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# Body size, developmental instability and climate change

Anders Pape Møller<sup>1</sup>, Johannes Erritzøe<sup>2</sup> and Stefan van Dongen<sup>3</sup>

<sup>1</sup> *Ecologie Systématique Evolution, Université Paris-Sud, CNRS,  
AgroParisTech, Université Paris-Saclay, F-91405 Orsay Cedex, France*

<sup>2</sup> *Taps Old Rectory, DK-6040 Christiansfeld, Denmark*

<sup>3</sup> *Department of Biology, Campus Drie Eiken, Building D. D. 137,  
Universitetsplein 1, University of Antwerp, B-2610 Wilrijk, Belgium*

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Correspondence to APM:

Tel: (+33) 1 69 15 56 88

Fax: (+33) 1 69 15 56 96

E-mail: anders.moller@u-psud.fr, erritzoe@birdresearch.dk,

stefan.vandongen@uantwerpen.be

Running headline:

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23

24

25 Development is often temperature-dependent. We hypothesized smaller size and  
26 larger asymmetry with increasing temperatures. However, we also predicted  
27 associations with asymmetry to differ among traits that differ in their degree of  
28 functional importance (especially the functional wings in migratory birds were  
29 predicted to be more canalized), timing of development (skeletal (femur, tarsus  
30 and humerus) vs feather (wing and tail traits), although it is difficult to make  
31 strong predictions a priori. We analyzed a large dataset of which we included to  
32 species with at least 20 specimens resulting in 5533 asymmetry values in 1593  
33 individuals from 66 species. There was a consistent significant decrease in size  
34 with temperature across all traits. Fluctuating asymmetry for wings and femur  
35 was on average lower, suggesting higher canalization, and it decreased with  
36 migration distance, while that was not the case for the other traits. Fluctuating  
37 asymmetry increased with increasing temperature for wings, but not for the  
38 other characters, where the different responses of different characters to  
39 temperature was significant. Since there was no significant three-way  
40 interaction between temperature, migration distance and character, the  
41 asymmetry-temperature response was similar in migratory and resident species.  
42 These findings imply that climate warming reduces size of all traits and  
43 decreases developmental instability of wings in birds. Further research will be  
44 required to study the specific role of more intense selection and/ or canalization  
45 to predict the effects of environmental changes on the developmental instability  
46 of different traits.

47

48 **KEY WORDS:** Birds, body size, climate change, development, fluctuating  
49 asymmetry, migration distance.

50

51

## 52 **Introduction**

53 Carl Bergmann (1847) documented that temperature drives spatial patterns of  
54 body size. This general phenomenon of increasing size with latitude was  
55 subsequently termed Bergmann's rule. However, an extensive scientific  
56 literature dealing with spatial and temporal patterns of phenotypic variation has  
57 reported many exceptions to this rule (e. g. Olson et al. 2009; Teplitsky and  
58 Millien 2014).

59         The metabolic underpinnings of Bergmann's rule are that larger  
60 individuals conserve body heat more efficiently than small conspecifics  
61 (Bergmann 1847). It is important to emphasize that this is only one of several  
62 explanations for this pattern since Bergmann's rule also applies to many  
63 poikilotherms. Furthermore, larger individuals may suffer from hyperthermia  
64 because of low heat loss efficiency. If we consider spatial patterns of variation  
65 in size as stated by Bergmann's rule, such geographical differences in body size  
66 may come about for different reasons. For example, James (1970) suggested  
67 that different phenotypes may have evolved in different climates, or that spatial  
68 variation in selection results in spatial clines in size as described by Bergmann.  
69 Therefore, the potential causes of temporal body size shifts include effects of  
70 temperature on development, fecundity and mortality because climate  
71 variability increases with climate change.

72         Recently, Bergmann's rule and other patterns of spatial and temporal  
73 variation in size have attracted increasing attention because climate change may

