

Body size, developmental instability, and climate change

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Development is often temperature-dependent. We hypothesized smaller size and larger asymmetry with increasing temperatures. However, we also predicted associations with asymmetry to differ among traits that differ in their degree of functional importance (especially the functional wings in migratory birds were predicted to be more canalized), timing of development (skeletal [femur, tarsus, and humerus] vs. feather [wing and tail traits]). We analyzed a large dataset of which we included species with at least 20 specimens resulting in 5533 asymmetry values in 1593 individuals from 66 species. There was a consistent significant decrease in size with temperature across all traits. Fluctuating asymmetry (FA) for wings and femur was on average lower, suggesting higher canalization, and it decreased with migration distance, however that was not the case for the other traits. FA increased with increasing temperature for wings, but not for the other characters, where the different responses of different characters to temperature were significant. Because there was no significant three-way interaction between temperature, migration distance, and character, the asymmetry–temperature response was similar in migratory and resident species. These findings imply that climate warming reduces size of all traits and decreases developmental instability of wings in birds.

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

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

The metabolic underpinnings of Bergmann's rule are that larger individuals conserve body heat more efficiently than small conspecifics (Bergmann 1847). It is important to emphasize that this is only one of several explanations for this pattern because Bergmann's rule also applies to many poikilotherms. Furthermore, larger individuals may suffer from hyperthermia because of low heat loss efficiency. If we consider spatial patterns of variation in size as stated by Bergmann's rule, such geographical

differences in body size may come about for different reasons. For example, James (1970) suggested that different phenotypes may have evolved in different climates, or that spatial variation in selection results in spatial clines in size as described by Bergmann. Therefore, the potential causes of temporal body size shifts include effects of temperature on development, fecundity, and mortality because climate variability increases with climate change.

Recently, Bergmann's rule and other patterns of spatial and temporal variation in size have attracted increasing attention because climate change may have predictable outcomes. Indeed, there is an extensive literature providing a link between temporal change in body size and climate change (reviews in Gardner et al. 2011; Yom-Tov and Geffen 2011; Van Buskirk et al. 2010). These

morphological changes can have important evolutionary consequences. For example, Van Gils et al. (2016) showed for the long distance migratory knot *Calidris canutus* that recent body shrinkage of birds in the Arctic has resulted in a deterioration in survival prospects. This pattern of change in body size was until recently so pronounced that it was considered a general consequence of climate warming (reviews in Daufresne et al. 2009; Gardner et al. 2011; Sheridan and Bickford 2011). However, a decline in body size caused by climate warming is far from ubiquitous (Meiri et al. 2009; Gardner et al. 2014a; Teplitsky and Millien 2014). Although some studies found decreases in body size when temperatures increased (e.g., Yom-Tov et al. 2008; Gardner et al. 2009; Van Buskirk et al. 2010), others found no change (e.g., Meiri et al. 2009; Salewski et al. 2010, 2014a,b), and yet others showed an increase (e.g., Gardner et al. 2014b; Björklund et al. 2015). An explanation for this heterogeneous pattern of change in body size may be that it is context dependent such as depending on different sites or even on the same sites in different years (Yom-Tov et al. 2006; Meiri et al. 2009; Collins et al. 2017). Thus, phenotypic changes may depend on short- and long-term effects of climate (Kruuk et al. 2015).

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

Previous studies of climate change effects on morphology have focused on reductions in size, however there is an extensive history of studies dealing with effects of temperature on developmental instability (DI), as shown by temporal changes in asymmetry (a measure of DI) with environmental fluctuations (e.g., Beardmore 1960; Siegel and Doyle 1975; Mooney et al. 1985; Gest et al. 1986). Absolute fluctuating asymmetry (AFA) reflected as the difference in size between the sides of a character has been shown more generally to increase with adverse environmental conditions including increased and stressful temperatures (reviews in Møller and Swaddle 1997; Beasley et al. 2013). Not only can this be important for evaluating the effects of climate change on how it causes stress during development, but causal effects of climate change on asymmetry can have functional implications as well, where, for example, larger wing asymmetry

decreases flight performance (Swaddle and Witter 1997). Thus, on the one hand, if DI reflects stress, health, and/or “individual quality,” one would expect associations between AFA and, for example, temperature to be expressed in all traits. However, there is evidence that the AFA–stress relationship may be trait-specific, and little is known about the factors affecting this heterogeneity (Lens et al. 2002; Van Dongen 2006; but see Van Dongen et al. 2009; De Coster et al. 2013), especially because very large sample sizes are required to detect such differences in responses between traits in single studies, a problem that is not present in this study.

