

Growth rate and locomotor performance tradeoff is not universal in birds

Tao Zhao¹ and Zhiheng Li²

¹ State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, Nanjing, China

² Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, Beijing, China

ABSTRACT

Though a tradeoff between growth rate and locomotor performance has been proposed, empirical data on this relationship are still limited. Here we statistically analyze the associations of growth rate and flight ability in birds by assessing how growth rate is correlated with three wing parameters of birds: flight muscle ratio, wing aspect ratio, and wing loading. We find that fast-growing birds tended to have higher flight muscle ratios and higher wing loadings than slow-growing birds, which suggests that fast-growing birds may have better takeoff performance, but lower efficiency in maneuvering flight. Accordingly, our findings suggest that the relationship between growth rate and flight ability is more complex than a simple tradeoff. Since the hindlimbs also contribute greatly to the locomotion of birds, future investigations on the relationship between growth rate and hindlimb performance will provide more insights into the evolution of birds.

Subjects Evolutionary Studies, Zoology

Keywords Birds, Growth rate, Flight ability, Flight muscles, Wing span, Wing area, Wing aspect ratio

INTRODUCTION

Growth rates vary considerably among different taxa and organisms ([Arendt, 1997](#); [Case, 1978](#); [Ricklefs, 1973, 1968](#)). It has been suggested that the growth rate for an organism results from a compromise between benefits and costs of rapid growth within physiological constraints ([Arendt, 1997](#); [Dmitriew, 2011](#)). Rapid growth allows organisms to shorten the duration of reaching maturity when they are vulnerable to predators ([Case, 1978](#)). However, rapid growth may reduce longevity ([Gabriela, 2018](#); [Metcalf & Monaghan, 2003](#)) and reduce investment in other functions, because overall resources are limited ([Arendt, 1997](#); [Dmitriew, 2011](#); [Martin et al., 2011](#)). One of the main functions that are suggested to be negatively affected by rapid growth is locomotor performance ([Billerbeck, Lankford & Conover, 2001](#); [Dmitriew, 2011](#); [Lee, Monaghan & Metcalfe, 2010](#)). For example, [Billerbeck, Lankford & Conover \(2001\)](#) showed that within the Atlantic silversides (*Menidia menida*), the fast-growing fish have lower maximum prolonged and burst swimming speeds than slow-growing ones.

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Corresponding authors

Tao Zhao, taozhao@nigpas.ac.cn

Zhiheng Li, lizhiheng@ivpp.ac.cn

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Birds are ideal for testing factors that are suggested to influence growth rate, because previous studies have accumulated relatively abundant data ([Martin, 2004](#); [Remeš & Martin, 2002](#); [Starck & Ricklefs, 1998](#)). By far, the variation of growth rate in birds has been found to be associated with a suite of factors. Growth rate is inversely correlated with body mass, and precocial birds tend to grow slower than altricial birds ([Ricklefs, 1973](#)). [Royle et al. \(1999\)](#) suggested that growth rate is associated with sibling competition. Several studies on passerines have shown that growth rates increase with nest predation rates ([Cheng & Martin, 2012](#); [Martin et al., 2011](#); [Remeš & Martin, 2002](#)). [Sandvig, Coulson & Clegg \(2019\)](#) found that birds from high latitudes tend to grow faster than birds from lower latitudes, and that birds nesting in open nests grow faster than birds nesting in enclosed nests. An inverse relationship between growth rate and locomotor performance at the interspecific level has also been proposed for songbirds ([Martin, 2015](#)). However, contradictory evidence exists at the intraspecific level. For example, [Coslovsky & Richner \(2011\)](#) found that within great tits (*Parus major*), the nestlings that grow faster tend to have longer wings at maturity. Moreover, statistical tests on the relationship between growth rate and locomotor performance in birds at the interspecific level are still lacking.

Here we empirically assess how growth rate is associated with three wing parameters of birds: flight muscle ratio, wing aspect ratio, and wing loading. The mass of flight muscles is important in determining the power that flight muscles can produce ([Pennycuik, 2008](#)). Wing loading and aspect ratio are key parameters for the aerodynamics of flight, which can be calculated based on body mass, wing span, and wing area ([Pennycuik, 2008](#)).

