

# **Broad Support for Bergmann's Rule in Birds**

by

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## **Abstract**

The observation that species, and individuals within species, tend to be larger in the colder parts of their range was long considered to be one of the few rules in ecology (Bergmann's Rule). However, recent efforts to test the generality of this rule at large scales have failed to find support for Bergmann's Rule. In birds, one challenge that has precluded a large-scale test of Bergmann's Rule has been a lack of data to estimate size variation between and within species across a sufficient gradient of temperature.

We use 3,016 skeletal specimens from 734 passerine species across the Americas to test whether variation in body size is associated with temperature. We find a negative relationship between temperature and both inter- and intra-specific differences in size. Our results are evidence of widespread conformation to Bergmann's Rule in birds.

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## **Introduction**

Higher temperatures have long been observed to correlate with smaller body size, a pattern known as Bergmann's Rule (Bergmann 1847). While Bergmann's Rule is widely considered to be one of the few laws of ecology, recent large-scale analyses of body size variation across mammals and birds have called the generality of Bergmann's Rule into question (Riemer et al. 2018). Understanding the spatial relationships between temperature and morphology has taken on new urgency, as spatial associations between morphology and temperature may be useful in predicting species responses to climate change (Tian and Benton 2020).

One challenge to assessing the empirical support for large-scale relationships between body size and temperature is that the metrics of size that have been sampled at the necessary scale and across sufficient numbers of species (e.g., mass) tend to be poor indicators of intra-specific differences in size. For example, in birds, mass is highly correlated with skeletal metrics of size, but temperature-driven reductions in size are less clear when estimated using mass as opposed to skeletal-based measures (Weeks et al. 2020). Birds, with their extensive representation in skeletal collections of natural history museums have the potential to be a powerful system for assessing the evidence of Bergmann's Rule.

In birds, the length of the tarsus (a bone in the lower leg) is an effective metric of intra-specific differences in size (Senar & Pascual 1997). However, variation in leg length relative to body size among species can be driven—both systematically and idiosyncratically—by ecology (Weeks et al. 2020), making the tarsus a poor predictor of inter-specific differences in size. First axes of principal component analyses of morphological traits have long been interpreted as indices of size (Jolicoeur 1963). In birds, the first axis of Principal Component Analyses (PCAs)

based on multiple skeletal elements are often considered the most reliable estimate of intra- and inter-specific differences (Albert et al. 2010; Grant & Grant 2008; Rising and Somer 1989). However, generating skeletal trait measurements is difficult, and as a result, much work with birds has focused on museum skin-based functional traits (Tobias et al. 2022), which do not provide reliable estimates of size (Freeman and Jackson 1990).

Here, we build a large-scale comparative dataset of skeleton-based avian body size estimates using museum specimens to simultaneously estimate the intra- and inter-specific relationships between body size and temperature in passerines across the Americas.

## **Materials and Methods**

### ***Sampling***

We measured all passerine skeleton specimens in the University of Michigan Museum of Zoology ornithological collection. To do this, each skeletal specimen was photographed, and then estimates of bone lengths were generated using Skelevision, a computer vision-based approach to generating length estimates of bird bones from photographs (Weeks et al. 2022). Taxonomy was unified to match a global phylogeny of birds (Jetz et al. 2012) and a global dataset of avian wing morphology (Sheard et al. 2020).

We use temperature at breeding localities because temperature on the breeding grounds appears to be the main driver of size reductions in birds (Weeks et al. 2020), and because migratory birds may spend little time at individual locations where they are found during migration. To do this, we only include specimens of non-migratory species and migratory bird species that were collected between the months of June and August, when they were presumably within their breeding range.

### ***Environmental Data***

We estimated breeding temperature for each specimen by calculating the mean annual temperature at their collection locality; we did this using the 2.5-minute resolution WorldClim bioclimatic variables data set and extracted temperatures and precipitations for each latitude and longitude using the raster and sp packages (Fick and Hijmans 2017; Pebesma and Bivand 2005) in R (R Core Team 2021).

### ***Principal Component Analysis***

To estimate size, we used skelevision to measure the length of the humerus, keel, tarsus, and skull. We then conducted a principal component analysis (PCA) to reduce the dimensionality of the data, and treated score of each species on the first axis of a PCA (PC1) as a metric of body size (Freeman and Jackson 1990; Senar and Pascual 1997). To estimate the PCA, we used the ‘princomp’ function in the stats package (R Core Team 2021) with a variance-covariance matrix.