74 have predictable outcomes. Indeed, there is an extensive literature providing a  
75 link between temporal change in body size and climate change (reviews in  
76 Yom-Tov and Geffen 2011; Gardner et al. 2011; Van Buskirk et al. 2010).  
77 These morphological changes can have important evolutionary consequences.  
78 For example, Van Gils et al. (2016) showed for the long distance migratory knot  
79 *Calidris canutus* that recent body shrinkage of birds in the Arctic has resulted in  
80 a deterioration in survival prospects. This pattern of change in body size was  
81 until recently so pronounced that it was considered a general consequence of  
82 climate warming (reviews in Daufresne et al. 2009; Gardner et al. 2011;  
83 Sheridan and Bickford 2011). However, a decline in body size caused by  
84 climate warming is far from ubiquitous (Meiri et al. 2009; Teplitsky and Millien  
85 2014; Gardner et al. 2014a). While some studies found decreases in body size  
86 when temperatures increased (e.g. Yom-Tov et al. 2008; Gardner et al. 2009;  
87 Van Buskirk et al. 2010), others found no change (e.g. Meiri et al. 2009;  
88 Salewski et al. 2010, 2014a, b), and yet others showed an increase (e.g.  
89 Björklund et al. 2014; Gardner et al. 2014b). An explanation for this  
90 heterogeneous pattern of change in body size may be that it is context  
91 dependent such as depending on different sites or even on the same sites in  
92 different years (Yom-Tov et al. 2006; Meiri et al. 2009; Collins et al. 2017).  
93 Thus, phenotypic changes may depend on short and long term effects of climate  
94 (Kruuk et al. 2015).

95 Changing body size changes may emerge through effects of  
96 environmental conditions on body growth, in particular the effects of protein  
97 content of the diet for growth of juveniles (e.g. Searcy et al. 2004; Bonaparte et  
98 al. 2016), although again alternative explanations are common. The size of  
99 endothermic organisms such as birds is affected by growth conditions and  
100 duration of the growth period (Yom-Tov and Geffen 2011). Climatic conditions  
101 can directly affect growth rates. Because temperature affects thermoregulation  
102 of juveniles, these changes may impact metabolic rates and variation in energy  
103 allocation to body growth (Gillooly et al. 2001). While climate conditions may  
104 affect growth rates, they may also affect eventual body size due to size-  
105 dependent mortality (such as that caused by heat waves or dehydration  
106 (McKechnie and Wolf 2010)).

107 Previous studies of climate change effects on morphology have focused  
108 on reductions in size, while there is an extensive history of studies dealing with  
109 effects of temperature on developmental instability (DI), as shown by temporal  
110 changes in asymmetry (a measure of DI) with environmental fluctuations (e.g.  
111 Beardmore 1960; Siegel and Doyle 1975; Mooney et al. 1985; Gest et al. 1986).  
112 Absolute fluctuating asymmetry (AFA) reflected as the difference in size  
113 between the sides of a character has been shown more generally to increase with  
114 adverse environmental conditions including increased and stressful  
115 temperatures (reviews in Møller and Swaddle 1997; Beasley et al. 2013). Not  
116 only can this be important for evaluating the effects of climate change on how it

117 causes stress during development, but causal effects of climate change on  
118 asymmetry can have functional implications as well, where, for example, larger  
119 wing asymmetry decreases flight performance (Swaddle, 1997). Thus, on the  
120 one hand, if DI reflects stress, health and/or ‘individual quality’, one would  
121 expect associations between AFA and for example temperature to be expressed  
122 in all traits. However, there is evidence that the AFA-stress relationship may be  
123 trait-specific, and little is known about the factors affecting this heterogeneity  
124 (Lens et al., 2002; Van Dongen, 2006; but see Van Dongen et al., 2009; De  
125 Coster et al., 2013), especially because very large sample sizes are required to  
126 detect such differences in responses between traits in single studies, a problem  
127 that is not present in this study.

128         A third component of phenotypic variation is canalization, which reflects  
129 the ability of a genotype to produce relatively constant phenotypes under  
130 different environmental conditions (Waddington 1942; Scharloo 1991). Not all  
131 traits are canalized similarly because traits vary in their functional importance.  
132 Hence the degree to which such traits have been selected to result in similar  
133 developmental trajectories even when encountering different or adverse  
134 environmental conditions may vary. As such, the degree of canalization may  
135 affect the effects of adverse conditions on DI and thus AFA. It can thus be  
136 predicted that due to the evolutionary history of traits, effects of climate change  
137 vary among different body parts. Indeed, Van Dongen et al. (2009) and De  
138 Coster et al. (2013) showed that the evolutionary history of a trait can influence

139 the association between AFA and stress. Similarly, it is likely that the time  
140 window during which stress is experienced may make some traits more  
141 vulnerable to increased DI than others. Making specific predictions is often  
142 difficult as different factors can simultaneously influence particular traits. For  
143 example, some traits, like the tarsus in birds, develop largely before fledging,  
144 while size and asymmetry of feathers can change after each molt (e.g., Swaddle,  
145 1997). Nevertheless, we predict that wings in particular are highly stabilized  
146 traits given their functional importance, and that should particularly be the case  
147 in birds migrating over very long distances. To what extent higher canalization  
148 would, if any, either increase or decrease DI of such traits is currently unknown,  
149 and is a specific aim of this study.