MATERIALS AND METHODS

Data collection

Two datasets were compiled: one (81 species) to assess the relationship between growth rate and flight muscle ratio ([Table S1](#)), and the other (125 species) to assess the relationship between growth rate and wing aspect ratio and wing loading ([Table S2](#)). Body mass, development mode (precocial or altricial), nest type (open or enclosed), clutch size, latitude, and migratory status (migratory or not) were included as control variables. Data on growth rate (“K” in the logistic function) were taken from AnAge Database ([Tacutu et al., 2013](#)) and [Tholon & Queiroz \(2007\)](#); body mass and mass of flight muscles (m. pectoralis and m. supracoracoideus) from [Wright, Steadman & Witt \(2016\)](#) and [Viscor & Fuster \(1987\)](#); body mass, wing span, and wing area from [Pennycuik \(2008\)](#) and [Serrano et al. \(2016\)](#); development mode from [Starck & Ricklefs \(1998\)](#); clutch size from [Myhrvold et al. \(2015\)](#); nest type from [Sibly et al. \(2012\)](#) and [Harrison & Greensmith \(1993\)](#); latitude from [BirdLife International & Handbook of the Birds of the World \(2018\)](#); migratory status from [BirdLife International \(2019\)](#). Data on body mass were taken from different sources for different sets of species. Flight muscle ratio was calculated as mass of flight muscles divided by body mass; aspect ratio as wing span squared divided by wing area; wing loading as body mass divided by wing area.

Data analysis

Nine models were tested. Three models were tested to assess the relationship between growth rate and three wing parameters (flight muscle ratio, wing aspect ratio, and wing loading), respectively, while controlling for body mass, development mode, clutch size, nest type, latitude, and migratory status. Another three models were tested to assess the relationship between latitude and these three wing parameters, respectively, while controlling for body mass, development mode, clutch size, nest type, and migratory status. The last three models were tested to assess the relationship between growth rate and these three wing parameters, respectively, while controlling for body mass, development mode, clutch size, nest type, and migratory status, with latitude dropped.

All analyses were carried out in R (*R Development Core Team, 2019*) using the packages “ape” (*Paradis, Claude & Strimmer, 2004*), “caper” (*Orme et al., 2018*), and “phytools” (*Revell, 2012*). To account for phylogeny, we used 1,000 time-calibrated phylogenetic trees from birdtree.org (*Jetz et al., 2012*) for each dataset in our study, from which a majority rule consensus tree was derived using the function “consensus.edges” in the package “phytools”. The phylogenetic generalized least squares (PGLS) analyses with Pagel’s λ were performed using the function “pgls” in the package “caper”. Before analyses, growth rate, body mass, flight muscle ratio, wing aspect ratio, wing loading, and clutch size were log₁₀-transformed, while the absolute values of latitude were used. The effect size “ r ” (for continuous variables) or “Hedges’ d ” (for categorical variables) was calculated from t -values obtained from PGLS models (*Nakagawa & Cuthill, 2007*).

To visualize the relationship between growth rate and wing parameters, residuals of these variables were obtained by regressing them against the control variables.

RESULTS

In order to assess the relationship between growth rate and wing parameters, we tested nine models (Tables 1–3). There are phylogenetic signals in all these models, indicating that the phylogenetic non-independence should be accounted for in these analyses.

When controlling for body mass, development mode, clutch size, nest type, latitude, and migratory status, among the three wing parameters, only flight muscle ratio was significantly correlated with growth rate ($P = 0.007$, effect size = 0.31), while wing aspect ratio ($P = 0.593$, effect size = -0.05) and wing loading ($P = 0.090$, effect size = 0.16) were not (Models 1–3 in Table 1). Birds with higher flight muscle ratios tended to grow faster than birds with smaller flight muscle ratios (Fig. 1). In all these three models, latitude was significantly correlated with growth rate ($P = 0.032$, effect size = 0.25 in model 1; $P = 0.001$, effect size = 0.29 in model 2; $P = 0.002$, effect size = 0.28 in model 3); birds from higher latitudes tended to grow faster than birds from lower latitudes.

Latitude was significantly correlated with wing aspect ratio ($P = 0.010$, effect size = -0.23) and wing loading ($P = 0.041$, effect size = 0.19), but not with flight muscle ratio ($P = 0.315$, effect size = 0.12), when controlling for body mass, development mode, clutch size, nest type, and migratory status (Models 4–6 in Table 2).

After dropping latitude from the models, growth rate was significantly correlated with flight muscle ratio ($P = 0.006$, effect size = 0.31) and wing loading ($P = 0.028$, effect

Table 1 PGLS models of growth rate in relation to flight muscle ratio (Model 1), wing aspect ratio (Model 2), and wing loading (Model 3), while controlling for body mass, development mode, clutch size, nest type, latitude, and migratory status. Effect size “*r*” was calculated for continuous variables, while “Hedges’ *d*” for categorical variables.

