species is no longer recognized in the  
122 latest HBW-BirdLife Taxonomic Checklist (version 3.0, November 2018) or because the species' range is  
123 too small to be matched to bioclimatic data at the chosen grid resolution, leaving n=515 with annual mean

124 temperature data. The full dataset used for analysis, along with associated R code and additional relevant  
125 files, is available in the Supporting Information.

126

## 127 **Classifying nest types**

128

129 Here, we consider nest type to be more complex than simply the structure of the nest itself, because the  
130 location in which the nest is built also strongly affects its exposure to climatic conditions (Mainwaring et  
131 al. 2014). For example, open cup-shaped nests built in vegetation should be more exposed to  
132 environmental conditions than open cup-shaped nests built inside tree cavities (von Haartman 1957).  
133 Therefore, we combine both aspects of the structure and location of birds' nests to produce an appropriate  
134 single nest design factor as follows. Nest structure is classified following Hansell (2000) in figure 3.2 as  
135 either cup, plate, scrape, bed, dome, dome and tube or burrow, while nest location is classified as open,  
136 semi-open or enclosed in which open refers to fully exposed nest sites (such as waders nesting on bare  
137 ground), semi-open refers to those nests that are largely concealed from all sides by, for example, being  
138 located in dense vegetation and enclosed refers to nests in tree cavities and alike (von Haartman 1957,  
139 Alerstam and Hogstedt 1981, Hansell 2000). We then combine information on nest structure and location  
140 to classify species' overall nest type as either open, semi-open or enclosed (**Table S1**). We consider as  
141 'open' nest types only open nest structures (cup, plate, scrape or bed nests) built in open locations. We  
142 consider as 'enclosed' nests both nests of any structure located inside cavities, and enclosed nest  
143 structures (dome, dome and tube or burrow) built in any location. Finally, we treat open nest structures  
144 (cup, plate, scrape or bed nests) built in 'semi-open' locations as 'semi-open' nests, an intermediate state  
145 between fully open and fully enclosed nest designs. In Supporting Information, we present the results of  
146 additional analyses treating nest structure and location separately.

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## 151 **Quantifying breeding climate**

152

153 Bergmann's rule is generally tested using measures of climatic conditions across a species' entire range.  
154 However, since our predictions concern how body mass may be affected by exposure to climatic  
155 conditions while breeding, here we investigate relationships between species' body mass and climatic  
156 conditions of the breeding range specifically. We used two variables to capture climatic conditions in the  
157 breeding range: breeding range latitude and breeding range temperature. We obtained northernmost and  
158 southernmost latitudes of the breeding ranges for each species from distribution maps in the Birds of the  
159 Western Palearctic book series (Cramp and Simmons 1977, 1980, 1983, Cramp 1985, 1988, 1992, Cramp  
160 and Perrins 1993, 1994a, 1994b). For analyses, we used a single latitudinal measure, 'breeding latitude  
161 midpoint', taken as the mean of the northernmost and southernmost breeding latitudes. To estimate  
162 breeding range temperature, we matched annual mean temperature data from WorldClim (Fick and  
163 Hijmans 2017) to species' ranges from BirdLife International (BirdLife International & Handbook of the  
164 Birds of the World 2018) using functions from the R packages 'rgdal' (Bivand et al. 2018) and 'letsR'  
165 (Vilela and Villalobos 2015). Species' ranges were converted to presence-absence matrices with 0.5  
166 degree grid cell resolution (~55km at the equator), counting a species as present if its range covered 10%  
167 or more of a cell. We exclude uncertain records (presence codes 2 = 'probably extant', 3 = 'possibly  
168 extant' and 6 = 'presence uncertain') and records from outside of species' native ranges (all except origin  
169 code 1 = 'native' and 2 = 'reintroduced'). To limit records to ranges in which birds may breed, we select  
170 only records from the birds' resident or breeding season ranges (season codes 1 = 'resident' or 2 =  
171 'breeding season'), thereby excluding non-breeding season and passage ranges, and records of uncertain  
172 seasonality (season codes 3 = 'non-breeding season', 4 = 'passage' and 5 'seasonal occurrence  
173 uncertain'). We obtained annual mean temperature data at 10 minutes of a degree resolution, matching it  
174 to each grid cell where a species is present. Since the climatic data is higher resolution than the presence  
175 absence matrix, we average climatic data across cells at the coarser 0.5-degree resolution to match the  
176 presence absence matrix. Finally, we summarise breeding range temperature at the species-level by taking  
177 the mean of annual mean temperature across all occupied cells in each species' presence-absence matrix.

178

## 179 **Quantifying body sizes**

180

181 We measured species' body sizes as the mean body mass of males and females during the breeding  
182 season, preferring estimates from the UK (where appropriate) due to larger sample sizes, using data from  
183 the Birds of the Western Palearctic (Cramp and Simmons 1977, 1980, 1983, Cramp 1985, 1988, 1992,  
184 Cramp and Perrins 1993, 1994a, 1994b). Body masses of unknown sex were used where body mass was  
185 not reported separately for males and females, following e.g. Møller et al. (2010).