150 The objectives of this study were to assess (1) whether size decreased  
151 with summer temperature, varied among characters and whether the temperature  
152 effect differed among characters, (2) whether absolute fluctuating asymmetry  
153 (AFA; a measure of developmental instability) differed among characters and  
154 with summer temperature and migration distance, and (3) whether the observed  
155 differences in AFA-temperature associations could be explained by trait  
156 functionality, canalization and/or timing of development. To this end, we  
157 analyzed a total of 8993 specimens belonging to 387 species of birds. The  
158 analyses were eventually restricted to 66 species with a minimum of 20  
159 specimens per species, and in total 5533 asymmetry values in 1593 birds from  
160 Christiansfeld and surroundings, Denmark.

161

162 *Materials and methods*163 **STUDY SITES AND ORIGIN OF SPECIMENS**

164 Johannes Erritzøe (JE), who is a taxidermist, receives dead birds delivered by  
165 the public from the surroundings of Christiansfeld, Denmark (55°36N, 9°49'E),  
166 Denmark. He has collected such specimens since 1960. The general area, where  
167 the specimens were found, is largely agricultural with small plantations and  
168 villages. The specimens are found dead, killed by collision with wires, windows  
169 or cars, shot or found dead for other reasons. All specimens are sexed and aged  
170 using gonads or plumage characteristics as reported in Svensson (2006).

171

172 **MEASUREMENTS**

173 JE measured more than 40 characters, including the five characters that were  
174 measured twice to allow discrimination between measurement error and  
175 fluctuating asymmetry. JE measured twice right and left side of the flattened  
176 wing for 2459 individual birds, tail length for 1247, tarsus length for 1816,  
177 femur length for 1840 and humerus length for 1963 individual birds to allow for  
178 estimation of size and size-scaled and log-transformed absolute fluctuating  
179 asymmetry (AFA). All feather measurements were made with a ruler to the  
180 nearest 0.5 mm and skeletal measurements were made with a digital caliper with  
181 a precision of 0.01 mm when bones had been fully cleaned, removed from  
182 specimen and measured as described above. Repeat measurements were made

183 first by measuring the character on the right side, then the left side, then the  
184 right side and finally the left side to avoid any bias in measurements. JE took  
185 great care to use clearly defined landmarks at the two ends of skeletal characters  
186 before making the measurements as described above. All specimens were  
187 measured by JE thereby avoiding any variation among observers. The  
188 measurements were made blindly with respect to the hypotheses under test,  
189 thereby preventing any observer expectations.

190

## 191 **ENVIRONMENTAL CONDITIONS**

192 We used mean summer temperature during the months May-August estimated  
193 as the temperature anomaly for all years 1949-2017  
194 ([http://cib.knmi.nl/mediawiki/index.php/European\\_climate\\_in\\_2017](http://cib.knmi.nl/mediawiki/index.php/European_climate_in_2017)). Surface  
195 air temperatures are measured at an extensive network of weather stations in  
196 Europe. These data are collected and aggregated into European temperatures.  
197 The annual mean values in this E-OBS  
198 (<http://www.ecad.eu/download/ensembles/ensembles.php>) dataset are estimated  
199 for the land area between 35°- 75°N and 25°W-45°E. We decided to rely on  
200 aggregated weather data over large spatial scales because the specimens that we  
201 obtained derived from a large spatial scale during migration and reproduction.  
202 Local climate data from the main study site at Taps, Christiansfeld, Denmark  
203 provided very similar conclusions.

204

**205 MIGRATION DISTANCES**

206 We estimated migration distance as the difference in latitude between the mean  
207 of the northernmost and the southernmost breeding distribution in degree  
208 latitude and the mean of the northernmost and the southernmost winter  
209 distribution in degree latitude, relying on information in Cramp and Perrins  
210 (1977-1994) and del Hoyo et al. (1995-2008). Migration distance ranged from 0  
211 to 71° latitude with a mean value of 13.9° (SE = 2.22) for the 66 species that  
212 were included in the analyses.

