Title: Bird wings are shaped by thermoregulatory demand for heat dissipation

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Abstract:

The tendency for animals in warmer climates to be longer-limbed (Allen's Rule) is widely attributed to the demands of thermoregulation. However, it remains unclear whether this pattern is driven by selection for efficient heat retention at low temperatures or increased demand for heat dissipation at high temperatures. Using comparative phylogenetic models, we find that occurrence in warmer climates is associated with longer wing bones for 1,520 species of passerine birds. The highly vascularized musculature along these bones functions in heat exchange during flight when the overwhelming thermoregulatory challenge is dissipating heat, suggesting longer wing-bone length is driven by heat dissipation demands. Our findings reveal the pervasive impacts of thermoregulation on even the most critical features of vertebrate anatomy, and establish a clear mechanism linking spatial and temporal trends in appendage length.

One-Sentence Summary:

Bird wing bones are longer in warmer climates to meet higher demand for heat loss.

Main Text:

The need to balance energy production with heat dissipation is a fundamental imperative for endotherms. Animal species have overcome this thermoregulatory challenge in numerous ways, including via morphological adaptations to climatic niches. These adaptations form the basis for classic ecogeographic patterns, including the tendencies to have smaller bodies [Bergmann's Rule (*1*)] and longer limbs [Allen's Rule (*2*)] in warmer climates, which have been reported in a wide range of animals (*3*–*5*), including humans (*6*). While the standard explanation for these Rules is that body size and appendage length are shaped by selection for either cold tolerance or heat dissipation, their mechanistic basis remains unclear. This uncertainty has important implications for understanding morphological evolution (*7*), constraints on energy expenditure (*8*), and the potential utility of spatial correlations between morphology and temperature as predictors of the impacts of global warming (*9*).

Focusing on Allen's Rule, we ask whether demand for shedding excess heat – as opposed to conserving heat – can drive large-scale trends in appendage length. Much of what we know about the effects of temperature on appendage length comes from studies of the beaks and leg bones of birds (*10*). There is a limit to what these appendages can tell us, however, because they regulate both heat dissipation (*11*) and cold tolerance (*12*), complicating the identification of underlying mechanisms. A more mechanistic understanding can be achieved by focusing on the vascularized components of wings.

The high energetic demands of flight require a 10-23-fold increase in metabolism (*13*), and the underlying conversion of chemical energy to mechanical energy results in nearly 90% of the metabolic energy expended during flight being converted to heat (*14*). Consequently, during prolonged flights, less than 1% of the heat generated by a bird is retained (*15*). This presents a critical thermoregulatory challenge: during flight much more heat is generated than when at rest, and nearly all of it must be dissipated to the environment. The requisite increase in heat dissipation is primarily achieved through convective heat loss from the vascularized brachial

areas of the wings (*16*). This is in stark contrast to the negligible amounts of heat lost from the wings when individuals are not flying and may need to retain heat, as the wings are held against the torso with the vascularized tissue well insulated (*17*).

We characterize wing heat dissipation capacity for 1,520 species of passerines (~33% of all passerines) by using a neural network (*18*) to measure key skeletal components of the wing – the humerus and the ulna – on digital photographs of 7,366 museum skeletal specimens originating from across the globe (Fig. 1). The lengths of these wing bones determine the extent of the vascularized brachial regions of the wings, which are the main windows of heat exchange with the environment during flight (*16*), and are therefore expected to determine the heat dissipation capacity of the wings (Fig. 2 and fig. S1). We couple these skeletal data with estimates of primary flight feather length and body mass (*19*) to quantify macroecological patterns in wing structure. Specifically, we test the hypothesis that hotter temperatures are associated with longer wing bones, driven by demand for increased heat dissipation capacity in warmer climates.

After controlling for the range of geographic and aerodynamic variables that are expected to influence wing structure, we find a significant positive relationship between temperature and the length of the wing bones ($\beta = 0.05$; $P < 0.001$; Fig. 2). Our model explains nearly all of the variation in wing-bone length (marginal $R^2 = 0.97$; conditional $R^2 > 0.99$). Given the importance of wings in heat dissipation but not cold tolerance, the positive relationship between wing-bone length and temperature likely reflects increased demand for heat dissipation efficiency from the wings in warmer climates, making it an example of Allen's Rule driven by heat dissipation demand.

The thermoregulation-associated pressures shaping wing structure play out within a selective landscape dominated by the demands of flight. The length of the wing bones is strongly predicted by scaling relationships, including a significant and strong positive relationship between wing-bone length and the length of the primary flight feathers ($\beta = 1.05$; P

< 0.001; Fig. 2). This relationship is not surprising, given the constraints on total wing length imposed by body size, and the positive scaling relationships between mass, wing-bone length, and the length of the primary flight feathers necessary to achieve flight (*20*).

