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Longer Wing Bones in Warmer Climates Suggest a Role of Thermoregulation in Bird Wing Evolution

Brian C. Weeks¹  | Christina Harvey²  | Joseph A. Tobias³ | Catherine Sheard⁴  | Zhizhuo Zhou^{5,6} | David F. Fouhey^{5,7,8}

¹School for Environment and Sustainability, University of Michigan, Ann Arbor, Michigan, USA | ²Department of Mechanical and Aerospace Engineering, University of California Davis, Davis, California, USA | ³Department of Life Sciences, Imperial College London, London, UK | ⁴School of Earth Sciences, University of Bristol, Bristol, UK | ⁵Department of Computer Science and Engineering, University of Michigan, Ann Arbor, Michigan, USA | ⁶School of Computer Science, Carnegie Mellon University, Pittsburgh, Pennsylvania, USA | ⁷Computer Science, Courant Institute of Mathematical Sciences, New York University, New York, New York, USA | ⁸Electrical & Computer Engineering, Tandon School of Engineering, New York University, New York, New York, USA

Correspondence: Brian C. Weeks (bcweeks@umich.edu)

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ABSTRACT

Aim: The tendency for animals in warmer climates to be longer-limbed (Allen's Rule) is widely attributed to the demands of thermoregulation. The role of thermoregulation in structuring bird wings, however, has been overshadowed by the selective demands placed on wings by flight. We test whether occurrence in warmer climates is associated with longer wing bones.

Location: Global.

Time Period: Current.

Major Taxa Studied: Aves: Passeriformes.

Methods: Using computer vision, we measure wing-bone length from photographs of museum skeletal specimens for 1520 species of passerine birds. We then model the relationship between wing-bone length and temperature, accounting for allometry, the demands of flight efficiency and manoeuvrability, and a range of ecological and environmental variables.

Results: Wing bones are longer in warmer climates. Our models, largely as a result of allometric effects, explain nearly all the variation in wing-bone length in our data, with a marginal $R^2 = 0.80$ and a conditional $R^2 > 0.99$.

Main Conclusions: Across 1520 species of birds, higher temperatures are associated with longer wing bones, as predicted by Allen's Rule. The vascularised musculature along these bones is maximally uncovered when birds actively hold their wings away from their bodies to aid in cooling or during flight. Conversely, the musculature along the wing bones is insulated by feathering when at rest, such that wings play a minor role in heat exchange when individuals are less active and may need to retain heat. While our analyses do not directly establish the mechanistic basis underlying the pattern we recover, given the asymmetry in the role of wings in thermoregulation, we interpret the positive relationship between temperature and wing-bone length to reflect increased demand for heat dissipation in warmer climates. Our findings highlight the role of thermoregulation in shaping even the most critical features of vertebrate anatomy.

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1 | Introduction

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 tendency to have smaller bodies (Bergmann's Rule; Bergmann 1847) and longer limbs (Allen's Rule; Allen 1887) in warmer climates, both of which have been reported in a wide range of animals (Meiri and Dayan 2003; Symonds and Tattersall 2010; Campbell et al. 2021; Fröhlich et al. 2023), including humans (Katzmarzyk and Leonard 1998). While the standard explanation for these patterns is that body size and appendage length are shaped by selection for either cold tolerance or heat dissipation, their mechanistic basis remains unclear. Unravelling these selective mechanisms is an important step towards a more complete understanding of morphological evolution (Tattersall et al. 2017), constraints on energy expenditure (Speakman and Król 2010), and the potential utility of spatial correlations between morphology and temperature as predictors of the impacts of global warming (Tian and Benton 2020).

Much of what we know about the effects of temperature on appendage length comes from studies of the beaks and leg bones of birds (Ryding et al. 2021). There is a limit to what these appendages can tell us, however, because they regulate heat dissipation both to prevent overheating (Greenberg et al. 2012) and to improve cold tolerance (Friedman et al. 2017), complicating the identification of underlying mechanisms. A more mechanistic understanding may be achieved by focusing on the vascularised components of wings.