186

## 187 **Quantifying migratory behaviour**

188

189 Using data from the Birds of the Western Palearctic (Cramp and Simmons 1977, 1980, 1983, Cramp  
190 1985, 1988, 1992, Cramp and Perrins 1993, 1994a, 1994b), we categorised species' migratory behaviour,  
191 distinguishing between sedentary (non-migratory) species, short-distance migrants and long-distance  
192 migrants. Sedentary species are those species that remain in the same area year-round and are thus  
193 residents, whilst short-distance migrants migrate south each autumn to over-winter either in southern  
194 Europe or northern Africa, and long-distance migrants migrate south each autumn to over-winter in sub-  
195 Saharan Africa.

196

## 197 **Statistical analyses**

198

199 We test predictions using Bayesian phylogenetic generalized linear mixed models and phylogenetic  
200 generalized least squares regression, implemented in the MCMCglmm R package (Hadfield 2010) and  
201 BayesTraits software (Pagel 1999, Pagel et al. 2004, Meade and Pagel 2016) respectively. To test for  
202 Bergmann's rule across the whole sample of species, we fit body mass as the outcome variable, predicted  
203 by either breeding range latitude or temperature. To investigate whether conformity to Bergmann's rule is  
204 affected by nesting variables and migration, we include an interaction term allowing slopes of body mass



205 on latitude or temperature to vary between species with different nest characteristics and/or migratory  
206 strategies. For models incorporating interactions, sample sizes are sufficient that there are at least 10  
207 species for every slope estimated. Body mass is log<sub>10</sub>-transformed to correct for a strong positive skew,  
208 while breeding latitude and temperature are roughly normally distributed and are left untransformed.

209 Accounting for phylogenetic non-independence is essential in cross-species comparative analyses  
210 to avoid pseudoreplication and biased parameter estimates (Freckleton et al. 2002). We obtained trees  
211 from a comprehensive global bird phylogeny (Jetz et al. 2012), selecting a version constructed using only  
212 species with molecular data, based on the Hackett et al. (2008) ‘backbone’ phylogeny. For the majority of  
213 our analyses we use a single maximum clade credibility (MCC) phylogeny based on a posterior sample of  
214 10,000 trees, created with TreeAnnotator (Drummond et al. 2012). However, to ensure analyses are  
215 robust to phylogenetic uncertainty, we repeat one of our main analyses across a posterior distribution of  
216 3000 trees in BayesTraits (Pagel 1999, Meade and Pagel 2016). This approach uses MCMC to estimate  
217 model parameters across the posterior tree distribution, thereby incorporating both model and  
218 phylogenetic uncertainty into results (Pagel et al. 2004). We find qualitatively identical results, both when  
219 sampling trees in proportion to their likelihood and when visiting each tree for an equal number of  
220 iterations (**Table S2**). Therefore, we are confident that our results are not substantially affected by  
221 phylogenetic uncertainty. For MCMCgllmm analyses we quantify the influence of phylogeny on results by  
222 estimating heritability ( $h^2$ ), the proportion of residual variance attributable to phylogenetic relationships  
223 equivalent to Pagel’s  $\lambda$  for PGLS regression (Hadfield and Nakagawa 2010). Like Pagel’s  $\lambda$ ,  $h^2$  varies  
224 from 0, equivalent to an ordinary non-phylogenetic regression with a random error structure, to 1, where  
225 the covariation in residual errors is directly proportional to phylogenetic relationships, assuming a  
226 Brownian motion model of trait evolution (Pagel 1999, Freckleton et al. 2002).

227 For all models, we ran MCMC chains of sufficient length to obtain effective sample sizes of at  
228 least 1000 for all model parameters (MCMCgllmm = 501,000 iterations, sampling every 100 iterations,  
229 with a burn-in period of 1000 iterations; BayesTraits = 5,050,000 iterations, sampling every 1000  
230 iterations, with a burn-in of 50,000 iterations). For MCMCgllmm analyses, we use default, diffuse normal  
231 priors for predictor variables (mean=0, variance= $10^8$ ) and commonly used inverse-Wishart priors for the

232 residual variance and phylogenetic random effect (with  $V=1$ ,  $\nu=0.002$ ) (Hadfield 2019). For BayesTraits  
233 analyses, we use default minimally-informative, uniform prior distributions for all parameters, with a  
234 range of -100 to 100 for fixed effects and 0 to 1 for Pagel's  $\lambda$  (Meade and Pagel 2016). For every model,  
235 we ensured that chains had converged on the posterior distribution, that burn-in periods were sufficient  
236 and that chains did not have problematic levels of autocorrelation by confirming sufficient effective  
237 sample sizes and by visual examination of chain plots. For all parameter estimates, we report means and  
238 95% credible intervals from posterior distributions. Additionally, for each model we report  $R^2$  estimated  
239 as the squared Pearson's correlation of the observed and fitted Y values.

240

## 241 **Data deposition**

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243 Data will be made available in the Dryad Digital Repository upon acceptance.