	β	<i>P</i>	Effect size (<i>r</i> or <i>d</i>)	95% CI of effect size
Model 1 ($R^2_{\text{adjusted}} = 0.53$, Pagel’s $\lambda = 0.786$)				
Intercept	−0.58	<0.001	–	–
Body mass	−0.24	<0.001	−0.66	[−0.77, −0.52]
Development mode: precocial	−0.40	<0.001	−1.52	[−2.06, −0.99]
Clutch size	−0.02	0.818	−0.03	[−0.24, 0.19]
Nest type: open	-4.37×10^{-4}	0.991	-3.31×10^{-3}	[−0.56, 0.56]
Latitude	2.03×10^{-3}	0.032	0.25	[0.03, 0.44]
Migratory status: migratory	0.02	0.530	0.17	[−0.34, 0.69]
Flight muscle ratio	0.41	0.007	0.31	[0.10, 0.49]
Model 2 ($R^2_{\text{adjusted}} = 0.43$, Pagel’s $\lambda = 0.643$)				
Intercept	−0.94	<0.001	–	–
Body mass	−0.19	<0.001	−0.53	[−0.65, −0.39]
Development mode: precocial	−0.29	<0.001	−0.91	[−1.29, −0.53]
Clutch size	0.11	0.147	0.13	[−0.04, 0.30]
Nest type: open	0.05	0.116	0.33	[−0.07, 0.73]
Latitude	2.86×10^{-3}	0.001	0.29	[0.12, 0.44]
Migratory status: migratory	0.06	0.115	0.37	[−0.08, 0.82]
Aspect ratio	−0.11	0.593	−0.05	[−0.22, 0.13]
Model 3 ($R^2_{\text{adjusted}} = 0.44$, Pagel’s $\lambda = 0.667$)				
Intercept	−1.16	<0.001	–	–
Body mass	−0.25	<0.001	−0.47	[−0.59, −0.32]
Development mode: precocial	−0.32	<0.001	−1.00	[−1.38, −0.61]
Clutch size	0.13	0.073	0.16	[−0.01, 0.33]
Nest type: open	0.05	0.122	0.32	[−0.07, 0.72]
Latitude	2.67×10^{-3}	0.002	0.28	[0.11, 0.43]
Migratory status: migratory	0.04	0.202	0.30	[−0.15, 0.75]
Wing loading	0.18	0.090	0.16	[−0.02, 0.32]

size = 0.20, Fig. 1), but not with wing aspect ratio ($P = 0.237$, effect size = −0.11) (Models 7–9 in Table 3). Fast-growing birds tended to have higher flight muscle ratios and higher wing loadings than slow-growing birds.

DISCUSSION

Our results show that fast-growing birds tended to have higher flight muscle ratios and higher wing loadings than slow-growing birds, which suggests that the relationship between growth rate and flight ability in birds is more complex than a simple tradeoff. It has been shown that the takeoff ability of birds is largely dependent on flight muscle ratio (Hartman, 1961; Marden, 1987). Birds with higher flight muscle ratios can provide

Table 2 PGLS models of latitude in relation to flight muscle ratio (Model 4), wing aspect ratio (Model 5), and wing loading (Model 6), while controlling for body mass, development mode, clutch size, nest type, and migratory status.

	β	<i>P</i>	Effect size (<i>r</i> or <i>d</i>)	95% CI of effect size
Model 4 ($R_{\text{adjusted}}^2 = 0.13$, Pagel's $\lambda = 0.418$)				
Intercept	32.61	0.055	–	–
Body mass	7.82	0.027	0.25	[0.04, 0.45]
Development mode: precocial	7.10	0.257	0.29	[–0.19, 0.77]
Clutch size	8.17	0.353	0.11	[–0.11, 0.32]
Nest type: open	5.97	0.212	0.37	[–0.19, 0.94]
Migratory status: migratory	8.39	0.045	0.55	[0.03, 1.08]
Flight muscle ratio	17.32	0.315	0.12	[–0.10, 0.33]
Model 5 ($R_{\text{adjusted}}^2 = 0.16$, Pagel's $\lambda = 0.562$)				
Intercept	62.39	0.002	–	–
Body mass	8.03	0.005	0.26	[0.08, 0.41]
Development mode: precocial	14.64	0.015	0.47	[0.10, 0.84]
Clutch size	13.18	0.086	0.16	[–0.02, 0.32]
Nest type: open	1.09	0.748	0.07	[–0.33, 0.46]
Migratory status: migratory	11.88	0.001	0.76	[0.31, 1.22]
Aspect ratio	–54.19	0.010	–0.23	[–0.39, –0.06]
Model 6 ($R_{\text{adjusted}}^2 = 0.14$, Pagel's $\lambda = 0.56$)				
Intercept	1.10	0.920	–	–
Body mass	–0.09	0.984	-1.90×10^{-3}	[–0.18, 0.17]
Development mode: precocial	7.79	0.198	0.25	[–0.12, 0.61]
Clutch size	19.47	0.009	0.24	[0.07, 0.40]
Nest type: open	0.34	0.919	0.02	[–0.38, 0.42]
Migratory status: migratory	8.25	0.022	0.54	[0.09, 0.99]
Wing loading	22.73	0.041	0.19	[0.01, 0.35]