Wing length has not often been used for tests of Allen's Rule, potentially because wings are used in flight and are thus considered to be constrained by the demands of flight, but also because they are not typically thought of as important thermoregulatory organs. Bird wings are largely composed of thermodynamically inert feathers (Ward et al. 1999) and when they are not in use, they can be tucked against the body such that the vascularised portion of the wing is insulated by feathers (Rogalla et al. 2021). However, there is some evidence that the brachial regions of the wings may be significant sites of heat exchange, particularly during powered flight. In lovebirds (*Agapornis personatus*), for example, while the head and trunk are the main sites of nonevaporative heat dissipation when individuals are perched, during flight, forced convection of heat from ventral wing areas becomes the main type of nonevaporative heat dissipation, with 86% of nonevaporative heat dissipation occurring in the wings (Lewden et al. 2023). Similarly, earlier studies of common starlings (*Sturnus vulgaris*) found that the brachial regions of the wings become a primary site of heat dissipation during flight (Ward et al. 1999). While the brachial regions of the wing appear to be important for thermoregulation, there is little data on this aspect of bird morphology. Rather, the vast majority of large-scale data on bird wing length comes from measures of the wing chord (Weeks et al. 2020; Jirinec et al. 2021; Tobias et al. 2022; Youngflesh et al. 2022), which do not include the vascularised musculoskeletal components of the wing where heat dissipation occurs.

Given the role of wings in heat dissipation, we developed a global dataset of wing-bone length spanning passerine birds (Figure 1) to test the hypothesis that wing bones will compose a larger portion of the wing in warmer climates in adherence to Allen's Rule. Because the lengths of the arm bones in the wing reflect the extent of the vascularised brachial regions of the wings, should the extent of the vascularised tissue determine the heat dissipation capacity of the wings, they may be expected to be longer in warmer climates.

2 | Materials and Methods

2.1 | Morphological and Life History Data

We estimated the length of the humerus and ulna for 7366 individual birds of 1520 species using skeletal specimens in the University of Michigan Museum of Zoology (UMMZ). Each specimen was photographed from a consistent distance, and then measurements of the ulna and humerus were generated from the photographs with a neural network-based computer vision approach (Weeks et al. 2023). In brief, for this method, training data were generated by hand annotating a subset of the images of specimens using the VGG Image Annotator (Dutta et al. 2016) and the Toronto Annotation Suite (Kar et al. 2021), and then precise pixel-wise segmentations for bones of interest were annotated using AI-assisted annotation tools in the Toronto Annotation Suite (Kar et al. 2021). These partial annotations (pixel segmentations were only provided for the bones of interest) were then extended to fully annotated specimens using machine learning. Specifically, a U-Net (Ronneberger et al. 2015) was trained to determine whether each pixel was a bone or not based on preliminary annotations as well as additional synthesised samples. The U-Net was used to infer labels of all pixels in the annotated images. This annotated data set was then used to train an instance segmentation neural network (Mask-RCNN; He et al. 2020) to segment the bones. From these segmentations, the length of each bone of interest was estimated as the length of the longest diagonal. The size of the bone was determined using its known distance from the camera on a flat surface. For complete details and methodological validation, see Weeks et al. (2023). We photographed all of the passerine specimens at the UMMZ but filtered our data to only include estimates for bones that the network detected with high confidence, which we define as a detection where the most likely bone class has at least a 95% probability (Weeks et al. 2023). For each specimen, if multiple measurements of the humerus or ulna were available (i.e., if the model identified and measured the bones from both wings), the arithmetic mean of the measurements was used.

Estimates of the relaxed wing chord (the distance from the carpal joint to the tip of the unflattened longest primary), which we refer to as primary flight feather length, and the distance from the carpal joint to the longest secondary flight feather were recently measured for all birds (Tobias et al. 2022) and are publicly available for all of our species. Migratory status data are publicly available (Tobias et al. 2022), with each species classified as 1 = nonmigratory, 2 = partial/intermediate migrant, or 3 = long-distance migrant. Species mean mass data and the latitude of the