A third component of phenotypic variation is canalization, which reflects the ability of a genotype to produce relatively constant phenotypes under different environmental conditions (Waddington 1942; Scharloo 1991). Not all traits are canalized similarly because traits vary in their functional importance. Hence, the degree to which such traits have been selected to result in similar developmental trajectories even when encountering different or adverse environmental conditions may vary. As such, the degree of canalization may affect the effects of adverse conditions on DI and thus AFA. It can thus be predicted that due to the evolutionary history of traits, effects of climate change vary among different body parts. Indeed, Van Dongen et al. (2009) and De Coster et al. (2013) showed that the evolutionary history of a trait can influence the association between AFA and stress. Similarly, it is likely that the time window during which stress is experienced may make some traits more vulnerable to increased DI than others. Making specific predictions is often difficult as different factors can simultaneously influence particular traits. For example, some traits, such as the tarsus in birds, develop largely before fledging, whereas size and asymmetry of feathers can change after each molt (e.g., Swaddle and Witter 1997). Nevertheless, we predict that wings in particular are highly stabilized traits given their functional importance, and that should particularly be the case in birds migrating over very long distances. To what extent higher canalization would, if any, either increase or decrease DI of such traits is currently unknown, and is a specific aim of this study.

The objectives of this study were to assess (1) whether size decreased with summer temperature, varied among characters, and whether the temperature effect differed among characters, (2) whether AFA (a measure of DI) differed among characters and with summer temperature and migration distance, and (3) whether the observed differences in AFA–temperature associations could be explained by trait functionality, canalization, and/or timing of development. To this end, we analyzed a total of 8993 specimens belonging to 387 species of birds. The analyses were eventually restricted to 66 species with a minimum of 20 specimens per species, and in total 5533 asymmetry values in 1593 birds from Christiansfeld and surroundings, Denmark.

Materials and Methods

STUDY SITES AND ORIGIN OF SPECIMENS

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

MEASUREMENTS

JE measured more than 40 characters, including the five characters that were measured twice to allow discrimination between measurement error and fluctuating asymmetry (FA). JE measured twice right and left side of the flattened wing for 2459 individual birds, tail length for 1247, tarsus length for 1816, femur length for 1840, and humerus length for 1963 individual birds to allow for estimation of size and size-scaled and log-transformed AFA. All feather measurements were made with a ruler to the nearest 0.5 mm and skeletal measurements were made with a digital caliper with a precision of 0.01 mm when bones had been fully cleaned, removed from specimen, and measured as described above. Repeated measurements were made first by measuring the character on the right side, then the left side, then the right side, and finally the left side to avoid any bias in measurements. JE took great care to use clearly defined landmarks at the two ends of skeletal characters before making the measurements as described above. All specimens were measured by JE thereby avoiding any variation among observers. The measurements were made blindly with respect to the hypotheses under test, thereby preventing any observer expectations.

ENVIRONMENTAL CONDITIONS

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

MIGRATION DISTANCES

We estimated migration distance as the difference in latitude between the mean of the northernmost and the southernmost breeding distribution in degree latitude and the mean of the northernmost and the southernmost winter distribution in degree latitude, relying on information in Cramp and Perrins (1977–1994) and del Hoyo et al. (1992–2008). Migration distance ranged from 0 to 71° latitude with a mean value of 13.9° (SE = 2.22) for the 66 species that were included in the analyses.

ESTIMATING SIZE AND AFA

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

To obtain AFA estimates for each trait and individual, first a mixed model was run to separate FA from measurement error and to correct for directional asymmetry. To achieve this, signed asymmetries were calculated for each individual–trait combination on the basis of the first and the second repeated measurements. Both were divided by trait size such that all signed FAs were expressed as a proportion of trait size. Next, a mixed model was run with signed FA as response variable and individual as random effect. The intercept of this model will test for directional asymmetry, whereas the between-individual variation reflects real FA and the residual variation the degree of measurement error. The results are provided in Table 1, showing that measurement error was smaller than 10%, and that right-biased directional asymmetry was present for tails, wings, and femur, whereas for humerus directional asymmetry was left-biased. This DA could reflect a real biological phenomenon, or it could originate from the handedness of the measurer (Helm and Albrecht 2000). Differences in DA among traits have also been observed in humans and may have functional importance (related to behavioral lateralization; Auerbach and Ruff 2006), but also be of developmental origin (Van Dongen et al. 2014). Absolute values of the random individual effects were used as estimates of AFA, thus after correcting for measurement error and directional asymmetry.