larger mass-specific lift force and take off more steeply than birds with lower flight muscle ratios. The positive correlation between growth rate and flight muscle ratio suggests that fast-growing birds tend to have better escape performance from predators than slow-growing birds. In the fixed-wing model of maneuvering performance, the radius of turn is proportional to wing loading; that is, birds with lower wing loadings can make turns of smaller radii (Norberg & Norberg, 1971; Norberg, 1990; Pennycuik, 2008). However, it has been suggested that birds with high wing loadings can also effect turns of small radii, but requiring slowing and flapping, which is energetically more expensive (Warrick, Dial & Biewener, 1998; Warrick, Bundle & Dial, 2002). In other words, wing loading is associated with efficiency of maneuvering flight (Warrick, Bundle & Dial, 2002). The positive correlation between growth rate and wing loading suggests fast growth of birds may negatively affect the efficiency of maneuvering flight. Aspect ratio reflects the efficiency of flight; an increase of aspect ratio can increase the lift and reduce the drag (Norberg, 1990; Pennycuik, 2008). The lack of significant correlation between growth rate

Table 3 PGLS models of latitude in relation to flight muscle ratio (Model 7), wing aspect ratio (Model 8), and wing loading (Model 9), while controlling for body mass, development mode, clutch size, nest type, and migratory status, with latitude dropped.

	β	<i>P</i>	Effect size (<i>r</i> or <i>d</i>)	95% CI of effect size
Model 7 ($R_{\text{adjusted}}^2 = 0.51$, Pagel's $\lambda = 0.792$)				
Intercept	-0.52	0.001	-	-
Body mass	-0.22	<0.001	-0.63	[-0.75, -0.48]
Development mode: precocial	-0.38	<0.001	-1.42	[-1.95, -0.89]
Clutch size	4.84×10^{-4}	0.995	7.36×10^{-4}	[-0.22, 0.22]
Nest type: open	0.01	0.833	0.06	[-0.50, 0.62]
Migratory status: migratory	0.04	0.206	0.35	[-0.17, 0.86]
Flight muscle ratio	0.43	0.006	0.31	[0.10, 0.50]
Model 8 ($R_{\text{adjusted}}^2 = 0.37$, Pagel's $\lambda = 0.717$)				
Intercept	-0.79	<0.001	-	-
Body mass	-0.16	<0.001	-0.46	[-0.59, -0.31]
Development mode: precocial	-0.25	<0.001	-0.71	[-1.09, -0.34]
Clutch size	0.17	0.035	0.19	[0.02, 0.36]
Nest type: open	0.05	0.114	0.33	[-0.07, 0.73]
Migratory status: migratory	0.09	0.017	0.56	[0.11, 1.01]
Aspect ratio	-0.25	0.237	-0.11	[-0.28, 0.07]
Model 9 ($R_{\text{adjusted}}^2 = 0.38$, Pagel's $\lambda = 0.733$)				
Intercept	-1.17	<0.001	-	-
Body mass	-0.24	<0.001	-0.44	[-0.57, -0.29]
Development mode: precocial	-0.30	<0.001	-0.84	[-1.22, -0.46]
Clutch size	0.20	0.009	0.24	[0.06, 0.40]
Nest type: open	0.05	0.127	0.32	[-0.08, 0.72]
Migratory status: migratory	0.06	0.075	0.42	[-0.03, 0.87]
Wing loading	0.24	0.028	0.20	[0.03, 0.36]

and aspect ratio suggests that growth rate and efficiency of flight are likely to be disconnected.

While the tradeoff caused by limited resources can explain growth rate's negative association with wing area (birds with smaller wing areas have higher wing loadings), the mechanisms underlying the positive correlation between growth rate and the size of flight muscles remain to be explored. [Wright, Steadman & Witt \(2016\)](#) showed that island birds tend to evolve smaller flight muscles and found a positive correlation between the size of flight muscles and predation pressure, when using raptorial species richness and the presence of mammalian predators as proxies for predation pressure. [Sandvig, Coulson & Clegg \(2019\)](#) showed that among altricial birds, island birds tend to grow slower than continental birds, though the relationship is marginally non-significant. A positive correlation between growth rate and nest predation rate has been demonstrated in previous studies of passerines ([Cheng & Martin, 2012](#); [Martin et al., 2011](#); [Remeš & Martin,](#)