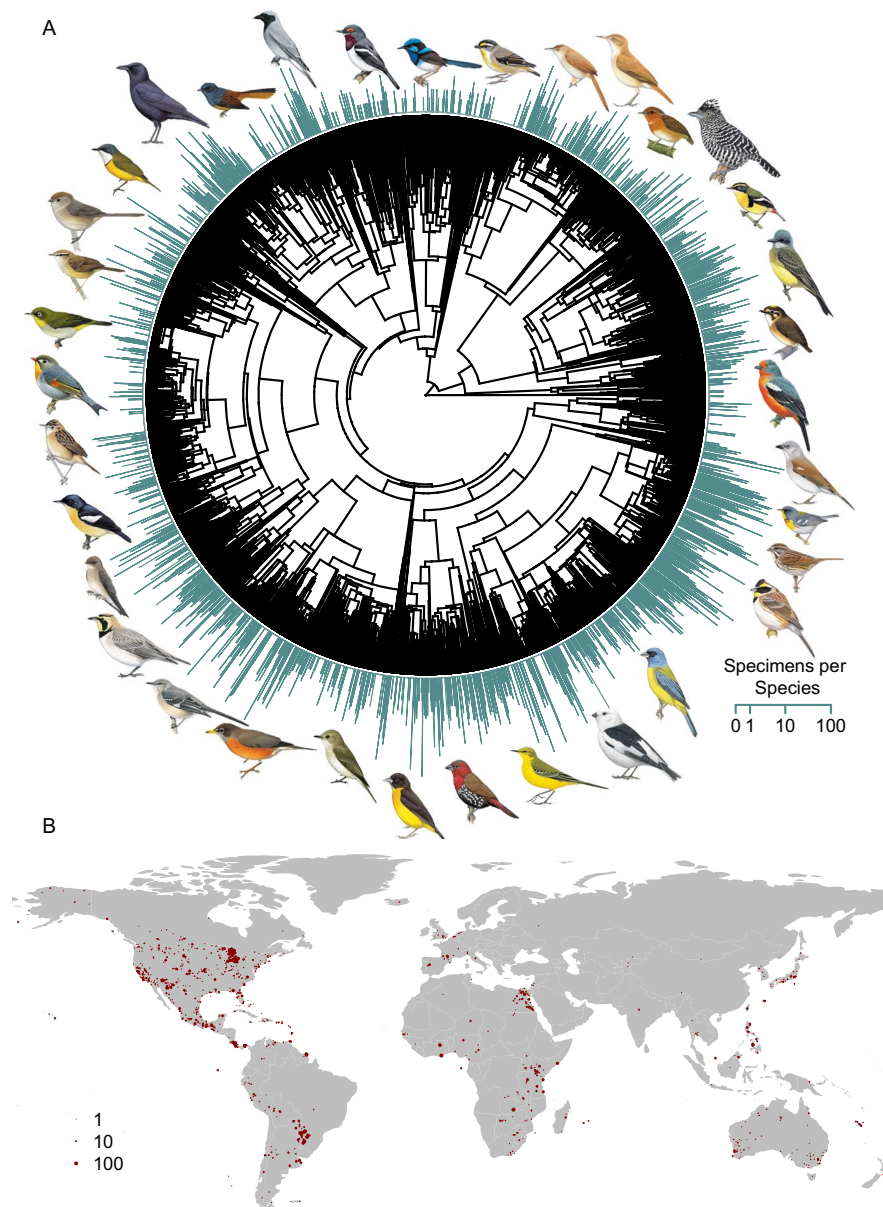


FIGURE 1 | Geographic and phylogenetic sampling of avian wing-bone morphology. Using measurements from 7366 skeletal specimens, we analyse variation in wing-bone length across 1520 bird species, representing approximately 25% of passerine diversity (Jetz et al. 2012). (A) Blue bars at branch tips show the number of specimens measured per species. (B) Red dots show the geographic distribution of specimen localities. For detailed information on the taxonomic sampling in the data set, see Table S9. Bird images are © Birds of the World Cornell Lab of Ornithology.

midpoint of the breeding range centroid were also obtained from Tobias et al. (2022).

2.2 | Environmental Data

Temperature and precipitation data were generated by overlapping species breeding and resident ranges obtained from Birdlife International with a 2.5-min resolution gridded map of the mean temperature of the warmest quarter and mean annual precipitation averaged across 1970–2000 using WorldClim v.2.1 (Fick and Hijmans 2017), and calculating the mean values of these variables within each species' range. All models were also refit using the 1970–2000 annual mean temperature and the maximum temperature of the warmest month (Fick and Hijmans 2017) (Supporting

Information S1). Conditions in the specific year in which specimens were collected cannot be used because many species means are the combination of multiple specimens collected at different timepoints, and the skeletal and plumage data are, by necessity, based on different individuals because they are derived from different specimen preparations. Species were categorised as occupying 1 of 10 ecological niches: vertivore, invertivore, scavenger, omnivore, aquatic predator, frugivore, herbivore (aquatic), herbivore (terrestrial), nectarivore or granivore, with each species assigned to a niche if the relevant food source accounts for at least 60% of the species' diet, based on (Tobias et al. 2022). We unified our taxonomy to the Birdtree taxonomy (Jetz et al. 2012) using the crosswalk in Tobias et al. (2022); only species with 1:1 correspondence (i.e., that were not differentially lumped or split by the UMMZ and Birdtree taxonomy) were included.