244

## 245 **Results**

246

### 247 **Support for Bergmann's rule**

248

249 We find support for Bergmann's rule across the whole sample: species' body mass increased with  
250 breeding range latitude midpoint ( $\beta = 0.002$  [ $<-0.001$ ,  $0.004$ ],  $n = 513$ ,  $h^2 = 0.990$  [ $0.973$ ,  $0.998$ ],  $R^2 =$   
251  $0.026$ , Fig. S1a) and decreased with breeding range temperature ( $\beta = -0.003$  [ $-0.005$ ,  $<0.001$ ],  $n = 515$ ,  
252  $h^2 = 0.989$  [ $0.973$ ,  $0.998$ ],  $R^2 = 0.019$ , Fig. S1b). These relationships are, however, fairly weak, with  
253 breeding climate explaining less than 3% of the variation in body mass. Translating effects to the data  
254 scale, the model predicts that body mass increases from 277g to 363g across the range of breeding  
255 latitudes (16 to 79.5 degrees), while body mass decreases from 384g to 297g from the lowest to the  
256 highest breeding range temperatures ( $-16^\circ\text{C}$  to  $28^\circ\text{C}$ ).

257

258

## 259 **Effects of nest design and migration on conformity to Bergmann's rule**

260

261 When modelling interactions of nest design and breeding climate, we find that nest design affects  
262 conformity to Bergmann's rule (Table 1). Specifically, in semi-open nesting species, we find similar  
263 effects to those found across the whole sample: body mass increases slightly with breeding range latitude  
264 and decreases with breeding range temperature. However, among open and enclosed nesting species,  
265 there is little to no relationship between body mass and either latitude or temperature. Repeating analyses  
266 for nest location and structure separately suggests that this pattern is driven primarily by nest location  
267 rather than structure (Tables S3, S4).

268 When including interaction terms for migration and breeding climate, we find support for the  
269 predicted effect of migration on conformity to Bergmann's rule: among sedentary species, body mass  
270 increases with breeding latitude and decreases with breeding range temperature, but not in short- or long-  
271 distance migrants (Table 2, Fig. 1).

272 When including a three-way interaction between breeding climate, nest type and migration, we  
273 find the predicted effects of nest type on conformity to Bergmann's rule within sedentary species. Among  
274 sedentary species, body mass increases with breeding range latitude and decreases with breeding range  
275 temperature for open and semi-open nesting species, but not enclosed nesting species. Short- and long-  
276 distance migrating species do not conform to Bergmann's rule at all, regardless of nest type (Table 3, Fig.  
277 2). When re-running analyses separating the effects of nest structure and location, we find similar patterns  
278 both for nest structure (Table S5) and location (Table S6).

279

## 280 **Discussion**

281

282 We find that conformity to Bergmann's rule, which predicts that species inhabiting colder environments  
283 should have larger body sizes (Bergmann 1847) depends strongly on migration and nest design in  
284 Western Palearctic birds. In both long- and short-distance migratory species, body mass is unaffected by  
285 climatic conditions in the breeding range, while among non-migrating sedentary species, conformity to

286 Bergmann's rule is greatest among species whose nests are most exposed to environmental conditions.  
287 Our results suggest that smaller bird species can adapt to colder climates either by migrating to avoid  
288 extreme winter temperatures, or by breeding in enclosed nests, while colder breeding climates favour  
289 larger body sizes in resident, open-nesting species. Therefore, among non-migratory species, enclosed  
290 nests may compensate for higher thermoregulatory costs of incubation in smaller-bodied adults breeding  
291 in colder climates, thus enabling smaller species to breed in colder climates than their body mass would  
292 otherwise allow. Our study is consistent with the idea that birds' behaviour, and particularly their nesting  
293 and migratory strategies, mediate the effect of environmental conditions on species' morphology.

294         Among resident species, we find evidence in support of Bergmann's rule only for species with  
295 open or semi-open nests, in which brooding parents are most exposed to adverse weather at northerly  
296 latitudes. Therefore, our results support the idea that enclosed nests serve to protect smaller birds against  
297 colder climatic conditions at higher latitudes. In additional analyses reported in the Supporting  
298 Information, we find the same pattern of results among resident species both for those building open nest  
299 structures and siting nests in open locations. Therefore, both enclosed nest structures and open structures  
300 built in protected locations can effectively buffer smaller-bodied species against colder conditions at  
301 higher latitudes. These results demonstrate the importance of considering not only aspects of nest  
302 structure but also of location when investigating ecological correlates of nest design. Our results contrast  
303 with a prior study testing the validity of Bergmann's rule at the intraspecific level within 106 bird species,  
304 which found that body mass was no more likely to increase in colder climates within open nesting than  
305 enclosed nesting species (Meiri and Dayan 2003). Our findings may differ from those of this study  
306 because we test predictions in a larger sample (>500 species) at the interspecific level, capturing far more  
307 variation in body mass and climatic conditions. Further, in contrast to prior studies we investigate  
308 relationships between body mass and environmental conditions in birds' breeding ranges specifically  
309 rather than across their entire ranges. Nest design is much more relevant to the former since birds' nests  
310 are generally temporary structures built for the purposes of breeding only.