213

**214 ESTIMATING SIZE AND ABSOLUTE FLUCTUATING ASYMMETRY**

215 After selecting species with 20 or more measured specimens, size was obtained  
216 for each trait and individuals were averaged across the repeated measurements  
217 on both sides. In order to be able to analyze the association between size and  
218 summer temperature, size was standardized for each species such that the scale  
219 of measurement was identical for all species.

220 To obtain absolute fluctuating asymmetry (AFA) estimates for each trait  
221 and individual, first a mixed model was run to separate FA from measurement  
222 error and to correct for directional asymmetry. To achieve this, signed  
223 asymmetries were calculated for each individual-trait combination on the basis  
224 of the first and the second repeated measurements. Both were divided by trait  
225 size such that all signed FA's were expressed as a proportion of trait size. Next,  
226 a mixed model was run with signed FA as response variable and individual as

227 random effect. The intercept of this model will test for directional asymmetry,  
228 whereas the between-individual variation reflects real FA and the residual  
229 variation the degree of measurement error. The results are provided in Table 1,  
230 showing that measurement error was smaller than 10%, and that right biased  
231 directional asymmetry was present for tails, wings and femur, while for  
232 humerus directional asymmetry was left biased. This DA could reflect a real  
233 biological phenomenon, or it could originate from the handedness of the  
234 measurer (Helm and Albrecht, 2000). Differences in DA among traits have also  
235 been observed in humans and may have functional importance (related to  
236 behavioral lateralization; Auerbach and Ruff, 2006), but also be of  
237 developmental origin (Van Dongen et al., 2014). Absolute values of the random  
238 individual effects were used as estimates of AFA, thus after correcting for  
239 measurement error and directional asymmetry.

240

## 241 **STATISTICAL ANALYSES**

242 The analysis of AFA in relation to summer temperature and migration distance  
243 was performed for all traits in one overall mixed model. In this model, summer  
244 temperature, migration distance, trait, all two-way interactions and the three-  
245 way interaction were treated as fixed effects. Individual, species, genus and  
246 family were added as random effects. In addition, the species-summer  
247 temperature interaction was also added as a random effect, to obtain the  
248 appropriate tests and degrees of freedom for the fixed effects analysis, thus

249 assuming that species are the independent unit of observation. A species-  
250 migration distance interaction could not be added as migration distance is a  
251 species-specific characteristic. Degrees of freedom were approximated using the  
252 Kenward-Roger method (Kenward and Roger 1997). In case of significant  
253 interactions between trait and either summer temperature or migration distance,  
254 indicating that associations between AFA and summer temperature or migration  
255 distance differed among traits, the above mixed model was run for each trait  
256 separately (and without the random individual effect, because there were no  
257 longer repeated measurements). A similar analysis was performed for trait size.  
258 However, since the size of each trait was standardized at the level of species for  
259 each trait, all variation among species, genera and families was a priori removed  
260 from the variation in size. In addition, as migration distance is a species-specific  
261 trait, it was also removed from the model. Thus, the mixed model contained  
262 trait, summer temperature and the trait-summer temperature interaction as fixed  
263 effects, and the summer temperature-species interaction as random effect.  
264 Degrees of freedom were approximated using the Kenward-Rogers method. The  
265 advantages of using such complex mixed models is that it allows to explicitly  
266 model and test for interactions and thus statistically compare patterns across  
267 traits.

268 All analyses were performed in the package R (version 3.3; R Core Team  
269 2017) using the package lmerTest and the function lmer.

270

271 **Results**

272 **CLIMATE CHANGE**

273 Climate changed significantly during 1948-2016. Annual temperature anomaly  
274 has increased since 1948 by +0.5921 (SE = 0.0546) °C/year, or by +0.0404 °C  
275 (SE = 0.0076) during 1948-2016 ( $F_{1,67} = 28.55$ ,  $R^2 = 0.29$ ,  $P < 0.0001$ ). Local  
276 temperature at the study site in Denmark was strongly positively correlated with  
277 the annual temperature anomaly during 1971-2017 ( $F_{1,44} = 22.28$ ,  $R^2 = 0.32$ ,  $P <$   
278  $0.0001$ , slope (SE) = 1.0397 (0.2203)).