2.3 | Flight Aerodynamics

For each species, we estimated an index of manoeuvrability and gliding flight efficiency. Flight manoeuvrability was quantified using a 'pitch index' that is a modified version of a pitch agility metric (Harvey et al. 2022) and quantifies the capacity of a bird to generate angular acceleration. To calculate the pitch index, we quantified wing area (S) and a static margin index (SMI) as:

$$S = L_s(H + U) + 0.2\pi L_s L_p \quad (1)$$

$$SMI = \frac{0.25 L_p}{M^{1/3}} \quad (2)$$

where L_s is the length from the carpal joint to the tip of the first secondary feather, H is the length of the humerus bone, U is the length of the ulna bone, L_p is the length from the carpal joint to the tip of the longest primary feather (referred to as the relaxed wing chord) and M is mass. We then used these variables to calculate the Pitch Index:

$$Pitch\ Index = \frac{(SMI)M^{0.24}S}{M^{5/3}} \quad (3)$$

Birds with higher pitch indices have a greater ability to generate angular acceleration around the pitch axis (Figures S1 and S2). To estimate gliding flight efficiency, we calculated an index of the aspect ratio of the wings as:

$$Aspect\ Ratio\ Index = \frac{(L_p + U + H)^2}{S} \quad (4)$$

We provide derivations of these equations, empirical validation and discussion of the necessary simplifying assumptions in the SI.

2.4 | Statistical Approach

In our models, we used species means for all variables. Wing-bone length (the sum of the humerus length and length of the ulna) was modelled in a phylogenetic linear mixed model as a function of primary feather length (i.e., the relaxed wing chord), mean temperature of the warmest quarter of the year, the latitude at the centre of the range, pitch index, aspect ratio, migration status and ecological niche, with species identity incorporated as a random effect that accounts for phylogenetic relatedness. Mass and wing area (Equation 1) were not included as predictors, as they were highly correlated with the length of the relaxed wing chord ($R=0.87$ and 0.95 , respectively); none of the remaining variables were highly correlated, with variance inflation factors, calculated using the method developed in Sheard et al. (2020), of all continuous variables < 5 (Table S6). We include the relaxed wing chord to control for allometry. All continuous variables were scaled to have a mean of 0 and a standard deviation of 1 prior to model fitting, and wing-bone length was log-transformed prior to scaling to improve the normality of the residual error distribution; migration was included as a categorical variable, with 1 being nonmigratory, 2 being partial/intermediate migrants

and 3 being long-distance migrants. To test for variation in the relationship between temperature and wing-bone length among migration strategies, we fit an identical model but with an interaction between temperature and migration strategy. We also constructed analogous models, controlling for log-transformed mass rather than the relaxed wing chord to understand the relationship between the variables and wing-bone length relative to body size (Table S4).

Models were fit using the 'MCMCglmm' function in the MCMCglmm package (Hadfield 2010) in R (R Core Team 2018), with uninformative inverse Wishart priors ($V=1$; $\nu=0.02$) for the residual and phylogenetic variance. To account for phylogenetic relatedness and uncertainty in those relationships, we randomly sampled 100 trees from the posterior distribution of a comprehensive phylogeny of birds (Jetz et al. 2012) constructed on the Hackett et al. (2008) backbone tree, and including species that were placed using taxonomy. Using a random tree from the posterior, we generated starting parameter estimates by running the models for 105,000 iterations, discarding the first 5000 iterations as burn-in and with a thinning rate of 10. Using these starting parameter estimates, we then ran the models for 105,000 iterations, with 5000 iterations discarded as burn-in and a thinning rate of 1000 for each of the 100 trees. The parameter estimates were derived by combining the posterior distributions based on each of the 100 trees. To test that our results were robust to our treatment of phylogenetic uncertainty, we also fit an analogous model, but used a maximum clade credibility consensus phylogeny to capture phylogenetic relatedness and ran the model for 500,000 iterations, with the first 50,000 discarded as burn-in and a thinning factor of 100. To test that our results were robust to sparse geographic sampling in some regions, we fit our main model using only the subset of specimens that were collected in the Nearctic. We confirmed that the models had converged by examining parameter trace plots and posterior distributions.