311         In contrast with our findings, two recent comparative analyses suggest that enclosed nests are  
312 protective against exposure to hotter and drier, rather than colder and wetter, climatic conditions. Among

313 diverse geographic regions, the proportion of passerine species with enclosed nests is 2 to 3 times greater  
314 in tropical or southern hemisphere regions than in north temperate regions (Martin et al. 2017). Within  
315 Australia, meanwhile, the proportion of passerine species building domed nests increases in areas with  
316 hotter, drier climates and less vegetative cover (Duursma et al. 2018). Direct comparisons between our  
317 results and these prior studies is challenging due to key methodological differences: these studies are  
318 based on geographical patterns rather than phylogenetically-informed relationships, and do not  
319 incorporate potential interactions with body mass. Discrepancies with our findings may also be partly  
320 explained, however, by different approaches to classifying nest types: in contrast to our study, these  
321 analyses did not count nests built in cavities as enclosed due to a focus solely on nest structure. In our  
322 sample, a substantial proportion (~20%) of species nest in cavities which may provide effective protection  
323 against colder breeding environments in the Northern hemisphere. Taken at face value, however, these  
324 differing results suggest that protective effects of enclosed nests against extreme climatic conditions may  
325 be region-specific. Enclosed nesting may only have the opportunity to evolve in response to colder  
326 climates within the Northern hemisphere, which encompasses far more potential breeding range in  
327 temperate and polar climatic zones than the Southern hemisphere.

328 Along with nest type, we also identify migration as an important mediator of conformity to  
329 Bergmann's rule. Consistent with some previous work at the intraspecific level (Meiri and Dayan 2003,  
330 but see Ashton 2002), we find that body mass increases in colder temperatures among sedentary species,  
331 but in neither short-distance or long-distance migrants. These findings support the idea that long-distance  
332 migrants are less exposed to selection pressures favouring large body size in colder climates as they avoid  
333 exposure to the coldest winter temperatures at high latitudes by spending the non-breeding season in  
334 warmer environments (Ashton 2002, Meiri and Dayan 2003). Teasing apart the effects of migration and  
335 nest type on conformity to Bergmann's rule, we find that migration has a stronger effect than nest type.  
336 While we find predicted effects of nest type within sedentary species, migratory species do not conform  
337 to Bergmann's rule at all, regardless of their nesting behaviour. Therefore, the thermoregulatory benefits  
338 of migration override those of nest design, such that enclosed nests provide no additional  
339 thermoregulatory benefits for migratory, small-bodied species. This is perhaps unsurprising because

340 migration results in species avoiding extreme winter conditions in the Northern hemisphere altogether,  
341 while nest design can only affect exposure to environmental conditions for relatively short periods during  
342 breeding. Taken together, our results reveal the interplay between nesting and migration in buffering  
343 small-bodied species against cold climates in the Northern hemisphere.

344         Alternative explanations for our findings may be related to potential systematic changes in the  
345 availability of nest sites (Hansell 2000) or food (Martin 1995) over latitudinal gradients: for example,  
346 natural cavities and food may be limited in forests at higher latitudes which may mean that smaller and  
347 competitively inferior tree cavity-nesting species are prevented from breeding at higher latitudes through  
348 competitive exclusion rather than environmental conditions alone. However, these alternatives seem  
349 unlikely as natural cavities are not usually in limited supply in the northern hemisphere (Wiebe 2011).  
350 Instead, our findings suggest that migration and nest morphology in birds and other animals may help  
351 species to breed in climates where they would not necessarily otherwise be able to. Meanwhile the need  
352 for streamlined body designs for efficient flight in migrant birds may play a greater role in determining  
353 their morphology than conditions on the breeding grounds alone. Nevertheless, these findings are  
354 consistent with a prediction of niche construction theory that susceptibility to abiotic selection pressures,  
355 such as environmental temperature, can be buffered by species' alteration of their environments through  
356 behaviour, particularly in terms of the location of nesting sites (Odling-Smee et al. 2003). However, since  
357 comparative analyses can only identify correlational rather than causal relationships (Nunn 2011), we  
358 cannot rule out the possibility of alternative causal explanations. Our results are therefore equally  
359 consistent with causal scenarios in which environmental selection pressures drive changes in behaviour  
360 rather than vice-versa, or where environmental selection pressures and behaviour influence one another in  
361 evolutionary feedback loops. In any case, our findings are significant in that they suggest that  
362 fundamental relationships between species' environments and morphology may be mediated by  
363 behaviour.

364         We have demonstrated that in Western Palearctic birds, body mass increases in colder climates as  
365 hypothesised by Bergmann's rule only in non-migratory species breeding in exposed nests. Our findings  
366 are consistent with the idea that migration and enclosed nests compensate for greater thermoregulatory

367 costs in smaller-bodied birds, allowing them to breed in colder environments than expected for their body  
368 size. Further research could usefully examine how species' modification of environments affects  
369 responses to environmental selection pressures across more diverse taxa and geographic regions,  
370 including across human populations. Our work should also guide future experimental studies on the  
371 potential mediating role of nesting and migratory behaviour on the influence of climatic conditions on  
372 parental and offspring fitness. We conclude that behaviour, particularly migration, nest-building and nest-  
373 site choice, is an important mediator of species' responses to climatic selection pressures.

374

375 *Acknowledgements* - We thank Sue Healy and Kevin Laland for useful comments.

376 *Author contributions* - MCM and SES designed the study, MCM collected the data, SES analysed the data and  
377 MCM and SES wrote the manuscript.

