Growth rate and locomotor performance trade-off is not universal in birds

Tao Zhao Corresp., 1, Zhiheng Li Corresp. 2

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

Corresponding Authors: Tao Zhao, Zhiheng Li
Email address: taozhao@nigpas.ac.cn, lizhiheng@ivpp.ac.cn

Though a trade-off 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 loading 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 insight into the evolution of birds.
Growth rate and locomotor performance trade-off is not universal in birds

Tao Zhao¹, Zhiheng Li²

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

Authors for correspondence:

Tao Zhao: taozhao@nigpas.ac.cn

Zhiheng Li: lizhiheng@ivpp.ac.cn
Abstract

Though a trade-off 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 loading 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 insight into the evolution of birds.

Key words: birds, growth rate, flight ability, flight muscles, wing span, wing area, wing aspect ratio
Introduction

Growth rates vary considerably among different taxa and organisms (e.g., Arendt 1997; Case 1978; Ricklefs 1973; Ricklefs 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; Metcalfe & 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 (e.g., Billerbeck et al. 2001; Dmitriew 2011; Lee et al. 2010). For example, Billerbeck et al. (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.

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 variations 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 faster 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 et al. (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. Flight muscles mass is important in determining the power that flight muscles can produce (Pennycuick 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 (Pennycuick 2008).

Materials & 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 et al. (2016) and Viscor & Fuster (1987); body mass, wing span and wing area from Pennycuick (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 and 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 muscles 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 in total. 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 Core Team 2019) using the packages “ape” (Paradis et al. 2004), “caper” (Orme et al. 2018) and phytools (Revell 2012). To account for phylogeny, we used 1000 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 9 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, 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 mass of flight muscle ratio ($P = 0.006$, effect size $= 0.31$) and wing loading ($P = 0.028$, effect 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 larger flight muscle ratios and larger 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 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 loading can make turns of smaller radii (Norberg et al. 1971; Norberg 1990; Pennycuick 2008). However, it has been suggested that birds with high wing loading can also effect turns of small radii, but requiring slowing and flapping, which is energetically more expensive (Warrick et al. 1998; Warrick et al. 2002). In other words, wing loading is associated with efficiency of maneuvering flight (Warrick et al. 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; Pennycuick 2008). The lack of significant correlation between growth rate 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 associations with wing areas (birds with smaller wing areas have higher wing loading), the mechanisms underlying the positive correlation between growth rate and the size of flight muscles remains to be explored. Wright et al. (2016) showed that islands 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 et al. (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 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 (e.g., Martin 2015; McCarty 2001; Ricklefs 1968; Ricklefs 1976; Sandvig et al. 2019). Moreover, latitude may confound growth rate’s associations 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 flight muscle mass (Wright et al. 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; Zheng et al. 2012). However, how the absence or the small size of the sternal keel in early birds could affect the size of flight muscles remain to be elucidated (Mayr ...
Recent prolific studies suggest that growth rates of extinct taxa can be estimated from their bone histology (Cubo et al. 2012; Erickson 2005; Erickson 2014; Erickson et al. 2009; Erickson et al. 2001; Padian et al. 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 lower wing loading, 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 et al. 2013; Zeffer et al. 2003). Moreover, wings and legs are highly linked during avian evolution (Allen et al. 2013; Heers & Dial 2015; Zhao et al. 2017). Further studies on the relationship between growth rate and hindlimb performance will provide more insights into the evolution of birds.
Acknowledgements

We are grateful to Prof. Zhonghe Zhou for discussion and Dr. Zhenchao Wang for help with ArcGIS.

References

Allen V, Bates KT, Li Z, and Hutchinson JR. 2013. Linking the evolution of body shape and locomotor biomechanics in bird-line archosaurs. Nature 497:104-107. 10.1038/nature12059

Arendt JD. 1997. Adaptive intrinsic growth rates: an integration across taxa. The Quarterly Review of Biology 72:149-177.

Billerbeck JM, Lankford TE, and Conover DO. 2001. Evolution of intrinsic growth and energy acquisition rates. I. Trade-offs with swimming performance in Menidia menidia. Evolution 55:1863-1872.

BirdLife International. 2019. IUCN Red List for birds. Downloaded from 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. The Quarterly Review of Biology 53:243-282.
Cheng Y-R, and Martin TE. 2012. Nest predation risk and growth strategies of passerine species: grow fast or develop traits to escape risk? *The American Naturalist* 180:285-295. 10.1086/667214

Coslovsky M, and Richner H. 2011. Predation risk affects offspring growth via maternal effects. *Functional Ecology* 25:878-888. 10.1111/j.1365-2435.2011.01834.x

Cubo J, Le Roy N, Martinez-Maza C, and Montes L. 2012. Paleohistological estimation of bone growth rate in extinct archosaurs. *Paleobiology* 38:335-349. 10.1666/08093.1

Dmitriew CM. 2011. The evolution of growth trajectories: what limits growth rate? *Biological Reviews* 86:97-116.

Erickson GM. 2005. Assessing dinosaur growth patterns: a microscopic revolution. *Trends Ecol Evol* 20:677-684. 10.1016/j.tree.2005.08.012

Erickson GM. 2014. On dinosaur growth. *Annual Review of Earth and Planetary Sciences* 42:675-697.