Additionally, variation in the length of the wing bones relative to the length of the primary flight feathers is expected to impact flight dynamics. To control for the demands of flight, we take advantage of aerodynamic theory to develop a modified index of pitch agility (*21*) that measures the ability of a bird to generate angular acceleration around the pitch axis (i.e. longitudinal maneuverability; fig. S1), and calculate the aspect ratio of the wings, a determinant of gliding flight efficiency (*14*, *22*, *23*). We find that wing-bone length is significantly negatively associated with pitch index (β = -0.04; $P < 0.001$) and aspect ratio (β = -0.23; $P < 0.001$), suggesting that birds with relatively short wing bones tend to be more agile with greater flight efficiency.

We further account for flight performance-associated drivers of wing structure by constraining our data to passerines, thus avoiding potential confounding effects related to coarse differences in flight style on wing morphology (*24*). For example, heat production during flight may be significantly reduced in birds that habitually soar or glide, but this confounding factor is removed in passerines, all of which use flapping flight. By focusing on a clade with a relatively consistent flight style, and including other contextual factors, such as ecological niche (primary food source), latitude, and migratory strategy (Fig. 2), our models achieve high explanatory power (conditional $R^2 > 0.99$), suggesting that we are not overlooking any major aerodynamic or ecological factor driving variation in wing-bone length.

After controlling for the non-thermal demands of flight, our analyses show that bird wings conform to Allen's Rule primarily as a result of heat dissipation demand. This may help to explain the widespread increases reported in the wing lengths of migrant and resident birds, despite ongoing reductions in body size over recent decades (*25*, *26*). The opposing trajectories of body size and wing length evolution have mainly been attributed to the need for increasingly

efficient flight (*25*, *26*), but our results suggest that the anomaly may be explained by heat dissipation demand selecting for longer wing bones and associated increases in the carpal and "hand" bones.

More broadly, our findings highlight the importance of heat dissipation as a key mechanism driving phenotypic responses to warming temperatures. These responses will not only affect morphological traits associated with food acquisition (*27*) but also with fundamental aspects of locomotion, such as flight. In such cases, the evolutionary outcomes of higher temperature are shaped by biophysical constraints on organismal performance. Further analyses are needed to understand how this trade-off between thermoregulation and flight performance will impact the capacity of birds and other volant animals to respond to global warming via morphological adaptations.

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Investigation: BCW, CH, CS, ZZ, DFF

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Data and materials availability: Please contact BCW for access to the data. All code for generating bone measurement data is publicly available (*18*)

