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Functional Morphology of Gliding Flight II. Morphology Follows Predictions of Gliding Performance

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Abstract
The evolution of wing morphology among birds, and its functional consequences, remains an open question, despite much attention. This is in part because the connection between form and function is difficult to test directly. To address this deficit, in prior work we used computational modeling and sensitivity analysis to interrogate the impact of altering wing aspect ratio, camber, and Reynolds number on aerodynamic performance, revealing the performance landscapes that avian evolution has explored. In the present work, we used a dataset of three-dimensionally scanned bird wings coupled with the performance landscapes to test two hypotheses regarding the evolutionary diversification of wing morphology associated with gliding flight behavior: 1) gliding birds would exhibit higher wing aspect ratio and greater chordwise camber than their non-gliding counterparts; and 2) that two strategies for gliding flight exist, with divergent morphological conformations. In support of our first hypothesis, we found evidence of morphological divergence in both wing aspect ratio and camber between gliders and non-gliders, suggesting that wing morphology of birds that utilize gliding flight is under different selective pressures than the wings of non-gliding taxa. Furthermore, we found that these morphological differences also yielded differences in coefficient of lift measured both at the maximum lift to drag ratio and at minimum sinking speed, with gliding taxa exhibiting higher coefficient of lift in both cases. Minimum sinking speed was also lower in gliders than non-gliders. However, contrary to our hypothesis, we found that the maximum ratio of the coefficient of lift to the coefficient of drag differed between gliders and non-gliders. This may point to the need for gliders to maintain high lift capability for takeoff and landing independent of gliding performance, or could be due to the divergence in flight styles among gliders, as not all gliders are predicted to optimize either quantity. However, direct evidence for the existence of two morphologically defined gliding flight strategies was equivocal, with only slightly stronger support for an evolutionary model positing separate morphological optima for these strategies than an alternative model positing a single peak. The absence of a clear result may be an artifact of low statistical power owing to a relatively small sample size of gliding flyers expected to follow the “aerial search” strategy.
Keywords
avian, performance landscape, wing morphology, aspect ratio, camber, coefficient of lift

Introduction

Birds are diverse in their behavior, ecology, and morphology. Clades vary in their reliance on flight (ranging from flightless to spending most time aloft), flight style (gliding to hovering), and flight performance (burst take-off to high-efficiency soaring). Birds span four orders of magnitude in body mass, ranging from 3.5 cm (bee hummingbird, *Mellisuga helenae*) to more than 3 m in wingspan (wandering albatross, *Diomedea exulans*; Shaffer et al. 2001), and vary in habits from sedentary flightlessness to long-distance flights that nearly match the circumference of the Earth (Austin 1953).

Despite being well-studied as a group, the connections between wing morphology, the biomechanics of flight, and evolution are not well understood. Previous work has focused on studying morphology and its connection to other biological characteristics. Many studies have connected wing shape to migratory habits, with migrants having more pointed wingtips than non-migrants (Mönkkönen 1995; Lockwood et al. 1998; Bowlin and Wikelski 2008; Baldwin et al. 2010; but see Grilli et al. 2017). This pattern exists across species (Lockwood et al. 1998) and among migrant versus sedentary populations of the same species (Mönkkönen 1995). Wing shape among songbirds also correlates with the risk of predation from aerial predators; species that face more intense pressure have more pointed wings (Swaddle and Lockwood 1998). Sheard, et al. (2019) described latitudinal variation the hand-wing index (the ratio of the length over the width of the wing distal to the wrist; Kipp 1959) and correlations with territoriality and habitat preference. Additionally, wing shape is linked to other attributes of avian biology, such as egg morphology (Stoddard et al. 2017).

While these studies are informative, observed morphological variation does not necessarily yield variation in flight performance. Recent work connecting biomechanics to morphological variation suggests that many complex systems have “many-to-one mapping” in which different morphologies result in similar performance (Wainwright 2007; Anderson and
Thus, the connection between variation in morphology and biomechanical consequences requires clarification.