Erickson GM, Rauhut OW, Zhou Z, Turner AH, Inouye BD, Hu D, and Norell MA. 2009. Was dinosaurian physiology inherited by birds? Reconciling slow growth in Archaeopteryx. *PLoS ONE* 4:e7390.

Erickson GM, Rogers KC, and Yerby SA. 2001. Dinosaurian growth patterns and rapid avian growth rates. *Nature* 412:429-433.

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...
261 Stress in Mammals and Birds. *Integrative and Comparative Biology* 58:544-558.

262 Habib MB, and Ruff CB. 2008. The effects of locomotion on the structural characteristics of avian limb bones. *Zoological Journal of the Linnean Society* 153:601-624.

264 10.1111/j.1096-3642.2008.00402.x

265 Harrison C, and Greensmith A. 1993. *Birds of the World*. London: Dorling Kindersley.

266 Hartman FA. 1961. *Locomotor mechanisms of birds*: Smithsonian institution.

267 Heers AM, and Dial KP. 2015. Wings versus legs in the avian bauplan: development and evolution of alternative locomotor strategies. *Evolution* 69:305-320. 10.1111/evo.12576

269 Jetz W, Thomas GH, Joy JB, Hartmann K, and Mooers AO. 2012. The global diversity of birds in space and time. *Nature* 491:444-448.

270 Lee W-S, Monaghan P, and Metcalfe NB. 2010. The trade-off between growth rate and locomotor performance varies with perceived time until breeding. *The Journal of Experimental Biology* 213:3289. 10.1242/jeb.043083

274 Marden JH. 1987. Maximum lift production during takeoff in flying animals. *Journal of Experimental Biology* 130:235-258.

276 Martin TE. 2015. Age-related mortality explains life history strategies of tropical and temperate songbirds. *Science* 349:966-970.

278 Martin TE, Lloyd P, Bosque C, Barton DC, Biancucci AL, Cheng YR, and 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*
Mayr G. 2017. Pectoral girdle morphology of Mesozoic birds and the evolution of the avian supracoracoideus muscle. *Journal of Ornithology* 158:859-867.

McCarty JP. 2001. Variation in Growth of Nestling Tree Swallows Across Multiple Temporal and Spatial Scales. *The Auk* 118:176-190. 10.1642/0004-8038(2001)118[0176:Vigont]2.0.Co;2

Metcalf NB, and Monaghan P. 2003. Growth versus lifespan: perspectives from evolutionary ecology. *Experimental Gerontology* 38:935-940.

Myhrvold NP, Baldridge E, Chan B, Sivam D, Freeman DL, and Ernest SKM. 2015. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology* 96:3109-3109. doi:10.1890/15-0846R.1

Nakagawa S, and Cuthill IC. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews* 82:591-605. 10.1111/j.1469-185X.2007.00027.x

Norberg R, xc, ke, and Norberg UM. 1971. Take-off, landing, and flight speed during fishing flights of Gavia stellata (Pont.). *Ornis Scandinavica (Scandinavian Journal of Ornithology)* 2:55-67. 10.2307/3676239

Norberg U. 1990. *Vertebrate flight: mechanics, physiology, morphology, ecology and evolution*: Springer Berlin Heidelberg.

O'Connor JK, Zheng X, Wang X, Zhang X, and Zhou Z. 2015a. The gastral basket in basal birds
and their close relatives: size and possible function. *Vertebrata PalAsiatica* 53:133-152.

O'Connor JK, Zheng XT, Sullivan C, Chuong CM, Wang XL, Li A, Wang Y, Zhang XM, and Zhou ZH. 2015b. Evolution and functional significance of derived sternal ossification patterns in ornithothoracine birds. *J Evol Biol* 28:1550-1567. 10.1111/jeb.12675

Olson SL, and Feduccia A. 1979. Flight capability and the pectoral girdle of Archaeopteryx.

*Nature* 278:247-248.

Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, and Pearse W. 2018. caper: Comparative analyses of phylogenetics and evolution in R. R package version 1.0.1.

Padian K, de Ricqlès AJ, and Horner JR. 2001. Dinosaurian growth rates and bird origins.

*Nature* 412:405-408.

Paradis E, Claude J, and Strimmer K. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20:289-290. 10.1093/bioinformatics/btg412

Pennycuick CJ. 2008. *Modelling the flying bird*. Amsterdam: Elsevier.

R Core Team. 2019. R: A language and environment for statistical computing. 3. 5. 3 ed. Vienna, Austria: R Foundation for Statistical Computing.

Remeš V, and Martin TE. 2002. Environmental influences on the evolution of growth and developmental rates in passerines. *Evolution* 56:2505-2518.

Revell LJ. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 3:217-223. 10.1111/j.2041-210X.2011.00169.x
Ricklefs R. 1973. Patterns of growth in birds. II. Growth rate and mode of development. *Ibis* 115:177-201.