Supplementary Materials

Materials and Methods

Supplementary Text

Figs. S1 to S3

Tables S1 to S5

Data S1 to S3

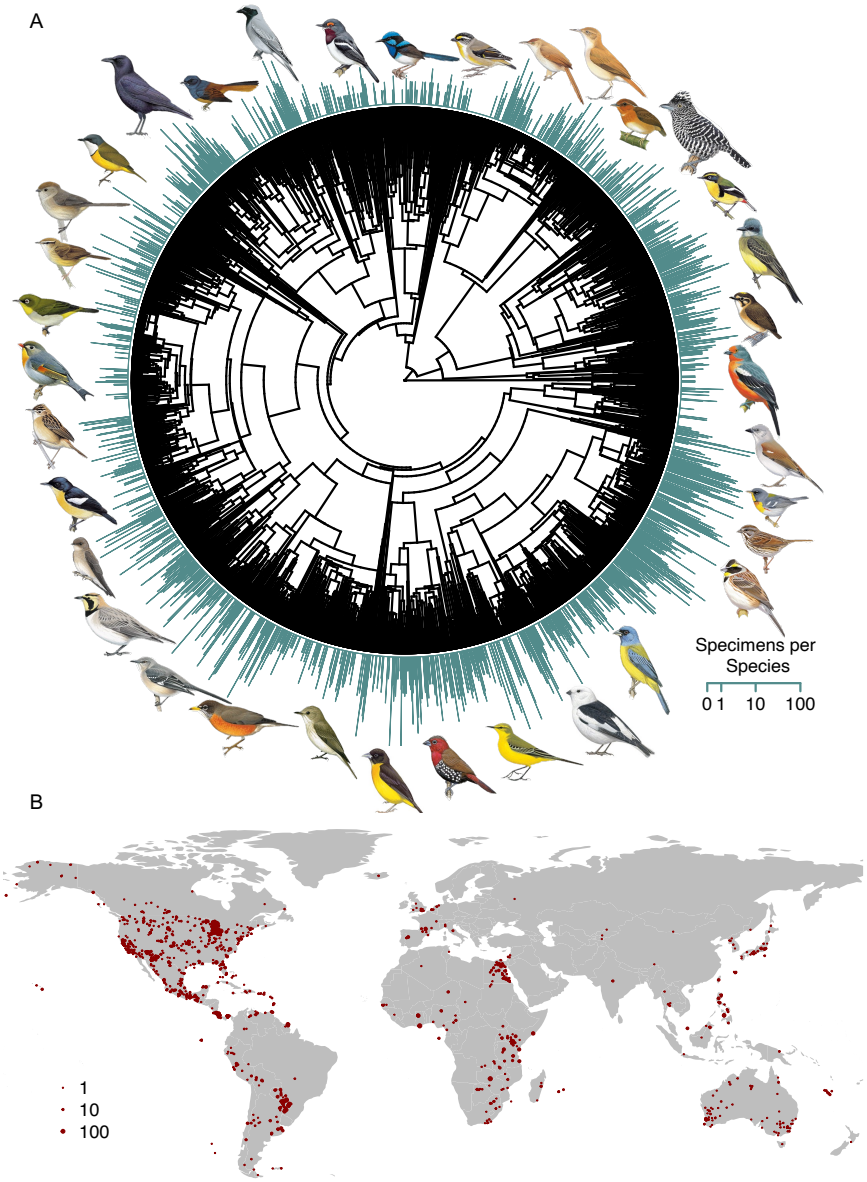

Fig. 1. Spatial and phylogenetic sampling of skeletal morphology. Using 7,366 specimens, we analyze wing-bone length across 1,520 bird species, representing ~33% of passerine diversity. (**A**) Blue bars at branch tips show the number of specimens measured per species. (**B**) Red dots show the broad geographic sampling of species from all continents except Antarctica. Images reproduced with permission from Cornell Lab of Ornithology.

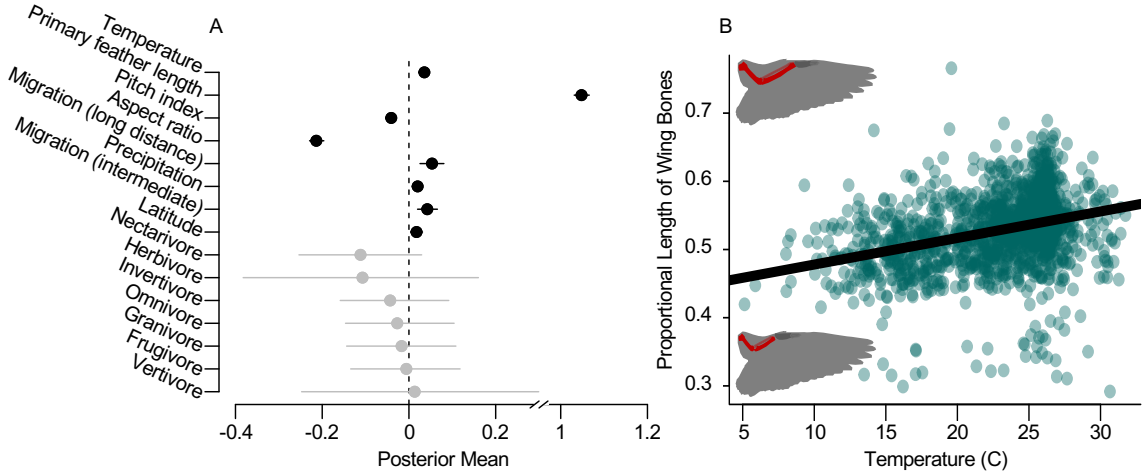

Fig. 2. Wings in warmer temperatures can dissipate more heat. (**A**) We find temperature during the warmest quarter of the year is significantly positively associated with wing-bone length after controlling for the length of the primary flight feathers and a range of ecological and geographic variables. Dots show means of the posterior distribution with bars indicating the 95% confidence interval for each estimate; those not overlapping zero are shown in black and those overlapping zero are shown in grey. (**B**) As expected, given the positive relationship between temperature and wing-bone length in our model, the vascularized section of wings is relatively large in warmer climates**.** The proportion of the wing that is vascularized (the sum of humerus and ulna length divided by the by the length of the primary flight feathers) is higher for species in warmer areas. Each dot represents the species average for each of the 1,502 species used in our models; a linear model of the bivariate relationship between temperature and the proportional length of the wing bones is shown.