Work in flight biomechanics has focused on flight performance of individuals within a single species (e.g.: Parrott 1970; Tucker and Heine 1990; Bowlin and Wikelski 2008; Weimerskirch et al. 2016) or comparative studies of a restricted number of species (e.g. Hedenström and Bone 1993; Altshuler 2003; Altshuler et al. 2004; but see Segre et al. 2015; Baliga et al. 2019). Many studies were conducted using non-phylogenetically explicit analyses (Lockwood et al. 1998; but see Taylor and Thomas 2014; Wang and Clarke 2015; Baliga et al. 2019). Direct measurement of flight performance in flying birds typically takes the form of birds flying in wind tunnels (Pennycuick 1968; Rosen and Hedenstrom 2001; Hedenstrom et al. 2006). While this type of work provides a mechanistic understanding of the flight of individual birds, it is too difficult and costly to implement in the broad taxonomic sampling required to understand trait evolution.

Computational modeling may provide an avenue to develop predictive relationships between morphological traits and their impact on biomechanical performance. When coupled with a survey of morphological specimens, such models could facilitate broader study of the evolution of performance traits. As an example, Tseng (2013) used numerical simulations to model the mechanical advantage of carnivorous mammal skulls across the plausible range of variation in three simple parameters of skull morphology – length, width, and depth. What resulted was a theoretical landscape linking biomechanical performance to varying morphological configurations (Tseng 2013). Similar work has also been performed by Polly et al. (2016), Keren et al. (2017), Waldrop et al. (2018), and Olsson et al. (2020) on different systems.

Here we focus on creating such performance landscapes based on flight style, a major difference in the ecology of many birds. While most birds engage in flapping flight, there are a few that mostly engage in gliding and soaring with stable, outstretched wings. Gliders trade potential energy, in the form of flight altitude, for forward motion, and the exchange rate of that transaction is largely determined by the efficiency of their wings (Vogel 1981). Soaring is a form of gliding flight wherein birds take advantage of updrafts in the air to gain altitude, and
thus energy, to power their flight without flapping. Birds that soar over land typically seek out thermals (Shannon et al. 2002; Ákos et al. 2010).

While gliding and soaring birds tend to have the same flight behavior, there are subtle differences in the way these birds use gliding and soaring. Staying in updrafts requires that birds must sense rising air and maneuver to stay within it (Vogel 1981; Williams et al. 2018). This favors relatively slow flight, meaning that the wings of these birds must produce sufficient lift at low airspeeds (Vogel 1981; Taylor and Thomas 2014). By contrast, birds that glide to travel long distances benefit from high speed and highly efficient flight – minimizing altitude lost per distance traveled (Vogel 1981; Weimerskirch et al. 1993; Taylor and Thomas 2014). Such differences in flight behavior may be associated with different selection regimes that could act to drive divergence in morphological features involved in flight. The obvious focus of these selective pressure would be the wings, but tail morphology is also known to influence aerodynamic forces (Usherwood 2005; Usherwood et al. 2020), and may also be subject to similar pressures. Furthermore, if differences in flight behavior are associated with differences in selective pressures, this may manifest in divergent trajectories toward disparate evolutionary optima, and possibly at different evolutionary rates ($\sigma^2$), for species that regularly engage in gliding flight versus those that do not.

In the preceding work, we created a computational model of fluid flow around simulated bird wings to construct aerodynamic performance landscapes of gliding flight (Waldrop et al. 2020). We used uncertainty quantification techniques to assess the sensitivity of performance to variation in three morphological metrics among birds: wing aspect ratio, camber, and body size. We found that aspect ratio and camber both strongly influenced gliding performance in maximum $C_L/C_D$ ratio, where $C_L$ and $C_D$ are the coefficients of lift and drag, as well as $C_L$. However, high performance in these metrics occurred at different combinations of morphology. High $C_L/C_D$ occurred at high aspect ratio and intermediate camber, while high $C_L$ was generated by high measures of both traits (see Waldrop et al. 2020). Based on the sensitivity analyses and performance landscapes, we proposed two hypotheses: 1) gliding birds would exhibit higher wing aspect ratio and greater chordwise camber than their non-gliding counterparts; and 2) that two strategies for gliding flight exist, which we have labeled “aerial
“searching” and “aerial perching”, and which are associated with divergent morphological conformations. The first hypothesis springs from the expectation that gliding birds will have a higher maximum \( C_l/C_D \) ratio, where \( C_l \) and \( C_D \) are the coefficients of lift and drag, respectively.