### ***Bayesian Modeling***

To control for phylogenetic relatedness, we fit Bayesian generalized linear mixed models with the ‘MCMCglmm’ function in the MCMCglmm package (Hadfield 2010) to investigate inter-specific and intra-specific relationships between PC1 and ambient temperature with ecological and environmental predictors. The fixed effects parameter estimates for the Bayesian model testing the changes in PC1 included the species-mean of the ambient temperature and corresponding temperature data points for each species. Other fixed effects were environmental and ecological predictors, including precipitation, diet, habitat, and migratory status. The models also included a random effect for species with a correlation structure accounting for phylogenetic dependency. To estimate phylogenetic relationships, we used a global phylogeny of the birds of the world (Jetz et al. 2012), with 1,000 of the most likely trees from the posterior distribution combined to form a 50% majority rule consensus tree (Sukumaran and Holder 2010; Rubolini et

al. 2015). Uninformative wishart distributions were used as priors for all parameters, chains were run for 500,000 iterations with a burn-in of 50,000 and were thinned by a factor of 500 to reduce autocorrelation. Convergence was confirmed by examining trace and posterior distribution plots for all parameters.

## **Results**

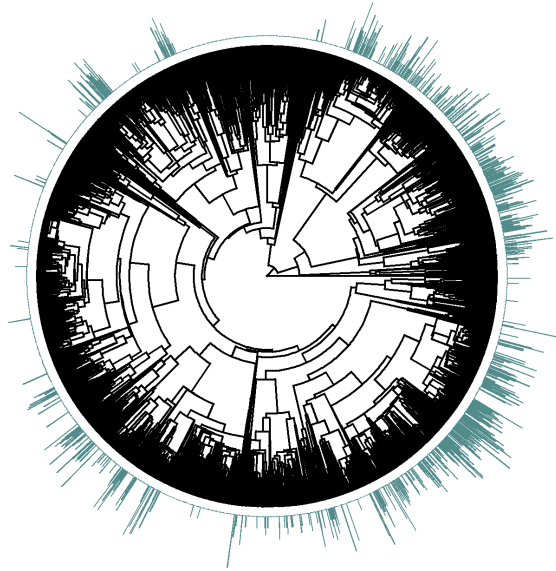
### ***Sampling***

Using a machine learning-based approach to automatically detecting and measuring skeletal elements from photographs of museum specimens (Weeks et al. 2022), we generate a PCA-based estimate of size using multiple bones (*Methods*) for 3,016 specimens from 734 passerine species that span 65 families. These specimens are distributed across the Americas (Fig 1& 2) and represent the entirety of the University of Michigan Museum of Zoology's passerine specimens from the Americas for which we were able to estimate the necessary bone lengths using the automated approach (*Methods*).



**Figure 1.** 3,016 Specimens with PCI scores on the American Continent. Non-continental locations are filtered out.





**Figure 2.** A phylogenetic tree of all 734 species in the dataset. Number of specimens per species are represented in bars on circumference of the circle.

While all species are passerines, they represent a diversity of life histories. Our data include 5 altitudinal migrants, 201 full migrants and 528 non-migratory species (BirdLife International 2018). Most of the species (303) were from dense habitats, with 292 from semi-open habitats, and 139 from open habitats (Tobias et al. 2016). The species' diets were similarly varied, with 83 frugivores, 443 invertivores, 5 nectarivores, 132 omnivores, 2 herbivores, 1 scavenger, 68 seed eaters (Wilman et al. 2014; Pigot et al. 2020; Sheard et al. 2020).

### ***Principal Component-based Index of Size***

We estimated size using a PCA of the length of the humerus, keel, tarsus, and skull (*Methods*). The first axis of the PCA (PC1) explained 91% of the variance, with positive loadings on humerus (0.42), keel (0.38), tarsus (0.58), and skull (0.59), suggesting that PC1 is positively associated with body size.