279

280 **SIZE, FA, CANALIZATION AND CLIMATE WARMING**

281 There was no significant interaction between trait and summer  
282 temperature for the mixed model analyzing trait size ( $F_{4,5990} = 0.46$ ,  $P = 0.76$ ),  
283 suggesting that the change in size with summer temperature is comparable for  
284 all traits. Indeed, the overall association between size and summer temperature  
285 was statistically significant ( $F_{1,135} = 9.47$ ,  $P = 0.003$ ), even though it was not  
286 statistically significant for each individual trait (Fig. 1).

287 AFA did not differ substantially among individuals (0.3%), species  
288 (0.7%), genera (0.6%) or families (1.9%), as these four hierarchical levels  
289 together explained only 3.5% of the variation in AFA. Average asymmetry did  
290 differ among traits, where the lowest values were observed for wing and femur  
291 (Table 1), suggesting that these traits were most strongly canalized.

292 For the mixed model of AFA, there was no significant three-way  
293 interaction between trait, summer temperature and migration distance ( $F_{4,94} =$   
294  $0.34, P = 0.85$ ), nor was there a significant interaction between summer  
295 temperature and migration distance ( $F_{1,556} = 0.20, P = 0.66$ ). A statistically  
296 significant interaction was found between trait and summer temperature ( $F_{4,77} =$   
297  $3.42, P = 0.01$ ) and between trait and migration distance ( $F_{4,3004} = 5.21, P =$   
298  $0.0004$ ). This indicates that the association between AFA and both summer  
299 temperature and migration distance differed among traits. Analyses for each  
300 trait separately showed that there was a significant increase in AFA with  
301 summer temperature for wings only (Fig. 2). In addition, AFA showed a  
302 significant negative association with migration distance for wings only (Fig. 3).

303

### 304 *Discussion*

305 There is an extensive literature on the effects of climate warming on size, albeit  
306 clearly heterogeneous (reviews in Gardner et al. 2011; Sheridan and Bickford  
307 2011). Here we have taken these analyses a step further by comparing patterns  
308 among characters which differ in functional importance, level of canalization  
309 and timing of development. In contrast, most previous studies have only  
310 analyzed one or a couple of characters and analyzed average AFA. However, it  
311 is not clear if DI can be considered to be an individual or ‘genome-wide’ trait  
312 and associations could vary among traits. This raises questions about the  
313 probability of demonstrating a consistent significant temporal or spatial pattern

314 as stated in recent reviews (Gardner et al. 2011; Sheridan and Bickford 2011),  
315 especially if there are good reasons to predict different responses of different  
316 characters.

317 Within- and among-individual variation in absolute fluctuating asymmetry  
318 (AFA) and size of two feather and three skeletal characters in birds during the  
319 last 57 years revealed a significant increase in wing asymmetry and a decrease  
320 in overall size with summer temperature. The degree of AFA differed among  
321 characters, with the lowest degree of FA in wings and femur, suggesting that  
322 these traits were more strongly canalized. Absolute fluctuating asymmetry in  
323 both wings and femur decreased with migration distance. These patterns of  
324 phenotypic variation imply that DI of the most important functional trait  
325 (wings) is more impacted by temperature than tails, tarsus, femur and humerus,  
326 and DI of the two most canalized traits is negatively related to migration  
327 distance.

328 Indeed, we hypothesized that migratory species should be subject to more  
329 intense selection against AFA in wings that are directly involved in flight and  
330 hence in long-distance migration. Indeed, the morphology of the flight  
331 apparatus is known to be related to migration with implications for wingspan,  
332 wing area, aspect ratio and wing loading (e.g. Norberg 1990; Rayner 1990;  
333 Vágási et al. 2016). In contrast, there was no comparable effect for tail, tarsus or  
334 humerus length. Migratory birds have been subject to a particularly intense  
335 history of selection, while that is not the case for resident species. Therefore, we

336 should expect that such traits subject to intense selection would have a high  
337 degree of canalization (Waddington 1942; Scharloo 1991). Indeed, there is  
338 currently strong selection on the locomotor apparatus in migrants (e. g. Møller  
339 et al. 2011a, b; Teplitsky et al. 2011). Canalization reflects the ability of a  
340 population to produce a single phenotype independent of variability in the  
341 environment (Waddington 1942; Scharloo 1991). However, not all traits are  
342 canalized similarly because traits vary in their functional importance and hence  
343 the degree to which such traits have been selected to result in similar  
344 developmental trajectories even under different adverse environmental  
345 conditions. Because the three-way interaction between temperature, migration  
346 distance and character was not statistically significant, the relationship between  
347 AFA and temperature was comparable for migratory and resident species.  
348 Indeed, for wings, the associations between AFA and both temperature and  
349 migration patterns are in agreement with our hypothesis that high functional  
350 importance would increase canalization and result in a trait DI that is more  
351 vulnerable for environmental stress, even though it is obviously important to  
352 note that we cannot prove this from our correlational data.