STATISTICAL ANALYSES

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

Table 1. Analysis of measurement error and directional asymmetry in the five characters of birds.

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

Variation in size-scaled signed asymmetry (expressed as a percentage relative to size) was partitioned into directional asymmetry (DA, positive values reflecting that the right side on average was larger than the left), variation in fluctuating asymmetry (FA), and variation in measurement error (ME).

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

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

Results

CLIMATE CHANGE

Climate changed significantly during 1948–2016. Annual temperature anomaly has increased since 1948 by $+0.5921^{\circ}\text{C}$ (SE = 0.0546) per year, or by $+0.0404^{\circ}\text{C}$ (SE = 0.0076) during 1948–2016 ($F_{1,67} = 28.55$, $R^2 = 0.29$, $P < 0.0001$). Local temperature at the study site in Denmark was strongly positively correlated with the annual temperature anomaly during 1971–2017 ($F_{1,44} = 22.28$, $R^2 = 0.32$, $P < 0.0001$, slope [SE] = 1.0397 [0.2203]).

SIZE, FA, CANALIZATION, AND CLIMATE WARMING

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

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

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

Discussion

There is an extensive literature on the effects of climate warming on size, albeit clearly heterogeneous (reviews in Gardner et al. 2011; Sheridan and Bickford 2011). Here we have taken these analyses a step further by comparing patterns among characters which differ in functional importance, level of canalization and timing of development. In contrast, most previous studies have only analyzed one or a couple of characters and analyzed average