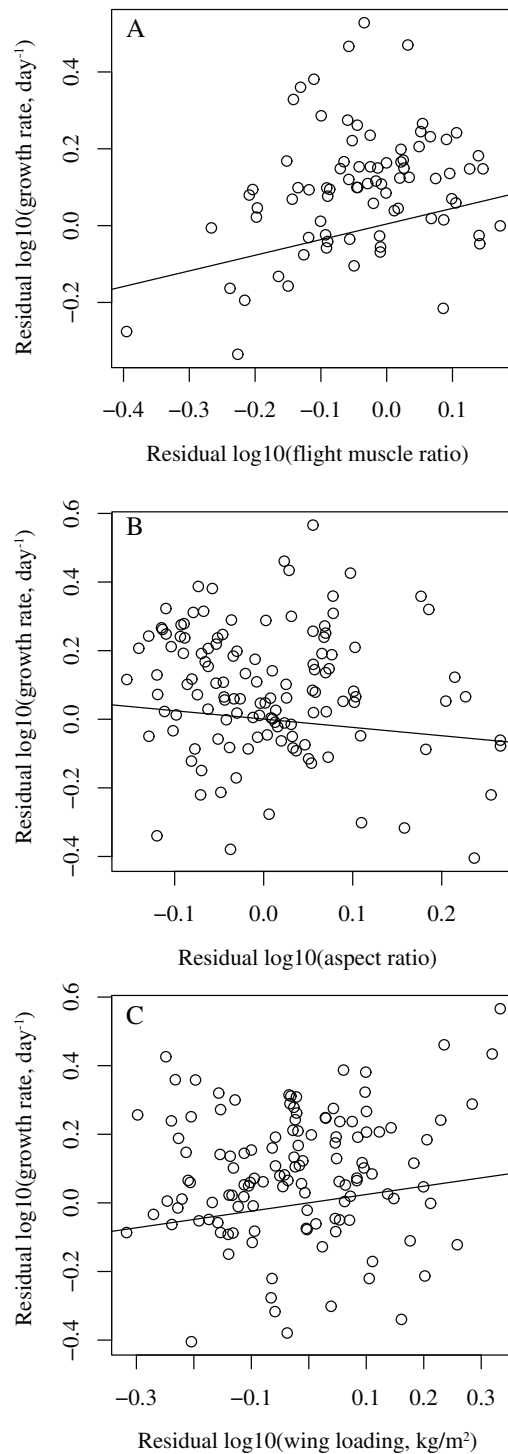


Figure 1 Bivariate plots showing the relationships between growth rate and wing parameters in birds. (A) residual log₁₀ (growth rate) vs. residual log₁₀ (flight muscle ratio); (B) residual log₁₀ (growth rate) vs. residual log₁₀ (aspect ratio); (C) residual log₁₀ (growth rate) vs. residual log₁₀ (wing loading). The lines are simple regressions between the residuals. In (A) the control variables are body mass, development mode, clutch size, nest type, latitude, and migratory status, while in (B) and (C) the control variables are body mass, development mode, clutch size, nest type, and migratory status, with latitude dropped.

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2002). These studies suggest that predation pressure can be a potential factor that drives the correlated evolution of growth rate and the size of flight muscles in birds.

The positive relationship found between growth rate and latitude is consistent with previous studies (Martin, 2015; McCarty, 2001; Ricklefs, 1968, 1976; Sandvig, Coulson & Clegg, 2019). Moreover, latitude may confound growth rate's association with wing loading. Martin (2015) suggested that the slower growth of tropical birds is associated with enhanced flight performance after fledging than temperate birds. The positive association of latitude with wing loading and the negative association of latitude with wing aspect ratio suggest that tropical birds may be more efficient in maneuvering flight and flight in general.

In extant birds, the sternal keel serves as the attachment of flight muscles (i.e., m. supracoracoideus and m. pectoralis) and the sternal keel length is positively correlated with the mass of flight muscles (Wright, Steadman & Witt, 2016). By contrast, in the earliest fossil birds, for example, *Archaeopteryx*, an ossified sternal keel is absent (Zheng et al., 2014), and an enlargement of the sternal keel along the lineage leading to crown birds has been well documented (O'Connor et al., 2015b; Zheng et al., 2014, 2012). However, how the absence or the small size of the sternal keel in early birds could affect the size of flight muscles remains to be elucidated (Mayr, 2017; O'Connor et al., 2015a; Olson & Feduccia, 1979). Recent prolific studies suggest that growth rates of extinct taxa can be estimated from their bone histology (Cubo et al., 2012; Erickson, 2005, 2014; Erickson et al., 2009; Erickson, Rogers & Yerby, 2001; Padian, De Ricqlès & Horner, 2001). Accordingly, our finding of the positive correlation between growth rate and the size of flight muscles suggests that bone microstructures may also be associated with the size of flight muscles. Further investigations on the relationship between bone histology and the size of flight muscles, and possibly other flight-related parameters, may provide a new avenue to understanding the early evolution of flight and change in growth rate.

CONCLUSIONS

Our study shows that growth rate and flight ability are correlated in avian evolution, and their relationship is more complex than a simple tradeoff as proposed in previous studies. Fast-growing birds tended to have higher flight muscle ratios and higher wing loadings, which means that fast-growing birds may have better takeoff performance, but lower efficiency in maneuvering flight. Besides wings, legs contribute greatly to the locomotion of birds and are important for birds to occupy different habitats (Habib & Ruff, 2008; Stoessel, Kilbourne & Fischer, 2013; Zeffler, Johansson & Marmebro, 2003). Moreover, wings and legs are highly linked during avian evolution (Allen et al., 2013; Heers & Dial, 2015; Zhao, Liu & Li, 2017). Further studies on the relationship between growth rate and hindlimb performance will provide more insights into the evolution of birds.