3 | Results

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 ($\beta=0.04$; $p<0.001$; Figure 2). The model has high explanatory power, explaining nearly all variation in wing-bone length (marginal $R^2=0.80$; conditional $R^2>0.99$), though importantly, allometry is by far the strongest predictor of wing-bone length in our models. The temperature relationship is consistent across a range of temperature metrics (Tables S1–S3). We conclude that higher temperatures are strongly associated with longer wing bones, as predicted by Allen's Rule.

The thermoregulation-associated pressures shaping wing structure likely 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 ($\beta=0.83$; $p<0.001$; Figure 2). Importantly, the effect size for this allometric relationship is 20 times larger than the relationship between temperature and wing-bone length. The length of the primary flight feathers

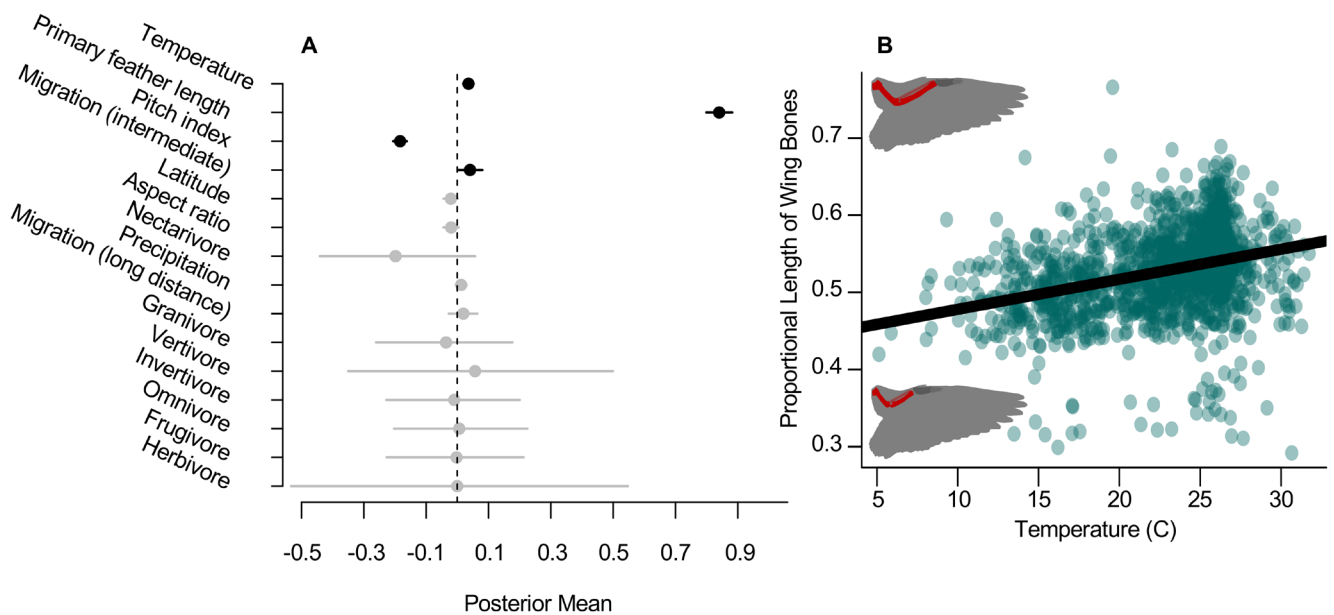


FIGURE 2 | Higher temperatures are associated with increased length of avian wing bones. (A) Temperature during the warmest quarter of the year is significantly positively associated with wing-bone length after controlling for the length of the primary flight feathers and a range of ecological and geographic variables (*Methods*). 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) To visualise the relationship between temperature and the proportion of the wing that is vascularise, here we plot the proportion of the wing that is vascularized (the sum of humerus and ulna length divided by the length of the primary flight feathers). Dots represent species averages for each of the 1502 species used in our models. To help visualise the trend in these data, a simple linear model of the bivariate relationship between temperature and the proportional length of the wing bones is shown.

is highly correlated with mass (Pearson's Correlation (R) = 0.88), and when mass is included as a predictor in the model rather than primary flight feather length, mass is similarly positively associated with wing-bone length ($\beta = 1.04$; $p < 0.001$; Table S4). Thus, unsurprisingly, wing bones are longer in larger birds and for species that have longer primary flight feathers.