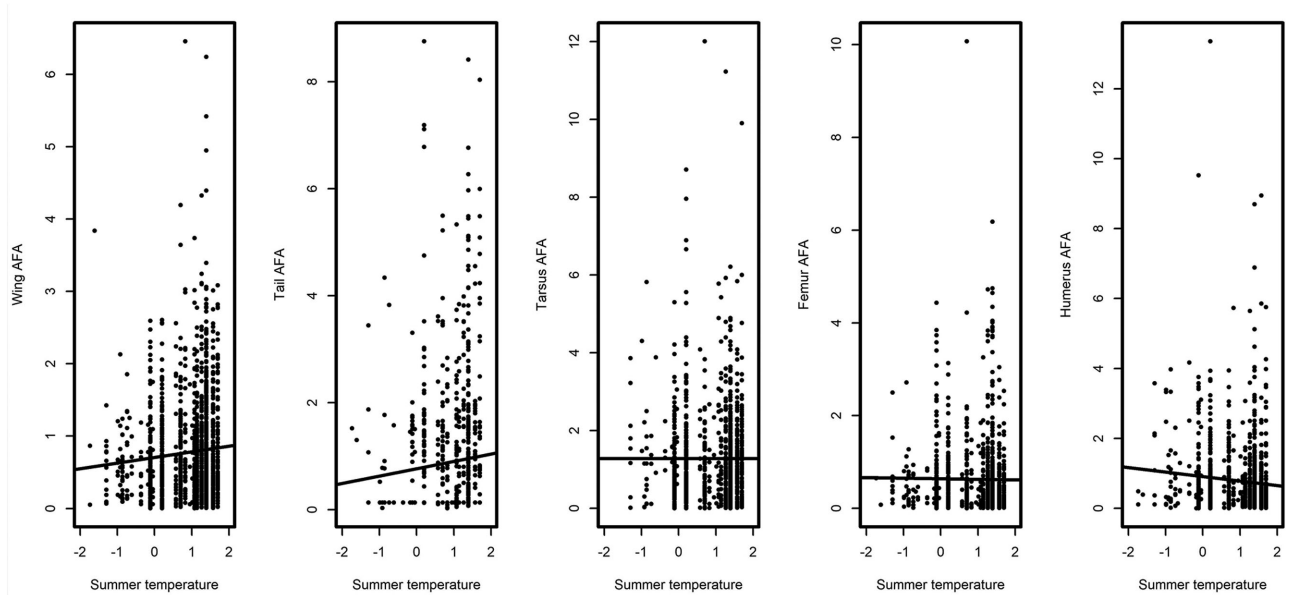


Figure 1. Absolute fluctuating asymmetry (AFA, expressed as a percentage of trait size) in relation to annual temperature anomaly for five different morphological characters in 66 species of birds. The associations were statistically significant for wing ($\beta = 0.079 \pm 0.031$; $t_{42} = 2.55$, $P = 0.01$), but not for tail ($\beta = 0.058 \pm 0.034$; $t_{25} = 1.63$, $P = 0.12$), tarsus ($\beta = 0.013 \pm 0.032$; $t_{26} = 0.38$, $P = 0.71$), femur ($\beta = -0.019 \pm 0.032$; $t_{26} = -0.58$, $P = 0.57$), and humerus ($\beta = -0.040 \pm 0.030$; $t_{29} = -1.27$, $P = 0.15$). The lines are the linear regression lines.

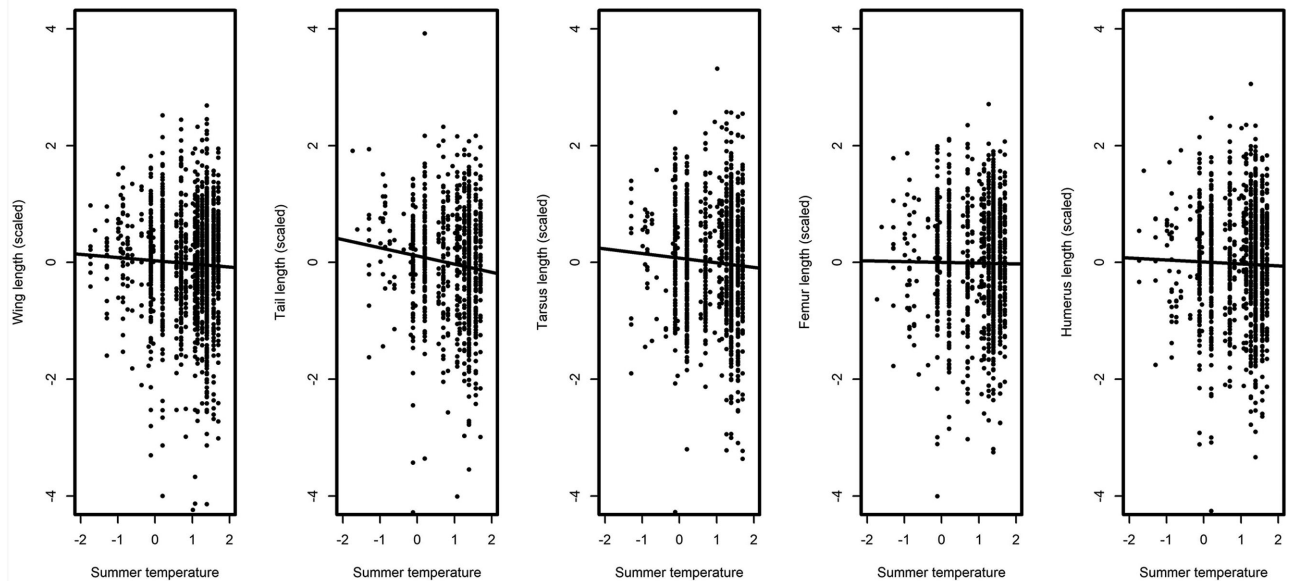


Figure 2. Size of five morphological characters in relation to annual temperature in 66 species of birds. The associations were significant for tail ($\beta = -0.141 \pm 0.046$; $t_{932} = -3.04$, $P = 0.002$) and tarsus ($\beta = -0.081 \pm 0.041$; $t_{1126} = -1.98$, $P = 0.05$), but not for wing ($\beta = -0.053 \pm 0.033$; $t_{1700} = -1.64$, $P = 0.10$), femur ($\beta = -0.012 \pm 0.041$; $t_{1074} = -0.30$, $P = 0.76$), and humerus ($\beta = -0.033 \pm 0.039$; $t_{1184} = -0.81$, $P = 0.40$). Because there was no significant interaction between trait and summer temperature, our results suggest that the size of all traits showed a similar association with summer temperature (see text for further details). The lines are the linear regression lines.