Within gliding taxa, the second hypothesis proposes a further split between aerial-perching birds that also exhibit high \( C_l \) and low minimum sinking speeds \( (V_{z,\text{min}}) \) and aerial searchers that do not. In the present work, we wielded a dataset of 3-dimensionally (3D) scanned wings to test the first hypothesis, and to provide a preliminary exploration of the second.

**Methods**

**Wing scanning and 3D wing morphology**

We collected morphological measurements from 3D scanned wings representing 163 species from three major ecotypes of birds, raptors (Accipitriformes and Falconiformes, also including two species of Strigiformes), seabirds, shorebirds and rails (Procellariiformes, Phaethontiformes, Charadriiformes, and Gruiformes), doves (Columbiformes), and songbirds (Passeriformes) from the collection of the North Carolina Museum of Natural Sciences (Raleigh, NC) using a NextEngine 3D Scanner Ultra HD laser scanner (NextEngine, Inc., Santa Monica, CA). Wings were scanned at resolutions of at least 200 dpi, but up to 16,000 dpi for small wings. The scanned wings were stripped down to their vertices, and 2D and 3D shape variables of the resulting point clouds were measured using a custom program in MATLAB (The MathWorks, Natick, MA, USA).

The scanned wings were aligned to \( X, Y, \) and \( Z \) axes in 3D space using a principal components (PC) analysis. The first, second and third PC axes represented the length (\( X \)), chord (\( Y \)), and thickness (\( Z \)) of the wings, respectively. Wing length was measured as \( X_{\text{max}} - X_{\text{min}} \). The wings were subdivided into chord-wise slices along their length, with the width of the slices scaled to \( 1/25^{\text{th}} \) of the distance between the wingtip and the wrist joint. This standardized the number of slices representing the hand portion of the wing, facilitating direct comparison across samples and taxa. The number of slices representing the arm portion of the wing varied, as wing proportions differ among species and higher order taxonomy. For each of these slices we measured wing chord as \( Y_{\text{max}} - Y_{\text{min}} \) and maximum section height as \( Z_{\text{max}} - Z_{\text{min}} \). The
proximal portion of the wings were subject to variable preservational artifacts, owing to their removal from the birds’ bodies during specimen preparation. Therefore, the proximal 1/3rd of the arm wing slices was excluded from chordwise analyses.

*Measuring wing geometry*

We measured wing aspect ratio \( (AR) \), mean camber \( (\bar{Q}) \), and estimated Reynolds number \( (Re) \) as a function of wing chord. Aspect ratio \( (AR) \) was calculated as

\[
AR = \frac{4r^2}{S}
\]

where \( S \) is wing area, and \( r \) is wing length. We were unable to account for the width of the body when calculating wingspan, owing to the removal of the wings during preparation. Therefore, our measurements of aspect ratio are underestimates. Camber \( (Q) \) for each of the wing slices was measured as the ratio of wing section thickness \( (t) \) over section chord length \( (C) \) (Fig. 1). Both \( t \) and \( Q \) varied along the span of the wings, so mean camber \( (\bar{Q}) \) and mean section thickness \( (\bar{t}) \) were calculated for each wing.

Reynolds number was calculated from mean chord \( (\bar{C}) \), while air density and kinematic viscosity were held constant at \( \rho = 1.225 \text{ kg m}^{-3} \) and \( \nu = 1.5 \times 10^{-5} \text{ m}^2 \text{ s}^{-1} \), respectively:

\[
Re = \frac{\nu \bar{C}}{\nu}
\]

To facilitate comparison across species, individual \( Re \) was estimated at an airspeed \( (V) \) of 8.0 ms\(^{-1} \), the minimum airspeed reported in Alerstam et al. (2007), and may therefore be an underestimate of the actual operating \( Re \) of some taxa in our sample.