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 impacts of the demands of flight on wing-bone length, we apply aerodynamic theory to estimate a 'pitch index', a modified index of pitch agility (Harvey et al. 2022) that measures the ability of a bird to generate angular acceleration around the pitch axis (i.e., longitudinal manoeuvrability; Figure S1). We also calculate the aspect ratio of the wings, a determinant of gliding flight efficiency (Norberg 1990; Pennycuik 2008; Harvey and Inman 2021). By controlling for pitch index and aspect ratio, we account for pressures associated with manoeuvrability and flight efficiency on the length of the wing bones. We find that pitch index is significantly negatively associated with wing-bone length ($\beta = -0.19$; $p < 0.001$). Wing aspect ratio is similarly negatively associated with wing-bone length, but the effect is marginally non-significant ($\beta = -0.02$; $p = 0.09$).

We also control for differences in migratory strategy, as long-distance movements are expected to exert strong selective pressure on wing shape and length (Sheard et al. 2020; Matyjasiak et al. 2023). We find that intermediate- and long-distance migration, both common life history strategies in birds adapted to highly seasonal environments (Winger et al. 2019), are positively associated with the length of the wing bones, but that

the relationship is only significant for intermediate/partial migrants (intermediate: $\beta = 0.04$; $p = 0.05$; long distance: $\beta = 0.02$; $p = 0.35$). When we allow the effects of temperature to interact with migratory strategy, the interactions are not significant and the support for the model is significantly lower than for a model without interactions (Table S8).

Given the range of important ecological factors that vary with latitude, such as ecological specialisation (Belmaker et al. 2012), species richness (Mittelbach et al. 2007), dispersal ability (Sheard et al. 2020) and geographical range size (Rapoport's Rule), we included latitude as a predictor in our model, based on the centroid of each species range. We find that the distance of this centroid from the equator (absolute value of latitude) is not significantly associated with wing-bone length ($\beta = -0.02$; $p = 0.10$). To further account for ecological differences, we include trophic niche as a predictor and find no significant relationships between niche and wing-bone length (Figure 2).

Our results were robust to our treatment of phylogenetic uncertainty (Table S5). The results were similarly consistent when using only the Nearctic species in our dataset (Table S7), suggesting the geographic gaps in our sampling are unlikely to be biasing our results.

4 | Discussion

The wings of flying animals are generally assumed to be shaped by the demands of aerodynamics and flight efficiency (Hedenström and Christoffer Johansson 2015; Sheard

et al. 2020). Our results add a new dimension by revealing a significant positive relationship between temperature and wing-bone length in a large sample of passerine birds, spanning over 80 families from all continents except Antarctica. This pattern is consistent across a range of temperature metrics, as well as robust to statistical controls for allometry (SI) and a suite of ecological, geographic and aerodynamic variables expected to influence wing structure. The anatomical trend we detect across global climatic gradients supports the hypothesis that thermoregulatory demands may be a widespread and overlooked driver of bird wing evolution.

As with other macroevolutionary studies that link appendage length variation with changes in temperature, our models cannot definitively distinguish between the impacts of heat dissipation demand in warmer climates and the demands for cold tolerance in colder climates. However, our interpretation of the tendency of wing bones to be longer in warmer climates can be informed by our understanding of the role of wings in thermoregulation. In birds, the high energetic demands of flight require a 10–23-fold increase in metabolism (Schmidt-Nielsen 1972), 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 (Norberg 1990). Consequently, during prolonged flights, in some contexts, less than 1% of the heat generated by a bird is retained (Craig and Larochelle 1991). This can present a critical thermoregulatory challenge: during flight, much more heat is generated than when at rest, and nearly all of it may need to be dissipated to the environment.