378

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459 **TABLES**

460

461 Table 1. Interaction of Bergmann's rule with nest design.

462

463 a) Latitude

<b>Nest design</b>	<b><math>\beta</math> Estimates &amp; 95% CI</b>	<b><math>h^2</math> &amp; 95% CI</b>	<b><math>n</math> species</b>	<b><math>R^2</math></b>
Open	<-0.001 [-0.003, 0.004]	0.987 [0.968, 0.998]	513	0.198
Semi-open	0.003 [-0.001, 0.006]			
Enclosed	0.002 [-0.003, 0.007]			

464

465 b) Temperature

<b>Nest design</b>	<b><math>\beta</math> Estimates &amp; 95% CI</b>	<b><math>h^2</math> &amp; 95% CI</b>	<b><math>n</math> species</b>	<b><math>R^2</math></b>
Open	0.001 [-0.003, 0.006]	0.988 [0.970, 0.998]	515	0.184
Semi-open	-0.005 [-0.009, -0.001]			
Enclosed	-0.004, -0.010, 0.002			

466

467  $\beta$  estimates = mean regression slopes from posterior distributions for body mass on a) latitude and b)

468 temperature, fitted for species with different nest designs,  $h^2$  = mean heritability (phylogenetic signal)

469 95% CI = 95% credible intervals.

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481 Table 2. Interaction of Bergmann's rule with migration.

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483 a) Latitude

Migration	$\beta$ estimates & 95% CI	$h^2$ & 95% CI	$n$ species	$R^2$
Sedentary	0.006 [0.002, 0.009]	0.991 [0.975, 0.999]	513	0.017
Short distance	-0.001 [-0.004, 0.003]			
Long distance	<0.001 [-0.004, 0.004]			

484

485 b) Temperature

Migration	$\beta$ estimates & 95% CI	$h^2$ & 95% CI	$n$ species	$R^2$
Sedentary	-0.008 [-0.012, -0.004]	0.991 [0.977, 0.999]	515	0.015
Short distance	0.001 [-0.004, 0.005]			
Long distance	0.002 [-0.003, 0.007]			

486

487  $\beta$  estimates = mean regression slopes from posterior distributions for body mass on a) latitude and b)

488 temperature, fitted for species with different migratory strategies,  $h^2$  = mean heritability (phylogenetic

489 signal) 95% CI = 95% credible intervals.

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503 Table 3. Interaction of Bergmann's rule with migration and nest design.

504

505 a) Latitude

Migration	Nest design	$\beta$ estimates & 95% CI	$h^2$ & 95% CI	$n$ species	$R^2$
Sedentary	Open	0.009 [0.002, 0.016]	0.988 [0.969, 0.998]	513	0.202
	Semi	0.006 [0.001, 0.010]			
	Enclosed	0.004 [-0.003, 0.010]			
Short	Open	-0.002 [-0.006, 0.004]			
	Semi	0.001 [-0.005, 0.006]			
	Enclosed	-0.002 [-0.010, 0.006]			
Long	Open	<-0.001 [-0.006, 0.006]			
	Semi	-0.002 [-0.008, 0.005]			
	Enclosed	0.004 [-0.006, 0.014]			

506

507 b) Temperature

Migration	Nest design	$\beta$ estimates & 95% CI	$h^2$ & 95% CI	$n$ species	$R^2$
Sedentary	Open	-0.008 [-0.016, <-0.001]	0.989 [0.972, 0.999]	515	0.188
	Semi	-0.009 [-0.014, -0.004]			
	Enclosed	-0.006 [-0.014, 0.004]			
Short	Open	0.003 [-0.003, 0.010]			
	Semi	-0.002 [-0.009, 0.005]			
	Enclosed	0.001 [-0.012, 0.014]			
Long	Open	0.003 [-0.004, 0.010]			
	Semi	0.002 [-0.006, 0.011]			
	Enclosed	-0.004 [-0.017, 0.010]			

508

509  $\beta$  estimates = mean regression slopes from posterior distributions for body mass on a) latitude and b)

510 temperature, fitted for species with different nest designs and migratory strategies,  $h^2$  = mean heritability

511 (phylogenetic signal) 95% CI = 95% credible intervals.

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513

## 514 **FIGURE LEGENDS**

515

516 Figure 1. Interaction of Bergmann's rule with migration. a) Species' body mass against breeding latitude  
517 midpoint with different slopes fitted for sedentary, short-distance migrating and long-distance migrating  
518 species. Mean slopes from posterior distributions are indicated by thick lines, while slopes from the entire  
519 posterior distributions are plotted as thinner, semi-transparent lines. b) density plot showing posterior  
520 distributions of slope estimates for sedentary, short-distance migrating and long-distance migrating  
521 species.

522

523 Figure 2. Interaction of Bergmann's rule with nest design within sedentary species. Species' body mass  
524 against breeding latitude midpoint with different slopes fitted for open, semi-open and enclosed nesting  
525 species, within sedentary species only. Mean slopes from posterior distributions are indicated by thick  
526 lines, while slopes from the entire posterior distributions are plotted as thinner, semi-transparent lines. b)  
527 density plot showing posterior distributions of slope estimates open, semi-open and enclosed nesting  
528 species, within sedentary species only.

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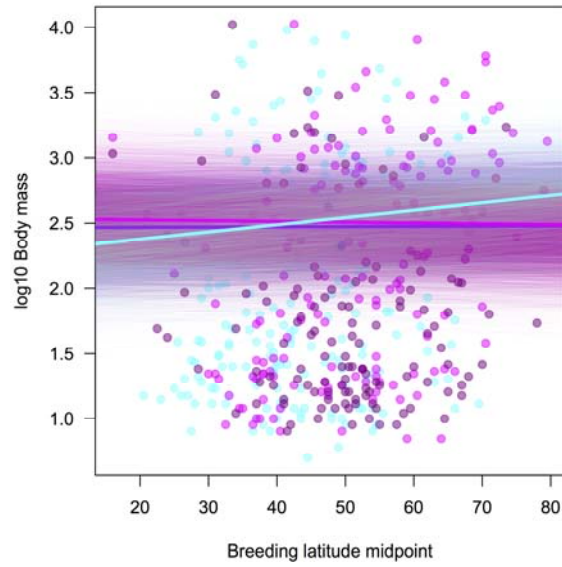
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542 Figure 1.