### ***Size is Negatively Associated with Temperature***

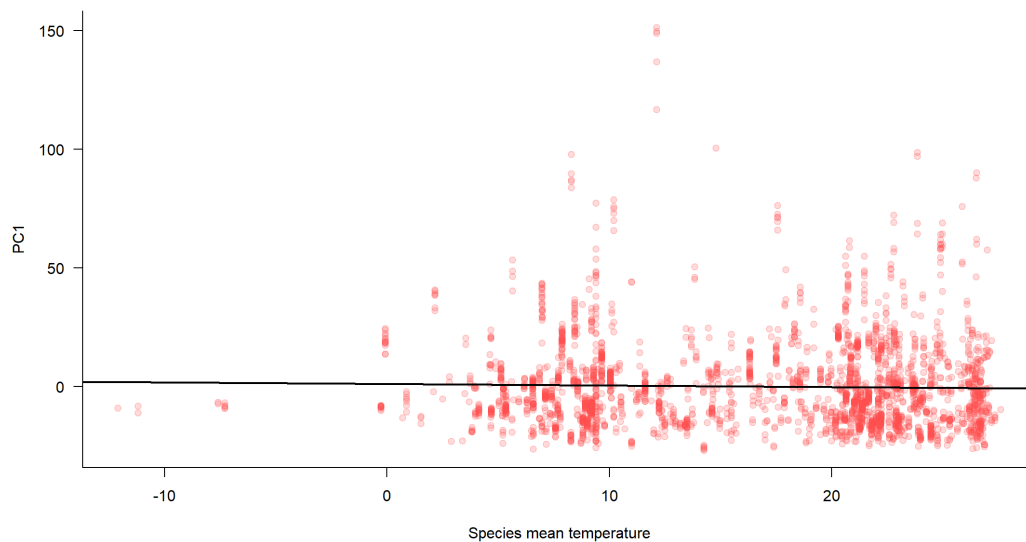
We used a phylogenetic mixed model to jointly estimate the effects of temperature on intra- and inter-specific differences in size while controlling for precipitation, migratory strategy, diet, and habitat affinity, and also controlling for phylogenetic relatedness in the structure of the model error (Table 1; *Methods*). We find that ambient temperature is negatively associated with both intra-specific ( $\beta = -0.0676$ , pMCMC = 0.709) and inter-specific ( $\beta = -0.104$ , pMCMC = 0.842) differences in size (Figure 3; Table 1).

We do not find significant size differences between species associated with precipitation, migratory strategy, habitat affinity or diet choice (Table 1).

Response variable	Explanatory variable	pm	Lower CI	Upper CI	pMCMC
PC1	Intercept	4.07	-13.6	21.8	0.687
	Species-mean temp	-0.104	-1.12	0.832	0.842
	Within-species temp	-0.0676	-0.480	0.275	0.709
	Precipitation	0.197	-0.0566	0.458	0.129
	Full Migrant	-2.52	-13.01	6.05	0.649
	Not a Migrant	0.567	-8.66	10.2	0.891
	Invertivore	-1.33	-4.43	2.17	0.413
	Nectarivore	-5.59	-17.9	7.91	0.404
	Omnivore	0.841	-2.10	4.39	0.620
	Herbivore	-1.84	-13.4	10.3	0.753
	Scavenger	-13.7	-27.2	2.36	0.0778

Seed eater	-3.68	-7.43	1.004	0.0956
Semi-open	0.0338	-1.76	1.71	0.996
Open	1.96	-0.493	4.50	0.144

**Table 1.** Changes in PCI in response to temperature. Results from Bayesian models testing the effects of ambient temperature on PCI. “Pm” refers to the posterior means, lower and upper CI indicate upper and lower bound of the 95% credible intervals, and pMCMC is used for significance testing in Bayesian models.



**Figure 3.** PCI on species mean temperature. There is a negative association between PCI and species mean temperature, which is converted to raw temperature from WorldClim data.

## **Discussion**

Size is perhaps the single most important determinant factor of the physiology and ecology of species. Thus, large scale ecogeographic gradients in size are likely to have broad ecological significance and to reflect important drivers of variation in life history, physiology, and the factors structuring of ecosystems. Passerines, with over 6,000 species, are the most diverse group of birds, constituting over 60% of avian diversity. For 734 species (~12% of all passerines and ~18% of passerines in the Americas), we find evidence that environmental

temperatures are negatively related to both intra- and inter-specific differences in a multivariate skeletal index of body size, although both relationships are not significant.

We attribute the differences between our findings and previous work that has found more mixed support for Bergmann's Rule to our ability to simultaneously precisely estimate intra- and inter-specific differences in size. However, our work does have important limitations that warrant further exploration. Increasing the effective sample size would potentially result in significant effects of ambient temperature on both intra- and inter-specific differences in body size, while the expanded intra-specific and inter-specific sampling would also allow for more direct analysis of the impacts of decisions about modeling frameworks and additional variables, like latitude, that may explain important variation in size.

However, our findings do provide further evidence of a general relationship between size and temperature in birds with important implications. In particular, understanding the relationship between temperature and size has assumed increased significance based on the idea that spatial patterns may predict change in size as the world warms (Tian and Benton 2020). While we do find evidence that birds tend to be smaller in warmer parts of their ranges, it is not clear if this association will be predictive of temporal change. The original formulation of Bergmann's Rule included a mechanism, suggesting that birds tended to be larger in colder regions because of greater selection for cold tolerance (Bergmann 1847). Conversely, recent work trying to understand the effects of changes in temperature through time on body size suggests that recent global warming may drive size reductions via developmental plasticity (Teplitsky and Millien 2014; Andrew et al. 2017; Weeks et al 2020). Understanding the mechanisms underlying the pattern we observe is critical to applying them to predict size impacts of climate change.

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