AFA. However, it is not clear if DI can be considered to be an individual or ‘genome-wide’ trait and associations could vary among traits. This raises questions about the probability of demonstrating a consistent significant temporal or spatial pattern as stated in recent reviews (Gardner et al. 2011; Sheridan and Bickford 2011),

especially if there are good reasons to predict different responses of different characters.

Within- and among-individual variation in AFA and size of two feather and three skeletal characters in birds during the last 57 years revealed a significant increase in wing asymmetry and a

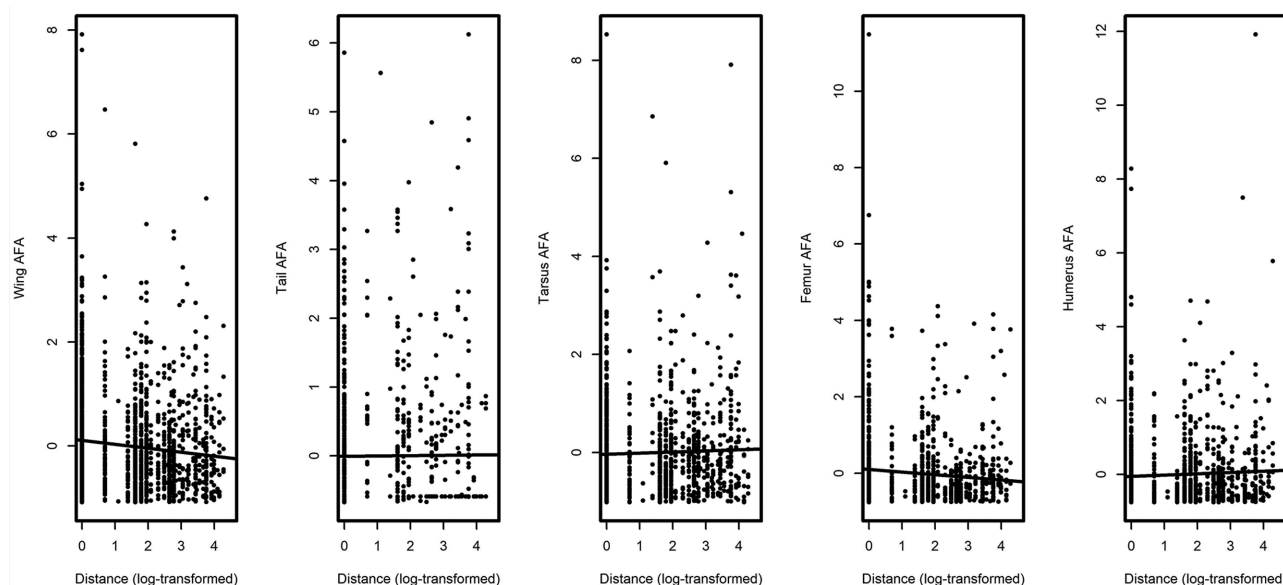


Figure 3. Absolute fluctuating asymmetry (AFA, expressed as a percentage of trait size) in relation to migration distance for five different morphological characters in 66 species of birds. The associations were statistically significant for wing ($\beta = -0.098 \pm 0.034$; $t_{56} = -2.89$, $P = 0.004$)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

decrease in overall size with summer temperature. The degree of AFA differed among characters, with the lowest degree of FA in wings and femur, suggesting that these traits were more strongly canalized. AFA in both wings and femur decreased with migration distance. These patterns of phenotypic variation imply that DI of the most important functional trait (wings) is more impacted by temperature than tails, tarsus, femur, and humerus, and DI of the two most canalized traits is negatively related to migration distance.

Indeed, we hypothesized that migratory species should be subject to more intense selection against AFA in wings that are directly involved in flight and hence in long-distance migration. Indeed, the morphology of the flight apparatus is known to be related to migration with implications for wingspan, wing area, aspect ratio, and wing loading (e.g., Norberg 1990; Rayner 1990; Vágási et al. 2016). In contrast, there was no comparable effect for tail, tarsus, or humerus length. Migratory birds have been subject to a particularly intense history of selection, however that is not the case for resident species. Therefore, we should expect that such traits subject to intense selection would have a high degree of canalization (Waddington 1942; Scharloo 1991). Indeed, there is currently strong selection on the locomotor apparatus in migrants (e.g., Møller et al. 2011a,b; Teplitsky et al. 2011). Canalization reflects the ability of a population to produce a single phenotype independent of variability in the environment (Waddington 1942; Scharloo 1991). However, not all traits are canalized similarly because traits vary in their functional importance and hence the degree to which such traits have

been selected to result in similar developmental trajectories even under different adverse environmental conditions. Because the three-way interaction between temperature, migration distance, and character was not statistically significant, the relationship between AFA and temperature was comparable for migratory and resident species. Indeed, for wings, the associations between AFA and both temperature and migration patterns are in agreement with our hypothesis that high functional importance would increase canalization and result in a trait DI that is more vulnerable for environmental stress, even though it is obviously important to note that we cannot prove this from our correlational data.