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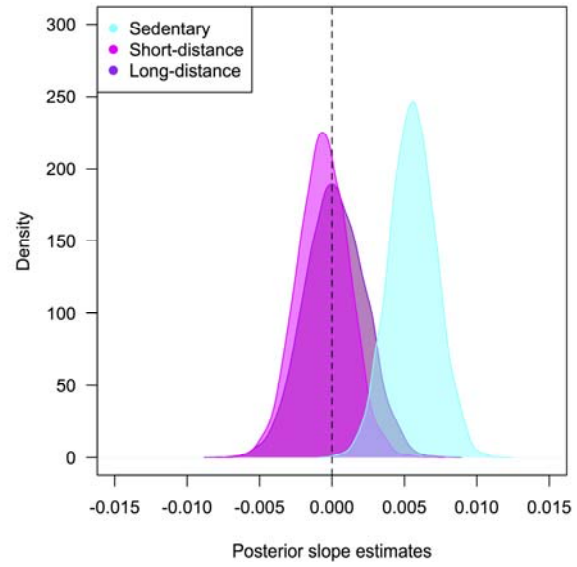
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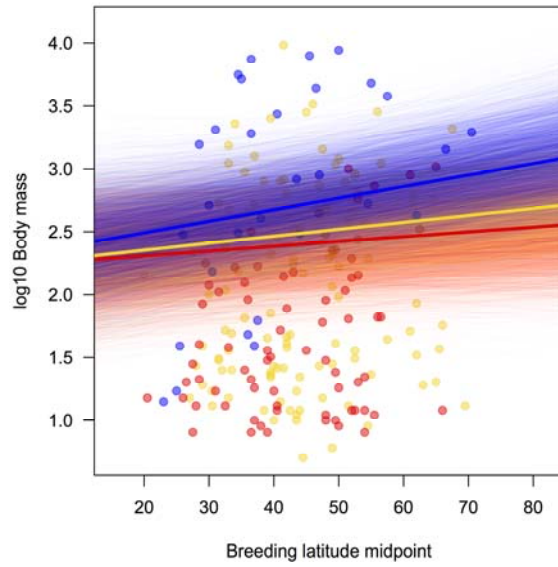
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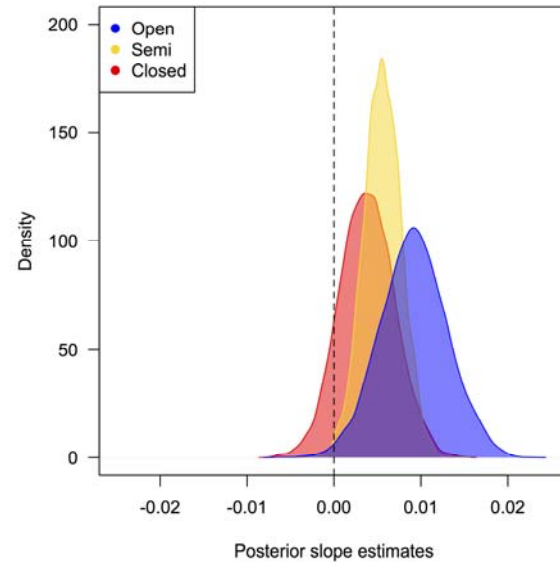


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566 **SUPPORTING INFORMATION**

567

568 Table S1. Nest design categorisation scheme.

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	<b>Open</b>	<b>Semi-open</b>	<b>Enclosed</b>
<b>Cup</b>	Open	Semi-open	Enclosed
<b>Plate</b>	Open	Semi-open	Enclosed
<b>Scrape</b>	Open	Semi-open	Enclosed
<b>Bed</b>	Open	Semi-open	Enclosed
<b>Dome</b>	Enclosed	Enclosed	Enclosed
<b>Dome &amp; tube</b>	Enclosed	Enclosed	Enclosed
<b>Burrow</b>	Enclosed	Enclosed	Enclosed

570

571 Scheme used to combine nest structure and location into a single nest design variable. Nest structure  
572 (rows) and nest location (columns) categories are combined to form a single nest design variable,  
573 capturing differing levels of exposure to environmental conditions influenced by both nest structure and  
574 location.

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590 Table S2. Incorporating phylogenetic uncertainty.