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ADDITIONAL INFORMATION AND DECLARATIONS

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Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Tao Zhao conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Zhiheng Li conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The raw data, phylogenetic trees, and R code are available as [Supplemental Files](#).

Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.8423#supplemental-information>.

REFERENCES

- Allen V, Bates KT, Li Z, Hutchinson JR. 2013. Linking the evolution of body shape and locomotor biomechanics in bird-line archosaurs. *Nature* 497(7447):104–107 DOI 10.1038/nature12059.
- Arendt JD. 1997. Adaptive intrinsic growth rates: an integration across taxa. *Quarterly Review of Biology* 72(2):149–177 DOI 10.1086/419764.
- Billerbeck JM, Lankford TE, Conover DO. 2001. Evolution of intrinsic growth and energy acquisition rates. I. Trade-offs with swimming performance in *Menidia menidia*. *Evolution* 55(9):1863–1872 DOI 10.1111/j.0014-3820.2001.tb00835.x.
- BirdLife International. 2019. IUCN Red List for birds. Available at <http://www.birdlife.org>.
- BirdLife International and Handbook of the Birds of the World. 2018. Bird species distribution maps of the world. Version 2018.1. Available at <http://datazone.birdlife.org/species/requestdis>.

- Case TJ. 1978.** On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *Quarterly Review of Biology* **53**(3):243–282 DOI [10.1086/410622](https://doi.org/10.1086/410622).
- Cheng Y-R, Martin TE. 2012.** Nest predation risk and growth strategies of passerine species: grow fast or develop traits to escape risk? *American Naturalist* **180**(3):285–295 DOI [10.1086/667214](https://doi.org/10.1086/667214).
- Coslovsky M, Richner H. 2011.** Predation risk affects offspring growth via maternal effects. *Functional Ecology* **25**(4):878–888 DOI [10.1111/j.1365-2435.2011.01834.x](https://doi.org/10.1111/j.1365-2435.2011.01834.x).
- Cubo J, Le Roy N, Martinez-Maza C, Montes L. 2012.** Paleohistological estimation of bone growth rate in extinct archosaurs. *Paleobiology* **38**(2):335–349 DOI [10.1666/08093.1](https://doi.org/10.1666/08093.1).
- Dmitriew CM. 2011.** The evolution of growth trajectories: what limits growth rate? *Biological Reviews* **86**(1):97–116 DOI [10.1111/j.1469-185X.2010.00136.x](https://doi.org/10.1111/j.1469-185X.2010.00136.x).
- Erickson GM. 2005.** Assessing dinosaur growth patterns: a microscopic revolution. *Trends in Ecology & Evolution* **20**(12):677–684 DOI [10.1016/j.tree.2005.08.012](https://doi.org/10.1016/j.tree.2005.08.012).
- Erickson GM. 2014.** On dinosaur growth. *Annual Review of Earth and Planetary Sciences* **42**(1):675–697 DOI [10.1146/annurev-earth-060313-054858](https://doi.org/10.1146/annurev-earth-060313-054858).
- Erickson GM, Rauhut OWM, Zhou Z, Turner AH, Inouye BD, Hu D, Norell MA. 2009.** Was dinosaurian physiology inherited by birds? Reconciling slow growth in Archaeopteryx. *PLOS ONE* **4**(10):e7390 DOI [10.1371/journal.pone.0007390](https://doi.org/10.1371/journal.pone.0007390).
- Erickson GM, Rogers KC, Yerby SA. 2001.** Dinosaurian growth patterns and rapid avian growth rates. *Nature* **412**(6845):429–433 DOI [10.1038/35086558](https://doi.org/10.1038/35086558).
- Gabriela AJ. 2018.** “The same thing that makes you live can kill you in the end”: exploring the effects of growth rates and longevity on cellular metabolic rates and oxidative stress in mammals and birds. *Integrative and Comparative Biology* **58**(3):544–558 DOI [10.1093/icb/icy090](https://doi.org/10.1093/icb/icy090).
- Habib MB, Ruff CB. 2008.** The effects of locomotion on the structural characteristics of avian limb bones. *Zoological Journal of the Linnean Society* **153**(3):601–624 DOI [10.1111/j.1096-3642.2008.00402.x](https://doi.org/10.1111/j.1096-3642.2008.00402.x).
- Harrison C, Greensmith A. 1993.** *Birds of the World*. London: Dorling Kindersley.
- Hartman FA. 1961.** *Locomotor mechanisms of birds*. Washington, D.C.: Smithsonian Institution.
- Heers AM, Dial KP. 2015.** Wings versus legs in the avian *bauplan*: development and evolution of alternative locomotor strategies. *Evolution* **69**(2):305–320 DOI [10.1111/evo.12576](https://doi.org/10.1111/evo.12576).
- Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012.** The global diversity of birds in space and time. *Nature* **491**(7424):444–448 DOI [10.1038/nature11631](https://doi.org/10.1038/nature11631).
- Lee W-S, Monaghan P, Metcalfe NB. 2010.** The trade-off between growth rate and locomotor performance varies with perceived time until breeding. *Journal of Experimental Biology* **213**(19):3289–3298 DOI [10.1242/jeb.043083](https://doi.org/10.1242/jeb.043083).
- Marden JH. 1987.** Maximum lift production during takeoff in flying animals. *Journal of Experimental Biology* **130**:235–258.
- Martin TE. 2004.** Avian life-history evolution has an eminent past: does it have a bright future? *The Auk* **121**:289–301.
- Martin TE. 2015.** Age-related mortality explains life history strategies of tropical and temperate songbirds. *Science* **349**(6251):966–970 DOI [10.1126/science.aad1173](https://doi.org/10.1126/science.aad1173).
- Martin TE, Lloyd P, Bosque C, Barton DC, Bianucci AL, Cheng Y-R, Ton R. 2011.** Growth rate variation among passerine species in tropical and temperate sites: an antagonistic interaction between parental food provisioning and nest predation risk. *Evolution* **65**(6):1607–1622 DOI [10.1111/j.1558-5646.2011.01227.x](https://doi.org/10.1111/j.1558-5646.2011.01227.x).
- Mayr G. 2017.** Pectoral girdle morphology of Mesozoic birds and the evolution of the avian supracoracoideus muscle. *Journal of Ornithology* **158**(3):859–867 DOI [10.1007/s10336-017-1451-x](https://doi.org/10.1007/s10336-017-1451-x).