Body mass \( (M_b) \) data were collected from museum tags and used to calculate the ratio of body mass over wing planform area (wing loading) for each individual. Because \( M_b \) can fluctuate dramatically in daily and seasonal cycles, we calculated median values of mass and wing loading for each taxon. Wing length and wing chord were non-dimensionalized relative to body mass by dividing by \( M_b^{0.33} \); transformed metrics are denoted by an \( ND \) subscript. This transformation assumes an isometric relationship between mass and length whereas birds as a whole or specific groups of birds may scale allometrically. This transformation leaves those allometries intact while controlling for the effect of body size on raw length measurements. The original measurement units are millimeters for lengths and grams for mass.
Modeling effects of wing geometry on gliding flight

We used the XFLR5 software (version 6.47; Deperrois 2009) to simulate airflow around wings of various morphological configurations with a simple elliptical wing planform geometry (Waldrop et al. 2020). Detailed methods can be found in Waldrop et al. (2020), but briefly, we tested prescribed combinations of three morphological parameters ($AR$, $Q$ and $Re$) of these model wings, spanning the plausible ranges for living birds, as indicated by the scanned wing data set. We extracted estimates of several wing performance metrics from XFLR5, including: 1) minimum sinking speed (assuming a constant bird mass of 0.9 kg; $V_{z,\text{min}}$), 2) coefficient of lift at minimum sinking speed ($C_L$ at $V_{z,\text{min}}$), and 3) maximum lift to drag ratio ($C_L/C_D$). We also checked that our assumption of constant bird mass didn’t bias our results by iterating our analysis of $V_{z,\text{min}}$ on estimates of $V_{z,\text{min}}$ calculated assuming constant wing loading.

Surrogate functions of output performance metrics were produced using uncertainty quantification techniques. The parameter input space was sampled and output surrogates were reconstructed using generalized polynomial chaos (gPC) expansion (Wiener 1938; Xiu and Karniadakis 2002). Global sensitivity analyses were conducted by calculating Sobol indices for each input parameter and their interactions on output performance (Sobol 1993; Sudret 2008). For additional details, see Waldrop et al (2020). In this study, gPC surrogate functions serve as performance landscapes for each output metric of flight ($V_{z,\text{min}}$, $C_L$ at $V_{z,\text{min}}$, and max $C_L/C_D$).

Analysis and hypothesis testing

All statistical analysis was conducted in R (R Development Core Team 2013). Comparative analyses of wing geometry were conducted on median values of each shape parameter for each species, and all analyses were conducted in a phylogenetically explicit framework. Phylogenetic trees were pruned from the Jetz et al. supertree (Jetz et al. 2012), acquired from birdtree.org (Rubolini et al. 2015). Phylogenetic signal was calculated using both Pagel’s $\lambda$ (Pagel 1999) and Blomberg’s $K$ (Blomberg et al. 2003) metrics using the “phylosig” command in the R package Phytools (Revell 2012).
Hypothesis 1: Wing morphology differs between gliders and non-giders

The global sensitivity analyses suggested that the effects of Re were small and that AR and $\bar{Q}$ had significant influences on all metrics of gliding flight performance (Waldrop et al. 2020), so we focused our attention on AR and $\bar{Q}$ for further analysis. Detailed discussion of the capabilities and limitations of the computational modeling is presented in the companion to this work (Waldrop et al. 2020). We classified each of the species in our sample as a glider or a non-glider based on descriptions of flight behavior from the Handbook of Birds of the World (Hoyo et al. 1992); if observations of gliding were mentioned in the text describing the species or family, the species was classified as a glider, and if the description of flight behavior did not mention gliding, species were classified as non-giders. Further, we classified seabirds, shorebirds, and swallows as “aerial searchers” based on descriptions of their long distance flight behavior (Weimerskirch et al. 1993, 2016; Shaffer et al. 2001; Warrick et al. 2016) and hawks and new-world vultures as “aerial perchers” because of their tendency to remain aloft within relatively confined geographic areas (DeVault et al. 2004; Monsarrat et al. 2013).