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592 a) Sampling trees in proportion to their likelihood

<b>Nest design</b>	<b><math>\beta</math> Estimates &amp; 95% CI</b>	<b><math>\lambda</math> &amp; 95% CI</b>	<b><i>n</i> species</b>	<b><math>R^2</math></b>
Open	<-0.001 [-0.004, 0.003]	0.970 [0.952, 0.983]	513	0.195
Semi-open	0.003 [-0.001, 0.006]			
Enclosed	0.002 [-0.002, 0.002]			

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594

595 b) Visiting all trees for an equal number of iterations

<b>Nest design</b>	<b><math>\beta</math> Estimates &amp; 95% CI</b>	<b><math>\lambda</math> &amp; 95% CI</b>	<b><i>n</i> species</b>	<b><math>R^2</math></b>
Open	<0.001 [-0.004, 0.004]	0.958 [0.936, 0.976]	513	0.200
Semi-open	0.003 [-0.001, 0.006]			
Enclosed	0.002 [-0.003, 0.007]			

596

597 Results of one of the main analyses (body mass predicted by an interaction of breeding latitude and nest  
598 design) repeated incorporating phylogenetic uncertainty by running the model across a posterior  
599 distribution of 3000 trees in BayesTraits. Initially trees were sampled in proportion to their likelihood (a),  
600 but this resulted in poor mixing between trees, likely caused by wide variation in tree likelihood across  
601 the sample. Results are qualitatively identical when forcing the chain to visit all trees in the sample for an  
602 equal number (1000) of iterations (b).  $\beta$  estimates = mean regression slopes from posterior distributions  
603 and  $\lambda$  = mean Pagel's lambda (phylogenetic signal) from posterior distributions with 95% credible  
604 intervals.

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614 Table S3. Bergmann's rule and nest structure.

615

616 c) Latitude

<b>Nest structure</b>	<b><math>\beta</math> estimates &amp; 95% CI</b>	<b><math>h^2</math> &amp; 95% CI</b>	<b><math>n</math> species</b>	<b><math>R^2</math></b>
Open	0.001 [-0.001, 0.004]	0.988 [0.971, 0.998]	513	0.055
Enclosed	0.005 [-0.002, 0.012]			

617

618 d) Temperature

<b>Nest structure</b>	<b><math>\beta</math> estimates &amp; 95% CI</b>	<b><math>h^2</math> &amp; 95% CI</b>	<b><math>n</math> species</b>	<b><math>R^2</math></b>
Open	-0.002 [-0.005, 0.001]	0.988 [0.970, 0.998]	515	0.050
Enclosed	-0.009 [-0.019, <0.001]			

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621 Results of models allowing the slope of body mass on a) latitude or b) temperature to vary between  
622 species with different nest structures (open = cup, plate, scrape or bed, closed = dome, dome and tube or  
623 burrow), regardless of location.  $\beta$  estimates = mean regression slopes from posterior distributions and  $h^2$   
624 = mean heritability (phylogenetic signal) from posterior distributions with 95% credible intervals.

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637 Table S4. Bergmann's rule and nest location.

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639 a) Latitude

<b>Nest location</b>	<b><math>\beta</math> estimates &amp; 95% CI</b>	<b><math>h^2</math> &amp; 95% CI</b>	<b><math>n</math> species</b>	<b><math>R^2</math></b>
Open	<0.001 [-0.003, 0.004]	0.987, [0.969, 0.998]	513	0.171
Semi-open	0.003 [<-0.001, 0.006]			
Enclosed	0.002 [-0.003, 0.008]			

640

641 b) Temperature

<b>Nest location</b>	<b><math>\beta</math> estimates &amp; 95% CI</b>	<b><math>h^2</math> &amp; 95% CI</b>	<b><math>n</math> species</b>	<b><math>R^2</math></b>
Open	0.001 [-0.003, 0.006]	0.989 [0.972, 0.988]	515	0.158
Semi-open	-0.005 [-0.009, -0.002]			
Enclosed	-0.003 [-0.011, 0.003]			

642

643 Results of models allowing the slope of body mass on a) latitude or b) temperature to vary between  
644 species with different nest locations (open, semi-open or enclosed), regardless of structure.  $\beta$  estimates =  
645 mean regression slopes from posterior distributions and  $h^2$  = mean heritability (phylogenetic signal) from  
646 posterior distributions with 95% credible intervals.

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659 Table S5. Interaction of Bergmann's rule with migration and nest structure.

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661 c) Latitude

Migration	Nest design	$\beta$ estimates & 95% CI	$h^2$ & 95% CI	<i>n</i> species	$R^2$
Sedentary	Open	0.005 [0.002, 0.008]	0.990 [0.972, 0.999]	513	0.048
	Enclosed	0.006 [-0.005, 0.017]			
Short	Open	<-0.001 [-0.004, 0.003]			
	Enclosed	-0.004 [-0.018, 0.012]			
Long	Open	-0.001 [-0.005, 0.004]			
	Enclosed	0.006 [-0.005, 0.018]			

662

663 d) Temperature

Migration	Nest design	$\beta$ estimates & 95% CI	$h^2$ & 95% CI	<i>n</i> species	$R^2$
Sedentary	Open	-0.007 [-0.012, -0.003]	0.990, [0.973, 0.998]	515	0.046
	Enclosed	-0.012 [-0.025, 0.002]			
Short	Open	0.001 [-0.004, 0.006]			
	Enclosed	0.005 [-0.020, 0.030]			
Long	Open	0.003 [-0.002, 0.008]			
	Enclosed	-0.009 [-0.024, 0.008]			

664

665 Results of models allowing the slope of body mass on a) latitude or b) temperature to vary between  
 666 species with different migratory strategies (sedentary, short- or long-distance) and nest structures (open =  
 667 cup, plate, scrape or bed, closed = dome, dome and tube or burrow).  $\beta$  estimates = mean regression  
 668 slopes from posterior distributions and  $h^2$  = mean heritability (phylogenetic signal) from posterior  
 669 distributions with 95% credible intervals.