For the femur, however, it remains difficult to explain why AFA would relate negatively to migration distance. A speculative explanation might be that the femur is morphologically associated with the muscles of the upper limb and thus have a relative high amount of mass. Subtle asymmetries might create mass imbalances between the two sides during flight and these need to be compensated for constantly and hence be energetically constant. However, to our knowledge, no research has been performed on the relationship between trait asymmetry and flight in birds, except for wings (Swaddle and Witter 1997). Even if one would be able to explain the higher canalization and the negative association between femur AFA and migration distance from a functional point of view, one would expect a positive correlation between femur AFA and temperature as well. Apparently, trait functionality and degree of canalization alone are not sufficient to explain our results.

In conclusion, climate warming has been predicted to affect body size and AFA. Here we have documented such effects for a large number of species and five different characters. Although some would argue that patterns in AFA should become expressed in all traits, we show the contrary and suggest that evolutionary history, functional importance, and degree of canalization of a trait may predict effects of environmental changes on DI. These novel findings are only to some extent consistent with predictions. Finally, we document that the effect of temperature, that is extensively documented in the literature, is similar in migratory and resident bird species, yet may mainly affect locomotor traits that can have functional consequences, especially in migratory birds. The comparison of AFA–stress associations among traits may offer an interesting strategy to explore the interplay of environmental changes and the evolutionary history of traits for DI and canalization. Ideally, an experimental approach should be adopted, but may be difficult to achieve when making comparisons among species with different properties, like being migratory or not. Because migrants and residents can be crossed readily, we hypothesize that these questions can be resolved using a quantitative genetic approach.

AUTHOR CONTRIBUTIONS

APM and SVD conceived the idea. JE collected the samples and measured specimens. APM and SVD analyzed the data. JE, APM, and SVD wrote the article. JE, APM, and SVD read and finally approved the manuscript.

DATA ARCHIVING

The doi for our data is <https://doi.org/10.5061/dryad.s0n86hq>.