Stochastic character mapping was used to map these flight behaviors onto the phylogeny (see Huelsenbeck et al. 2003; Bollback 2006) using the Phytools package in R (Revell 2012). We then used the OUWie package (Beaulieu and O’Meara 2012) to fit two different models of evolution to each of the morphological traits: 1) a single-peak Ornstein-Uhlenbeck (OU) model is a Brownian motion model with a tendency toward a single trait optimum; and 2) a two-peak OU model that allows for separate evolutionary rates ($\sigma^2$) and trait optima for each behavioral group (gliders and non-giders). We used AIC$_C$ and a Monte Carlo-based method (package “pmc” in R, see Boettiger et al. 2012) to assess which model best fit our trait data. Support for a two-peak model would suggest morphological divergence between flight styles, supporting our hypotheses. We checked that differences in trait means for AR and $\bar{Q}$ were significant using phylogenetic ANOVAs, implemented in R with the “phyLANOVA” command in the Phytools package (Revell 2012). We also conducted a discriminant function analysis with jackknife sampling to assess whether gliders and non-giders could be correctly classified based on the combination of AR and $\bar{Q}$. 
To assess whether wing morphology confers differences in glide performance among the flight styles, we used the performance landscapes (gPC surrogate functions) to estimate performance for combinations of AR and \( Q \) representing each species. We used phylogenetically-aware ANOVAs in the R package Phytools (Revell 2012) to quantify divergence in \( V_{z,\min} C_L \) at \( V_{z,\min} \) and max \( C_L/C_D \).

**Hypothesis 2: Two gliding strategies lead to disparate gliding morphotypes**

Our performance landscapes identified two regions of high gliding performance associated with different combinations of wing shape traits. The highest values of \( C_L/C_D \) were found at combinations of high AR and moderate \( Q \), while the highest values of \( C_L \) at \( V_{z,\min} \) were found at high AR and high \( Q \) (Waldrop et al. 2020). This led to the prediction that “aerial perchers” might possess wing morphologies that confer high \( C_L \) at low sinking speeds, and “aerial searchers” may display high \( C_L/C_D \) wings that minimize glide angle but may require higher airspeeds to generate sufficient lift. To test these predictions, we restricted the dataset to just those taxa identified above as gliders, which were then subset into aerial perchers – those species that glide to survey comparatively small areas (hawks, falcons, and vultures), and aerial searchers – species that use their gliding flight while transiting long distances either in migration or in search of foraging grounds (seabirds and shorebirds). We used a similar OUwie approach (see above) to ask whether AR and \( Q \) showed different evolutionary patterns between these groups. We also used phylogenetically aware ANOVAs to assess differences in flight performance (estimated sinking speed, \( V_{z,\min} \), as well as \( C_L \) at \( V_{z,\min} \), \( C_L \) at max \( C_L/C_D \) and max \( C_L/C_D \)).

**Data availability**

Wing data, XFLR5 files, and results available at: https://github.com/lindsaywaldrop/birdwingGPC.

**Results**

We scanned 1094 wings from 163 species in 30 major lineages of birds (see Figure 2 and supplemental data). Sample sizes for each species ranged from 1 to 49 with a median sample
size of 5 individuals. To our knowledge, this represents the largest data set of three-dimensional wing morphology presently available.