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678 Table S6. Interaction of Bergmann's rule with migration and nest location.

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680 a) Latitude

Migration	Nest location	$\beta$ estimates & 95% CI	$h^2$ & 95% CI	$n$ species	$R^2$
Sedentary	Open	0.009 [0.002, 0.016]	0.988 [0.971, 0.998]	513	0.172
	Semi-open	0.006 [0.002, 0.010]			
	Enclosed	0.003 [-0.004, 0.011]			
Short	Open	-0.002 [-0.006, 0.003]			
	Semi-open	0.001 [-0.004, 0.006]			
	Enclosed	<-0.001 [-0.010, 0.010]			
Long	Open	<-0.001 [-0.006, 0.006]			
	Semi-open	-0.002 [-0.008, 0.005]			
	Enclosed	0.003 [-0.009, 0.015]			

681

682 b) Temperature

Migration	Nest location	$\beta$ estimates & 95% CI	$h^2$ & 95% CI	$n$ species	$R^2$
Sedentary	Open	-0.008 [-0.016, <0.001]	0.989 [0.973, 0.999]	515	0.160
	Semi-open	-0.010 [-0.014, -0.005]			
	Enclosed	-0.006 [-0.015, 0.004]			
Short	Open	0.004 [-0.003, 0.010]			
	Semi-open	-0.002 [-0.009, 0.006]			
	Enclosed	-0.001 [-0.015, 0.014]			
Long	Open	0.003 [-0.004, 0.010]			
	Semi-open	0.002 [-0.006, 0.010]			
	Enclosed	-0.003 [-0.018, 0.012]			

683

684 Results of models allowing the slope of body mass on a) latitude or b) temperature to vary between  
 685 species with different migratory strategies (sedentary, short- or long-distance) and nest locations (open,  
 686 semi-open or enclosed).  $\beta$  estimates = mean regression slopes from posterior distributions and  $h^2$  = mean  
 687 heritability (phylogenetic signal) from posterior distributions with 95% credible intervals.

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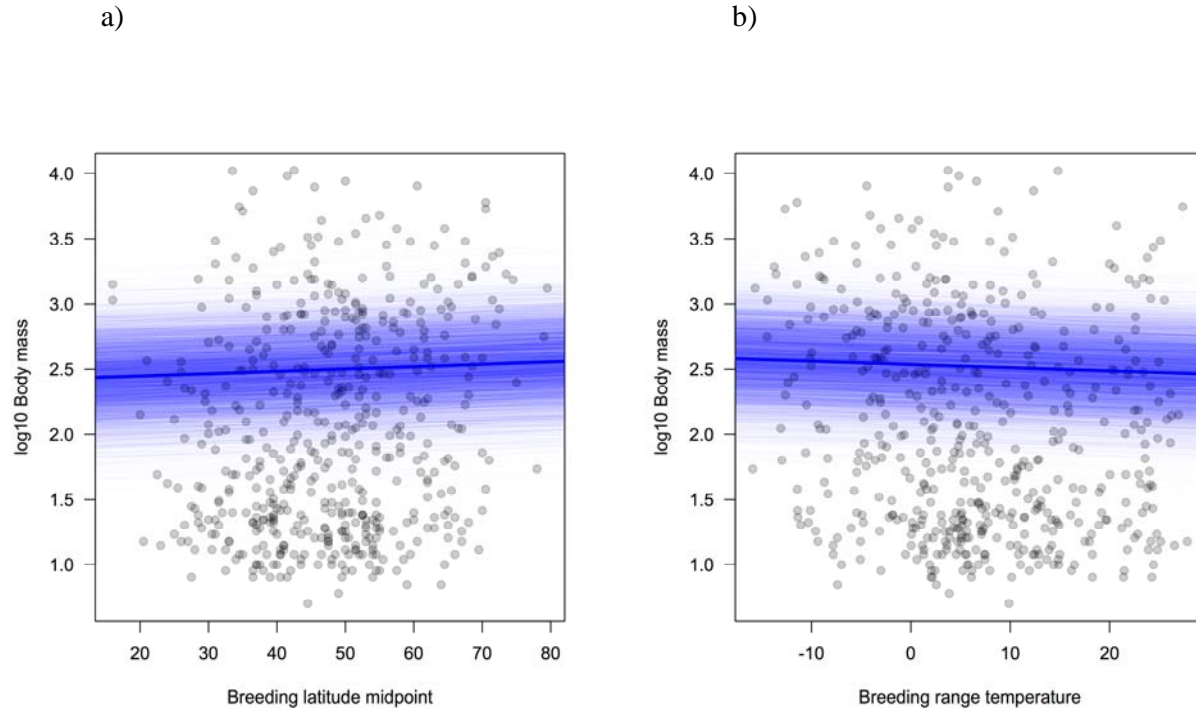
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695 Figure S1. Support for Bergmann's rule.

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700 Species' body mass against a) breeding latitude midpoint and b) breeding range mean temperature across  
701 the whole sample. Mean slopes from the posterior distributions are indicated by thicker, opaque lines,  
702 while slopes from the entire posterior distribution are plotted as thinner, semi-transparent lines.

703