Wings likely play a role in overcoming this heat dissipation challenge. During flight, the percentage of total nonevaporative heat loss achieved by convection increases dramatically (Lewden et al. 2023), and in some studies, the wings have been found to be the most significant windows of heat exchange with the environment during flight (Ward et al. 1999; Lewden et al. 2023). In a reflection of their capacity to dissipate excess heat, similar exposure of the brachial regions of the wing can be achieved intentionally when perched birds spread their wings to prevent overheating (Sharpe et al. 2022). While a flying bird likely needs to release large amounts of body heat to avoid overheating and to permit the sustained energy expenditure required to maintain flight, birds that are engaged in less energetically demanding tasks may have a greater demand for heat retention to aid in cold tolerance. Wings are expected to play a relatively minor role in involuntary heat loss when birds are not flying, as the wings can be held against the torso with the vascularised tissue well insulated under a dense layer of plumage (Rogalla et al. 2021). Given this, we interpret our findings to align with heat dissipation limit theory (Speakman and Król 2010) and suggest that increased demand for dissipating heat in warmer climates likely explains the widespread correlation between higher temperature and longer wing-bone length we find across passerines.

Our analyses suggest passerine wing length conforms to Allen's Rule, but further work is needed on the drivers and implications of this pattern. Much remains to be learned about the role of wings in heat dissipation, as estimates of their contribution to heat dissipation during flight vary widely (e.g., Craig and

Larochelle 1991; Ward et al. 1999) and there may be important differences in morphology–temperature relationships among taxonomic groups within birds (Baldwin et al. 2023). Further, while we focus on thermoregulation while in prolonged flight or at rest, these are endpoints on a spectrum of behaviours that occur in a wide variety of environmental contexts. It is possible, for example, that species living in cold climates may benefit from retaining more heat during flight. Similarly, heat loss during other less energetically taxing behaviours during which the wing can still be a site of heat exchange (e.g., climbing, foraging and interacting with other individuals) could conceivably impact the thermoregulatory demands on the wing. Thus, while bird wings certainly appear to be less important to heat exchange at times when birds are at rest and might be cold (Ward et al. 1999; Rogalla et al. 2021), it is possible that heat lost through the wings could result in selection for shorter wings in colder climates to improve cold tolerance. Although we do not find evidence that there is a significant interaction between migration strategy and temperature relationships with wing-bone length, we have a relatively small number of migratory species in our dataset. Given the global relationship between temperature and wing-bone length, expanding sampling to look at more nuanced variation in temperature and wing-bone length variation within major taxonomic groups and groups with similar life history strategies is an exciting avenue of future research.

Nearly all aspects of bird wing size and shape, including the structure of the forelimb, are expected to be broadly important to the physics of flight (Pennycuick 2008). Accordingly, we find a strong positive relationship between wing-bone length and primary flight feather length (Figure 2), reflecting the hard constraint on total wing length necessary to achieve flight that is imposed by body size (Sullivan et al. 2019). We also find a significant negative relationship between pitch index and wing-bone length. This suggests that flight manoeuvrability is maximised in wings with relatively short wing bones compared to the primary flight feathers. This nonthermal selective pressure on wing structure likely interacts via trade-offs with thermal mechanisms to determine the outcome of wing evolution. Better understanding these trade-offs in modern birds, and potentially at the very origin of flight when wings may have been more influenced by climate than aerodynamic requirements, represent exciting avenues for future research.

5 | Conclusions

Our results reveal that bird wings are complex traits shaped not only by flight adaptations but also by the imperative for efficient thermoregulation. The connection between wing-bone length and temperature remains strongly significant even when we account for allometry and a full range of other contextual factors, such as ecological niche (primary food source), latitude and migratory strategy (Figure 2). We also use aerodynamic theory to control for selection associated with flight performance (Pennycuick 2008; Harvey et al. 2022) and 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 (Wang et al. 2011).

Previous studies have shown that thermoregulatory demands can affect morphological traits that are critical to food acquisition (Tattersall et al. 2009), with consequences for individual fitness (Van Gils et al. 2016). Our analyses extend these previous findings by demonstrating that thermoregulation has altered the design of anatomical features fundamental to locomotion, including flight.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data and code used in this manuscript are publicly available for download on Dryad: DOI: [10.5061/dryad.7wm37pw4](https://doi.org/10.5061/dryad.7wm37pw4).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.