**Morphometric summary**

Median body mass among non-gliders ranged from 6.75 g to 194.75 g and estimated $Re$ from 16,000 to 54,500, while glider body mass ranged from 12.35 g to 2060.0 g, and $Re$ from 17,197 to 132,577. Median within-species wing loading among non-gliders varied from 1.90 g cm$^{-2}$ to 9.97 g cm$^{-2}$ with an overall median of 4.21 g cm$^{-2}$. Wing loading in gliders ranged from 2.30 g cm$^{-2}$ to 31.40 g cm$^{-2}$ with an overall median of 8.67 g cm$^{-2}$. $AR$ varied from 3.90 to 7.60 in non-gliders and from 5.27 to 13.26 in gliders, with medians of 5.33 and 7.58, respectively. $\bar{Q}$ was lower in non-gliders (range 0.06 to 0.12, mean = 0.094) than in gliders (range 0.08 to 0.17, mean = 0.124). Phylogenetic signal was high in all measured traits, with $\lambda > 0.8$ and $K > 0.4$ in all cases (see Table 1).

**Hypothesis 1:**

To address the hypothesis that wing morphology would differ between gliding taxa and non-gliders, we asked two questions: 1) are there different evolutionary optima for our morphological parameters, and 2) do evolutionary rates differ between flight styles? We found support for an Ornstein-Uhlenbeck (OU) model with two evolutionary optima for aspect ratio – with gliding birds being higher ($7.76 \pm 0.30$) than non-gliding taxa ($5.40 \pm 0.11$). This difference was supported by the results of a phylogenetic ANOVA ($p = 0.03$). We also found support for different evolutionary rates between the two groups ($\sigma^2 = 0.398$ and 0.042, respectively, $AIC_c$ weight = 0.99). Non-dimensional wing length ($r_{ND}$) was greater in gliders than non-gliders (dual-rate, two-optima OU model; estimates 55.71 ± 1.83 and 41.57 ± 1.82, respectively), and evolutionary rate also differed between the groups ($\sigma^2 = 5.78$, 2.19, respectively, $AIC_c$ weight = 0.99). In a dual-rate, two-optima OU model, non-dimensional wing chord ($C_{ND}$) had estimated optima of $14.80 \pm 0.67$ for gliders and $15.90 \pm 0.69$ for non-gliders, and $\sigma^2 = 0.73$ and 0.28, respectively; $AIC_c$ weight = 0.99. In this case the evolutionary rates differ substantially but the parameter optima for $C_{ND}$ are similar (7% difference). For camber ($\bar{Q}$), we also found support
for an OU model with two optima (supported by phylogenetic ANOVA; \( p = 0.03 \)), and again, the gliding birds had greater camber (\( 0.12 \pm 0.003 \) vs. \( 0.10 \pm 0.002 \), respectively). Evolutionary rate also differed between non-gliders and gliders (\( \sigma^2 = 2.51 \times 10^{-5} \), \( 1.0 \times 10^{-4} \), respectively; \( \text{AIC}_C \) weight = 0.99). Selection of OU over simpler Brownian motion models was supported by Monte Carlo simulations, as implemented using the “pmc” command in R (Boettiger et al. 2012).

Discriminant function analysis (DFA) also supported the existence of a morphological distinction between gliders and non-gliders, with an 89.6% correct classification rate. As DFA is not a phylogenetically-aware method, we urge caution in interpretation of these results beyond the suggesting that our recovered disparity between gliders and non-gliders is robust to varying assumptions of phylogenetic relatedness.

Maximum \( C_L/C_D \) and did not differ between gliders and non-gliders (\( p = 0.28 \)), but \( V_{z,\text{min}} \) was lower among gliding birds than non-gliders (\( 1.23 \pm 0.31 \) vs \( 1.89 \pm 0.31 \), \( p = 0.03 \)), and \( C_L \) at \( V_{z,\text{min}} \) was significantly greater (\( 1.02 \pm 0.12 \) vs. \( 0.78 \pm 0.06 \), \( p < 0.01 \)). This pattern was for both the assumption of constant body mass and constant wing loading. Despite disparity in mean body mass between the different flight styles, the difference was not significant (phylogenetic ANOVA, \( p = 0.09 \)), likely owing to the large dispersion within each group (482.25 \( \pm \) 447.46 g vs. 30.82 \( \pm \) 32.50 g, \( p = 0.1 \)). Wing loading, similarly, did not differ between groups (\( p = 0.16 \)).