Ricklefs RE. 1968. Patterns of growth in birds. *Ibis* 110:419-451. 10.1111/j.1474-919X.1968.tb00058.x

Ricklefs RE. 1976. Growth rates of birds in the humid New World tropics. *Ibis* 118:179-207. 10.1111/j.1474-919X.1976.tb03065.x

Royle NJ, Hartley IR, Owens IPF, and Parker GA. 1999. Sibling competition and the evolution of growth rates in birds. *Proceedings of the Royal Society of London Series B: Biological Sciences* 266:923.

Sandvig EM, Coulson T, and 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* 286:20181967.

Serrano FJ, Palmqvist P, Chiappe LM, and Sanz JL. 2016. Inferring flight parameters of Mesozoic avians through multivariate analyses of forelimb elements in their living relatives. *Paleobiology*:1-26. 10.1017/pab.2016.35

Sibly RM, Witt CC, Wright NA, Venditti C, Jetz W, and Brown JH. 2012. Energetics, lifestyle, and reproduction in birds. *Proceedings of the National Academy of Sciences* 109:10937. 10.1073/pnas.1206512109

Starck JM, and Ricklefs RE. 1998. Patterns of development: the altricial-precocial spectrum. In: *Avian growth and development: evolution within the*
*altricial-precocial spectrum.* New York: Oxford University Press, 3-30.

Stoessel A, Kilbourne BM, and Fischer MS. 2013. Morphological integration versus ecological plasticity in the avian pelvic limb skeleton. *J Morphol* 274:483-495. 10.1002/jmor.20109

Tacutu R, Craig T, Budovsky A, Wuttke D, Lehmann G, Taranukha D, Costa J, Fraifeld VE, and de Magalhães JP. 2013. Human Ageing Genomic Resources: integrated databases and tools for the biology and genetics of ageing. *Nucleic Acids Research* 41:D1027-D1033. 10.1093/nar/gks1155

Tholon P, and Queiroz S. 2007. Models for the analysis of growth curves for rearing tinamous (Rhynchotus rufescens) in captivity. *Brazilian Journal of Poultry Science* 9:23-31.

Viscor G, and Fuster JF. 1987. Relationships between morphological parameters in birds with different flying habits. *Comparative Biochemistry and Physiology Part A: Physiology* 87:231-249. Warrick DR, Bundle MW, and Dial KP. 2002. Bird maneuvering flight: blurred bodies, clear heads. *Integrative and Comparative Biology* 42:141-148. 10.1093/icb/42.1.141

Warrick DR, Dial KP, and Biewener AA. 1998. Asymmetrical force production in the maneuvering flight of pigeons. *The Auk* 115:916-928. 10.2307/4089510

Wright NA, Steadman DW, and Witt CC. 2016. Predictable evolution toward flightlessness in volant island birds. *Proceedings of the National Academy of Sciences* 113:4765-4770. 10.1073/pnas.1522931113

Zeffer A, Johansson LC, and Marmebro Å. 2003. Functional correlation between habitat use and
leg morphology in birds (Aves). *Biological Journal of the Linnean Society* 79:461-484.

Zhao T, Liu D, and Li Z. 2017. Correlated evolution of sternal keel length and ilium length in birds. *PeerJ* 5:e3622. 10.7717/peerj.3622

Zheng X, O'Connor JK, Wang X, Wang M, Zhang X, and 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* 111:13900-13905. 10.1073/pnas.1411070111

Zheng X, Wang X, O'Connor J, and Zhou Z. 2012. Insight into the early evolution of the avian sternum from juvenile enantiornithines. *Nat Commun* 3:1116.
Table 1 (on next page)

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      | P     | Effect size (r or d) | 95% CI of effect size |
|----------------------|--------|-------|----------------------|-----------------------|
| **Model 1** (R²_adj = 0.53, Pagel’s λ = 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** (R²_adj = 0.43, Pagel’s λ = 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** (R²_adj = 0.44, Pagel’s λ = 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)         |
Table 2 (on next page)

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.
| Model 4 (R²_adj = 0.13, Pagel’s λ = 0.418) | β     | P      | Effect size (r or d) | 95% CI of effect size |
|-----------------------------------------|--------|--------|----------------------|-----------------------|
| (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 (R²_adj = 0.16, Pagel’s λ = 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 (R²_adj = 0.14, Pagel’s λ = 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)          |
Table 3 (on next page)

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.
| Model 7 ($\text{R}^2_{\text{adj}} = 0.51$, Pagel’s $\lambda = 0.792$) |
|-----------------------------------------------|
| β            | P       | Effect size (r or d) | 95% CI of effect size |
| (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 | $4.84 \times 10^{-4}$ | 0.995               | 7.36$\times 10^{-4}$ | (-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 ($\text{R}^2_{\text{adj}} = 0.37$, Pagel’s $\lambda = 0.717$) |
|-----------------------------------------------|
| β            | P       | Effect size (r or d) | 95% CI of effect size |
| (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 ($\text{R}^2_{\text{adj}} = 0.38$, Pagel’s $\lambda = 0.733$) |
|-----------------------------------------------|
| β            | P       | Effect size (r or d) | 95% CI of effect size |
| (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)         |
Figure 1

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.
Manuscript to be reviewed