- McCarty JP. 2001. Variation in growth of nestling tree swallows across multiple temporal and spatial scales. *Auk* 118(1):176–190 DOI 10.1093/auk/118.1.176.
- Metcalfe NB, Monaghan P. 2003. Growth versus lifespan: perspectives from evolutionary ecology. *Experimental Gerontology* 38(9):935–940 DOI 10.1016/S0531-5565(03)00159-1.
- Myhrvold NP, Baldrige E, Chan B, Sivam D, Freeman DL, Ernest SKM. 2015. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology* 96(11):3109 DOI 10.1890/15-0846R.1.
- Nakagawa S, Cuthill IC. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews* 82(4):591–605 DOI 10.1111/j.1469-185X.2007.00027.x.
- Norberg RA, Norberg UM. 1971. Take-off, landing, and flight speed during fishing flights of *Gavia stellata* (Pont.). *Ornis Scandinavica (Scandinavian Journal of Ornithology)* 2(1):55–67 DOI 10.2307/3676239.
- Norberg U. 1990. *Vertebrate flight: mechanics, physiology, morphology, ecology and evolution*. Berlin: Springer.
- O'Connor JK, Zheng X-T, Sullivan C, Chuong C-M, Wang X-L, Li A, Wang Y, Zhang X-M, Zhou Z-H. 2015b. Evolution and functional significance of derived sternal ossification patterns in ornithothoracine birds. *Journal of Evolutionary Biology* 28(8):1550–1567 DOI 10.1111/jeb.12675.
- O'Connor JK, Zheng X, Wang X, Zhang X, Zhou Z. 2015a. The gastral basket in basal birds and their close relatives: size and possible function. *Vertebrata Palasiatica* 53:133–152.
- Olson SL, Feduccia A. 1979. Flight capability and the pectoral girdle of *Archaeopteryx*. *Nature* 278(5701):247–248 DOI 10.1038/278247a0.
- Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W. 2018. *CAPER: Comparative analyses of phylogenetics and evolution in R*. R package version 1.0.1. Available at <https://CRAN.R-project.org/package=caper>.
- Padian K, De Ricqlès AJ, Horner JR. 2001. Dinosaurian growth rates and bird origins. *Nature* 412(6845):405–408 DOI 10.1038/35086500.
- Paradis E, Claude J, Strimmer K. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20(2):289–290 DOI 10.1093/bioinformatics/btg412.
- Pennycuik CJ. 2008. *Modelling the flying bird*. Amsterdam: Elsevier.
- R Development Core Team. 2019. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at <http://www.R-project.org/>.
- Remeš V, Martin TE. 2002. Environmental influences on the evolution of growth and developmental rates in passerines. *Evolution* 56(12):2505–2518 DOI 10.1111/j.0014-3820.2002.tb00175.x.
- Revell LJ. 2012. Phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 3(2):217–223 DOI 10.1111/j.2041-210X.2011.00169.x.
- Ricklefs RE. 1968. Patterns of growth in birds. *Ibis* 110(4):419–451 DOI 10.1111/j.1474-919X.1968.tb00058.x.
- Ricklefs R. 1973. Patterns of growth in birds. II. growth rate and mode of development. *Ibis* 115:177–201.
- Ricklefs RE. 1976. Growth rates of birds in the humid new World tropics. *Ibis* 118(2):179–207 DOI 10.1111/j.1474-919X.1976.tb03065.x.