Hypothesis 2:
We found support for dual-optima and dual-rate OU models for both AR and \( \bar{Q} \) (\( \text{AIC}_C \) weight = 0.74 and 0.90, respectively) when comparing the “aerial perch” to the “aerial search” strategies. However, dual-optima and single-rate models also performed fairly well (\( \text{AIC}_C \) weight = 0.24 and 0.09, respectively). The estimated AR optima were greater among aerial searchers than aerial perchers in both single-rate (\( AR = 8.96 \pm 0.41 \) vs. \( 6.13 \pm 0.63 \)) and dual-rate models (\( AR = 8.92 \pm 0.44 \) vs. \( 6.34 \pm 0.35 \)). Despite \( \text{AICc} \) support for the dual-optima models for \( \bar{Q} \), the standard error bounds for the optima overlap in both the dual-rate (\( \bar{Q} = 0.12 \pm 0.005 \) vs. \( 0.12 \pm 0.003 \)) and single-rate (\( \bar{Q} = 0.12 \pm 0.006 \) vs. \( 0.12 \pm 0.007 \)) cases, lending some ambiguity to its interpretability. These results should be viewed with some caution because the sample sizes are small (\( n = 21 \) for aerial searchers and \( n = 17 \) for aerial perchers). Additionally, there were no
significant differences in estimated gliding flight performance parameters between searchers and perchers ($C_l/C_D, C_l$ at $V_{z_{\text{min}}}$; both $p > 0.09$). We did, however, find that aerial searchers had significantly lower $V_{z_{\text{min}}}$ than non-gliders (phylogenetic ANOVA, $p = 0.02$). The aerial perchers showed no such distinction from non-gliders ($p = 0.39$).

Discussion

In the preceding work, Waldrop et al. (2020) proposed two hypotheses based on the analysis of a computational model of gliding flight. The first predicted that gliding birds would exhibit different combinations of wing morphology than non-gliders. The second hypothesis posits that two gliding strategies exist: one characterized by maximizing horizontal travel relative to altitude lost, and the other simply minimizing sinking speed to enhance capacity for remaining aloft or to facilitate load-carrying. Further, Waldrop et al. (2020) suggested that these two gliding strategies may exert different selective pressures on the birds that conduct each type of flight which may result in divergence in wing morphology. As described below, we found strong support for our first hypothesis and equivocal support for our second hypothesis.

Performance landscapes predict differences in gliding performance

Consistent with the first hypothesis proposed in Waldrop et al. (2020), we found different evolutionary optima and rates ($\sigma^2$) in both wing aspect ratio ($AR$) and camber ($\bar{Q}$) for gliders and non-gliders. This result suggests that flight mode (i.e., gliding instead of flapping) exerts different selective pressures, shaping morphological evolution of bird wings. However, we caution that the present results do not show a definitive causal relationship between behavior and morphology, but rather, an evolutionary association.

Contrary to our hypothesis, we found that maximum $C_l/C_D$ did not differ between gliders and non-gliders. Gliding birds appear to be drawn toward morphological configurations that enhance the magnitude of lift production (high $C_l$) rather than efficiency of lift production (high $C_l/C_D$; see Fig. 3). This also translated to the hypothesized reduction in estimated $V_{z_{\text{min}}}$ and may therefore represent adaptation to low speed flight or load lifting. These birds, with their relatively high camber, high-aspect ratio wings did not occupy either of the regions of
especially high performance in the $C_l/C_D$ or $C_l$ landscapes, but rather seem to be settled into a valley between the optima (Fig. 3). This may reflect conflicting selective pressures that have led a Pareto optimization effect (Taylor and Thomas 2014), stemming from a tradeoff between the need for flight efficiency and the ability to generate sufficient lift to land, and takeoff, especially with large food loads. Furthermore, our proxy for wing camber is implicitly linked to cross-sectional thickness of the wing, as is the longitudinal stiffness of the wing structure. Wings may therefore be excluded from the region of highest $C_l/C_D$ by a lower bound on the thickness of the wing imposed by structural demands.