353         For the femur, however, it remains difficult to explain why AFA would  
354 relate negatively to migration distance. A speculative explanation might be that  
355 the femur is morphologically associated with the muscles of the upper limb and  
356 thus have a relative high amount of mass. Subtle asymmetries might create mass  
357 imbalances between the two sides during flight and these need to be

358 compensated for constantly and hence be energetically constant. However, to  
359 our knowledge, no research has been performed on the relationship between  
360 trait asymmetry and flight in birds, except for wings (Swaddle, 1997). Even if  
361 one would be able to explain the higher canalization and the negative  
362 association between femur AFA and migration distance from a functional point  
363 of view, one would expect a positive correlation between femur AFA and  
364 temperature as well. Apparently, trait functionality and degree of canalization  
365 alone are not sufficient to explain our results.

366

367         In conclusion, climate warming has been predicted to affect body size and  
368 AFA. Here we have documented such effects for a large number of species and  
369 five different characters. While some would argue that patterns in AFA should  
370 become expressed in all traits, we show the contrary and suggest that  
371 evolutionary history, functional importance and degree of canalization of a trait  
372 may predict effects of environmental changes on DI. These novel findings are  
373 only to some extent consistent with predictions. Finally, we document that the  
374 effect of temperature, that is extensively documented in the literature, is similar  
375 in migratory and resident bird species, yet may mainly affects locomotor traits  
376 that can have functional consequences, especially in migratory birds. The  
377 comparison of AFA-stress associations among traits may offer an interesting  
378 strategy to explore the interplay of environmental changes and the evolutionary  
379 history of traits for developmental instability and canalization. Ideally, an

380 experimental approach should be adopted, but may be difficult to achieve when  
381 making comparisons among species with different properties, like being  
382 migratory or not. Since migrants and residents can be crossed readily, we  
383 hypothesize that these questions can be resolved using a quantitative genetic  
384 approach.

385

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- 539

540 **Legends to figures**

541

542 **Figure 1.** Size of five morphological characters in relation to annual  
 543 temperature in 66 species of birds. The associations were significant for tail ( $\beta$   
 544 =  $-0.141 \pm 0.046$ ;  $t_{932} = -3.04$ ,  $p = 0.002$ ) and tarsus ( $\beta = -0.081 \pm 0.041$ ;  $t_{1126} = -$   
 545  $1.98$ ,  $p = 0.05$ ), but not for wing ( $\beta = -0.053 \pm 0.033$ ;  $t_{1700} = -1.64$ ,  $p = 0.10$ ),  
 546 femur ( $\beta = -0.012 \pm 0.041$ ;  $t_{1074} = -0.30$ ,  $p = 0.76$ ) and humerus ( $\beta = -0.033 \pm$   
 547  $0.039$ ;  $t_{1184} = -0.81$ ,  $p = 0.40$ ). Since there was no significant interaction between  
 548 trait and summer temperature, our results suggest that the size of all traits  
 549 showed a similar association with summer temperature (see text for further  
 550 details). The lines are the linear regression lines.

551

552 **Figure 2.** Absolute fluctuating asymmetry (AFA, expressed as a percentage of  
 553 trait size) in relation to annual temperature anomaly for five different  
 554 morphological characters in 66 species of birds. The associations were  
 555 statistically significant for wing ( $\beta = 0.079 \pm 0.031$ ;  $t_{42} = 2.55$ ,  $P = 0.01$ ), but not  
 556 for tail ( $\beta = 0.058 \pm 0.034$ ;  $t_{25} = 1.63$ ,  $P = 0.12$ ), tarsus ( $\beta = 0.013 \pm 0.032$ ;  $t_{26} =$   
 557  $0.38$ ,  $P = 0.71$ ), femur ( $\beta = -0.019 \pm 0.032$ ;  $t_{26} = -0.58$ ,  $P = 0.57$ ) and humerus ( $\beta$   
 558 =  $-0.040 \pm 0.030$ ;  $t_{29} = -1.27$ ,  $P = 0.15$ ). The lines are the linear regression lines.