LITERATURE CITED

- Auerbach, B. M., and Ruff, C. B. 2006. Limb bone bilateral asymmetry: variability and commonality among modern humans. *J. Hum. Evol.* 50:203–218.
- Beardmore, J. A. 1960. Developmental stability in constant and fluctuating temperatures. *Heredity* 14:411–422.
- Beasley, D. A. E., A. Bonisoli-Alquati, and T. A. Mousseau. 2013. The use of fluctuating asymmetry as a measure of environmentally induced developmental instability: a meta-analysis. *Ecol. Indic.* 30:218–226.
- Bergmann, C. 1847. Über die Verhältnisse des Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien*. 3:595–708.
- Björklund, M., A. Borrás, J. Cabrera, and J. C. Senar. 2015. Increase in body size is correlated to warmer winters in a passerine bird as inferred from time series data. *Ecol. Evol.* 5:59–72.
- Bonaparte, K. M., C. Riffle-Yokoi, and N. T. Burley. 2011. Getting a head start: diet, sub-adult growth, and associative learning in a seed-eating passerine. *PLoS One* 6:e23775.
- Collins, M. D., G. E. Relyaea, E. C. Brustein, and S. M. Badami. 2017. Heterogeneous changes in avian body size across and within species. *J. Ornithol.* 158:39–52.
- Cramp, S., and C. M. Perrins, eds. 1977–1994. *The birds of the Western Palearctic*. Vols. 1–9. Oxford Univ. Press, Oxford, U.K.
- Daufresne, M., K. Lengfellner, and U. Sommer. 2009. Smallest algae thrive as the Arctic Ocean freshens. *Proc. Natl. Acad. Sci. USA* 106:12788–12793.
- Dayan, T., D. Simberloff, E. Tchernov, and Y. Yom-Tov. 1991. Calibrating the paleothermometer: climate, communities, and the evolution of size. *Paleobiology* 17:189–199.
- De Coster, G., S. van Dongen, P. Malaki, M. Muchane, A. Alcántara-Exposito, and H. Matheve. 2013. Fluctuating asymmetry and environmental stress: understanding the role of trait history. *PLoS One* 8:e57966.
- del Hoyo, J., A. Elliott, and J. Sagartal, eds. 1992–2008. *Handbook of the birds of the world*. Lynx, Barcelona, Spain.
- Gardner, J. L., R. Heinsohn, and L. Joseph. 2009. Shifting latitudinal clines in avian body size correlate with global warming in Australian passerines. *Proc. Biol. Sci.* 276:3845–3852.
- Gardner, J. L., A. Peters, M. A. Kearney, J. Joseph, and L. Heinsohn. 2011. Declining body size: a third universal response to warming. *Trends Ecol. Evol.* 26:285–291.
- Gardner, J. L., T. Amano, P. R. Y. Blackwell, K. Ikin, W. J. Sutherland, and A. Peters. 2014a. Temporal patterns of avian body size reflect linear size responses to broadscale environmental change over the last 50 years. *J. Avian Biol.* 45:1–7.
- Gardner, J. L., T. Amano, B. Mackey, W. J. Sutherland, M. Clayton, and A. Peters. 2014b. Dynamic size responses to climate change: prevailing effects of rising temperature drive long-term body size increases in a semi-arid passerine. *Global Change Biol.* 20:206–2075.
- Gest, T. R., M. I. Siegel, and J. Anistranski. 1986. The long bones of neonatal rats stressed by cold, heat, and noise exhibit increased fluctuating asymmetry. *Growth* 50:385–389.
- Gillooly, J. F., J. H. Brown, G. B. West, V. W. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. *Science* 293:2248–2251.
- Helm, B., and Albrecht, H. 2000. Human handedness causes directional asymmetry in avian wing length measurements. *Anim. Behav.* 60:899–902.
- James, F. C. 1970. Geographic size variation in birds and its relationship to climate. *Ecology* 51:365–390.
- Kenward, M., and J. Roger. 1997. Small sample inference for fixed effects from restricted maximum likelihood. *Biometrics* 53:983–997.
- Kruuk, L. E. B., H. L. Osmond, and A. Cockburn. 2015. Contrasting effects of climate on juvenile body size in a Southern Hemisphere passerine bird. *Global Change Biol.* 21:2929–2941.
- Lens, L., S. Van Dongen, S. Kark, and E. Matthysen. 2002. Fluctuating asymmetry as an indicator of fitness: Can we bridge the gap between studies? *Biol. Rev.* 77:27–38.
- McKechnie, A. E., and B. O. Wolf. 2010. Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biol. Lett.* 6:253–256.
- Meiri, S., D. Guy, T. Dayan, and D. Simberloff. 2009. Global change and carnivore body size: data are stasis. *Global Ecol. Biogeogr.* 18:240–247.
- Møller, A. P., and J. P. Swaddle. 1997. *Asymmetry, developmental stability, and evolution*. Oxford Univ. Press, Oxford, U.K.
- Møller, A. P., C. Biard, F. Karadas, D. Rubolini, N. Saino, and P. F. Surai. 2011a. Maternal effects and changing phenology of bird migration. *Climate Res.* 49:201–210.
- Møller, A. P., R. Nuttall, S. E. Piper, T. Szép, and E. J. Vickers. 2011b. Migration, moult and climate change in barn swallows *Hirundo rustica* in South Africa. *Climate Res.* 47:201–205.
- Mooney, M. P., M. I. Siegel, and T. R. Gest. 1985. Prenatal stress and increased fluctuating asymmetry in the parietal bones of neonatal rats. *Am. J. Phys. Anthropol.* 68:131–134.
- Norberg, U. M. 1990. *Vertebrate flight: mechanisms, physiology, morphology, ecology and evolution*. Springer, Berlin, Germany.
- Olson, V. A., R. G. Davies, C. D. L. Orme, G. H. Thomas, S. Meiri, T. M. Blackburn, K. J. Gaston, I. P. F. Owens, and P. M. Bennett. 2009. Global biogeography and ecology of body size in birds. *Ecol. Lett.* 12:249–259.