- Royle NJ, Hartley IR, Owens IPF, Parker GA. 1999. Sibling competition and the evolution of growth rates in birds. *Proceedings of the Royal Society of London Series B: Biological Sciences* 266(1422):923–932 DOI 10.1098/rspb.1999.0725.
- Sandvig EM, Coulson T, Clegg SM. 2019. The effect of insularity on avian growth rates and implications for insular body size evolution. *Proceedings of the Royal Society B: Biological Sciences* 286(1894):20181967 DOI 10.1098/rspb.2018.1967.
- Serrano FJ, Palmqvist P, Chiappe LM, Sanz JL. 2016. Inferring flight parameters of Mesozoic avians through multivariate analyses of forelimb elements in their living relatives. *Paleobiology* 43(1):1–26 DOI 10.1017/pab.2016.35.
- Sibly RM, Witt CC, Wright NA, Venditti C, Jetz W, Brown JH. 2012. Energetics, lifestyle, and reproduction in birds. *Proceedings of the National Academy of Sciences of the United States of America* 109(27):10937–10941 DOI 10.1073/pnas.1206512109.
- Starck JM, Ricklefs RE. 1998. Patterns of development: the altricial-precocial spectrum. In: Starck JM, Ricklefs RE, eds. *Avian Growth and Development: Evolution Within the Altricial-Precocial Spectrum*. New York: Oxford University Press, 3–30.
- Stoessel A, Kilbourne BM, Fischer MS. 2013. Morphological integration versus ecological plasticity in the avian pelvic limb skeleton. *Journal of Morphology* 274(5):483–495 DOI 10.1002/jmor.20109.
- Tacutu R, Craig T, Budovsky A, Wuttke D, Lehmann G, Taranukha D, Costa J, Fraiefeld VE, De Magalhães JP. 2013. Human ageing genomic resources: integrated databases and tools for the biology and genetics of ageing. *Nucleic Acids Research* 41(D1):D1027–D1033 DOI 10.1093/nar/gks1155.
- Tholon P, Queiroz SA. 2007. Models for the analysis of growth curves for rearing tinamous (*Rhynchotus rufescens*) in captivity. *Brazilian Journal of Poultry Science* 9(1):23–31 DOI 10.1590/S1516-635X2007000100004.
- Viscor G, Fuster JF. 1987. Relationships between morphological parameters in birds with different flying habits, Bird maneuvering flight: blurred bodies, clear heads. *Comparative Biochemistry and Physiology Part A: Physiology* 87(2):231–249 DOI 10.1016/0300-9629(87)90118-6.
- Warrick DR, Bundle MW, Dial KP. 2002. Bird maneuvering flight: blurred bodies, clear heads. *Integrative and Comparative Biology* 42:141–148 DOI 10.1093/icb/42.1.141.
- Warrick DR, Dial KP, Biewener AA. 1998. Asymmetrical force production in the maneuvering flight of pigeons. *Auk* 115(4):916–928 DOI 10.2307/4089510.
- Wright NA, Steadman DW, Witt CC. 2016. Predictable evolution toward flightlessness in volant island birds. *Proceedings of the National Academy of Sciences of the United States of America* 113(17):4765–4770 DOI 10.1073/pnas.1522931113.
- Zeffer A, Johansson LC, Marmebro Å. 2003. Functional correlation between habitat use and leg morphology in birds (Aves). *Biological Journal of the Linnean Society* 79(3):461–484 DOI 10.1046/j.1095-8312.2003.00200.x.
- Zhao T, Liu D, Li Z. 2017. Correlated evolution of sternal keel length and ilium length in birds. *PeerJ* 5:e3622 DOI 10.7717/peerj.3622.
- Zheng X, O'Connor J, Wang X, Wang M, Zhang X, Zhou Z. 2014. On the absence of sternal elements in *Anchiornis* (Paraves) and *Sapeornis* (Aves) and the complex early evolution of the avian sternum. *Proceedings of the National Academy of Sciences of the United States of America* 111(38):13900–13905 DOI 10.1073/pnas.1411070111.
- Zheng X, Wang X, O'Connor J, Zhou Z. 2012. Insight into the early evolution of the avian sternum from juvenile enantiornithines. *Nature Communications* 3(1):1116 DOI 10.1038/ncomms2104.