559

560

561

562 **Figure 3.** Absolute fluctuating asymmetry (AFA, expressed as a percentage of  
563 trait size) in relation to migration distance for five different morphological  
564 characters in 66 species of birds. The associations were statistically significant  
565 for wing ( $\beta = -0.098 \pm 0.034$ ;  $t_{56} = -2.89$ ,  $P = 0.004$ ) and femur ( $\beta = -0.086 \pm$   
566  $0.038$ ;  $t_{56} = -2.29$ ,  $P = 0.02$ ), but not for tail ( $\beta = 0.020 \pm 0.041$ ;  $t_{55} = 0.49$ ,  $P =$   
567  $0.62$ ), tarsus ( $\beta = 0.042 \pm 0.038$ ;  $t_{56} = 1.12$ ,  $P = 0.26$ ) and humerus ( $\beta = 0.029 \pm$   
568  $0.038$ ;  $t_{56} = 0.77$ ,  $P = 0.44$ ). The lines are the linear regression lines.

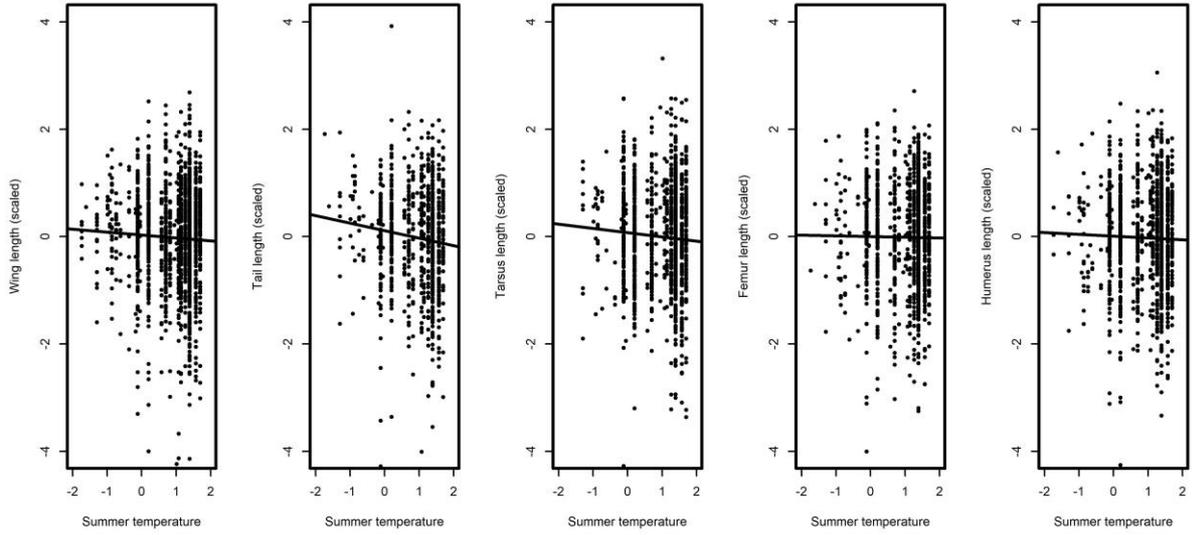
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572 Fig. 1