- R Development Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rayner, J. M. V. 1990. The mechanics of flight and bird migration performance. Pp. 283–299 in E. Gwinner, ed. Bird migration. Physiology and ecophysiology. Springer, Heidelberg, Germany.
- Salewski, V., W. Hochachka, and W. Fiedler. 2010. Global warming and Bergmann's rule: Do central European passerines adjust their body size to rising temperatures? *Oecologia* 162:247–260.
- Salewski, V., W. M. Hochachka, and H. Flinks. 2014a. Changes in stonechat *Saxicola torquata* morphology: A response to climate change? *J. Ornithol.* 155:601–609.
- Salewski, V., K.-H. Siebenrock, F. Woog, and W. Fiedler. 2014b. Morphological change to birds over 120 years is not explained by thermal adaptation to climatic change. *PLoS* 9:e101927.
- Scharloo, W. 1991. Canalization: genetic and developmental aspects. *Ann. Rev. Ecol. Syst.* 22:65–93.
- Searcy, W. A., S. Peters, and S. Nowicki. 2004. Effects of early nutrition on growth rate and adult size in song sparrows *Melospiza melodia*. *J. Avian Biol.* 35:269–279.
- Sheridan, J., and D. Bickford. 2011. Shrinking body size as an ecological response to climate change. *Nat. Clim. Change* 1:401–406.
- Siegel, M. I., and W. J. Doyle. 1975. The effects of cold stress on fluctuating asymmetry in the dentition of the mouse. *J. Exp. Zool. A* 193:385–389.
- Svensson, L. 2006. Identification guide to European passerines. British Trust for Ornithology, Thetford, U.K.
- Swaddle, J. P., and M. S. Witter. 1997. The effects of molt on the flight performance, body mass, and behavior of European starlings (*Sturnus vulgaris*): an experimental approach. *Can. J. Zool.* 75:1135–1146.
- Teplitsky, C., and V. Millien. 2014. Climate warming and Bergmann's rule through time: Is there any evidence? *Evol. Appl.* 7:156–168.
- Teplitsky, C., N. G. Mouawad, J. Balbontín, F. de Lope, and A. P. Møller. 2011. Quantitative genetics of migration syndromes: a study of two barn swallow populations. *J. Evol. Biol.* 24:2025–2039.
- Vágási, C., P. L. Pap, O. Vincze, G. Osváth, J. Erritzøe, and A. P. Møller. 2016. Morphological adaptations to migration in birds. *Evol. Biol.* 43:48–59.
- Van Buskirk, J., R. S. Mulvihill, and R. C. Leberman. 2010. Declining body sizes in North American birds associated with climate change. *Oikos* 119:1047–1055.
- Van Dongen, S. 2006. Fluctuating asymmetry and developmental instability in evolutionary biology: past, present and future. *J. Evol. Biol.* 19:1727–1743.
- Van Dongen, S., L. Lens, E. Pape, F. A. M. Volckaert, and J. A. M. Raeymaekers. 2009. Evolutionary history shapes the association between developmental instability and population-level genetic variation in three-spined sticklebacks. *J. Evol. Biol.* 22:1695–1707.
- Van Dongen, S., F. Galis, C. Ten Broek, K. Heikinheimo, L. C. D. Wijnaendts, S. Delen, and J. Bots. 2014. When right differs from left: human limb directional asymmetry emerges during very early development. *Laterality* 19:591–601.
- Van Gils, J. A., S. Lisovski, S. Lok, W. Meissner, A. Ozarowska, J. de Fouw, E. Rakhimberdiev, M. Y. Soloviev, M. Piersma, and M. Klaassen. 2016. Body shrinkage due to Arctic warming reduces red knot fitness in tropical wintering range. *Science* 352:819–821.
- Waddington, C. H. 1942. Canalization of development and the inheritance of acquired characters. *Nature* 150:563–565.
- Yom-Tov, Y., and E. Geffen. 2011. Recent spatial and temporal changes in body size of terrestrial vertebrates: possible causes and pitfalls. *Biol. Rev.* 86:531–541.
- Yom-Tov, Y., S. Yom-Tov, J. Wright, C. J. R. Thorne, and R. Du Feu. 2006. Recent changes in body weight and wing length among some British passerine birds. *Oikos* 112:91–101.
- Yom-Tov, Y., S. Yom-Tov, and G. Jarrell. 2008. Recent increase in body size of the American marten *Martes americana* in Alaska. *Biol. J. Linn. Soc.* 93:701–707.

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