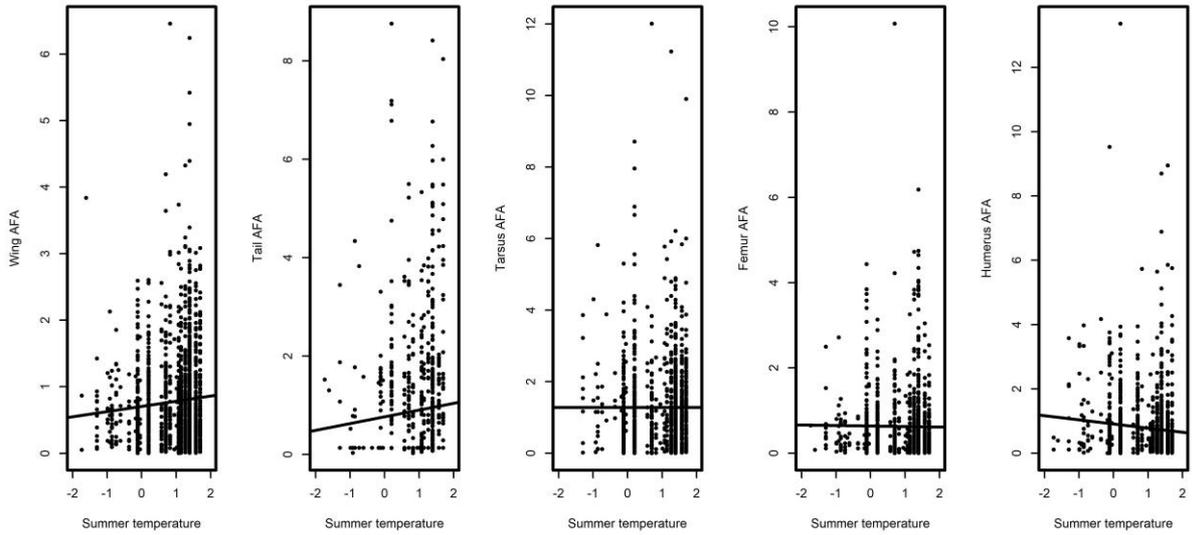
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576 Fig. 2



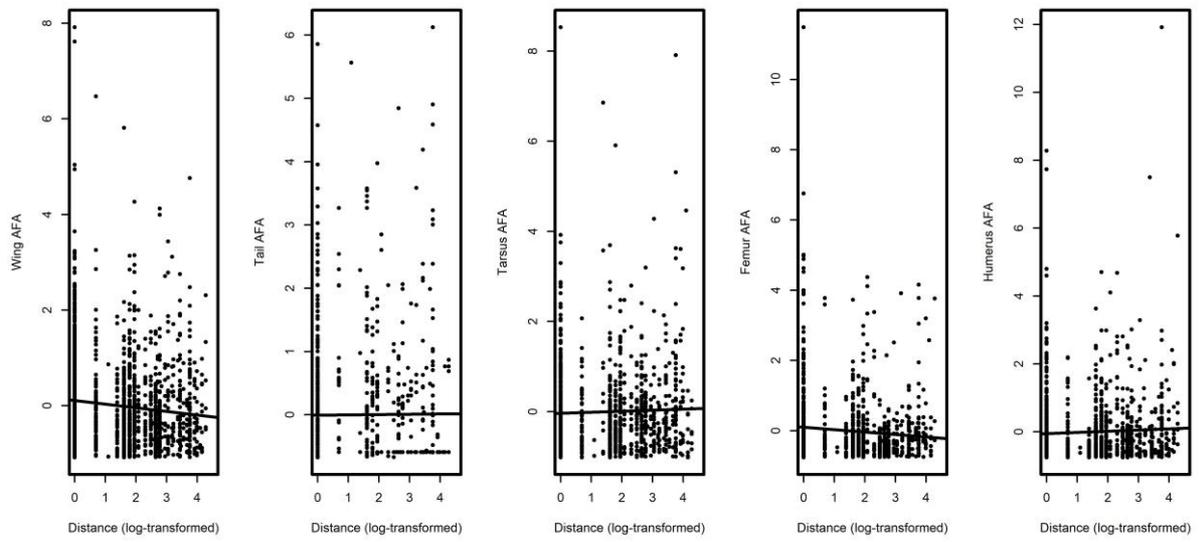
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581 Fig. 3



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583

584 **Table 1.** Analysis of measurement error and directional asymmetry in the five  
 585 characters of birds. Variation in size scaled signed asymmetry (expressed as a  
 586 percentage relative to size) was partitioned into directional asymmetry (DA,  
 587 positive values reflecting that the right side on average was larger than the left),  
 588 variation in fluctuating asymmetry (FA) and variation in measurement error  
 589 (ME).

590

591 Trait	FA	ME	%FA	DA [mean (SD), t-test]	<i>P</i>
592 Wing	1.21	0.12	91%	0.38 (0.02), $t_{2118} = 15.3 < 0.0001$	
593 Tail	2.28	0.08	97%	0.13 (0.05), $t_{1111} = 2.91$	0.004
594 Tarsus	3.35	0.35	91%	-0.04 (0.05), $t_{1517} = 0.80$	0.42
595 Femur	1.32	0.03	97%	0.20 (0.03), $t_{1425} = 6.40 < 0.0001$	
596 Humerus	1.82	0.12	94%	-0.12 (0.04), $t_{1552} = 3.25$	0.001

597

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