Significant distinctions in gliding performance were driven by greater values of both $AR$ and $Q$ in gliding taxa, relative to non-gliders, irrespective of body size and $Re$. Body size is tightly correlated with the phylogeny (Pagel’s $\lambda = 0.90$; Pagel 1999), so it may be difficult to explicitly disambiguate the effects of size and phylogeny in this relationship. High $AR$ wings are a known morphological adaptation to gliding and soaring flight (for example, see Taylor and Thomas 2014), but the interaction with $Q$ was previously unknown. Both $AR$ and $Q$, as measured herein, are non-dimensional ratios, but our data facilitated explicit exploration of which dimensional shape attributes appeared to be under selection. Average wing chord ($C_{ND}$) differed very little among flight styles, however, body mass corrected wing length ($r_{ND}$) was greater in gliding birds, leading to increased $AR$. Similarly, because $Q$ is the ratio of average wing section thickness ($\bar{t}$) over $C$, the relative lack of divergence in chord indicates that the wings of gliders have greater $\bar{t}$, which serves as a proxy measurement for more pronounced camber curvature.

It should be noted that few of the species in our sample are specialist gliders, as this behavior seems to be isolated to only a handful of lineages, including vultures and pelagic seabirds (Taylor and Thomas 2014), but many other lineages rely on gliding to reduce their cost of flight to varying degrees (Vogel 1981; Hoyo et al. 1992; Taylor and Thomas 2014). We used the non-gliding songbirds and rails as a point of reference to contrast with gliders. While the performance landscapes presented here leave us uncertain what adaptive value anchors the non-gliders in their region of morphospace, it is clear that gliders have diverged from them. Further exploration of how the $AR$ and $Q$ relate to other flight performance metrics, particularly those associated with flapping flight, may be illuminating.
Equivocal support for two gliding strategies

Birds use gliding and soaring flight to reduce their cost of transport, with two different goals, 1) to remain aloft in a relatively discrete area (which we have dubbed “aerial perching”), and 2) to transit long horizontal distances (“aerial searching”) (Ákos et al. 2008, 2010). Hawks, eagles, vultures, and other similar birds tend to forage in relatively small home ranges (Ákos et al. 2008, 2010) where they utilize discrete updrafts to remain aloft (Parrott 1970; McGahan 1973; Tucker and Heine 1990; Hedenström and Bone 1993). Pelagic seabirds such as petrels, fulmars, and albatrosses (Procellariiformes) transit long distances between island breeding sites and pelagic foraging sites (Weimerskirch et al. 1993, 2016; Ákos et al. 2008).

Based on the performance landscapes from Waldrop et al. (2020), we predicted that aerial perchers would be adapted to maximize $C_L$ and minimize $V_{z,min}$, and that aerial searchers would have morphological configurations that produced comparatively high $C_L/C_D$. Our results do not support or reject this hypothesis. Despite the lack of support for the predicted differences in gliding performance between the two strategies, models do support the presence of dual evolutionary optima for $AR$. However, while two peak statistical models of $\bar{Q}$ between searchers and perchers outperformed one-peak models, support was equivocal between single and dual rates, and the SE estimated confidence bounds of the two peaks overlap. However, the sample sizes of putative searchers and perchers were small, and OUwie modeling has been shown to be particularly sensitive to error at small sample sizes (Cooper et al. 2016). Additionally, most species in our sample that frequently glide are not specialist gliders like vultures (Tucker 1988) and albatrosses (Weimerskirch et al. 1993). Non-specialist species may be subject to tradeoffs imposed by flapping flight that would have less impact on gliding specialists. A more explicit test of this hypothesis should thus focus on these and similar specialist taxa.

On performance landscapes

Performance landscapes provide a useful tool to probe the relationship between form and function (Arnold 2003; Dickson and Pierce 2019). With the application of quantitative modeling
of the sensitivity of performance output to changes in morphological traits, a theoretical landscape can explore configurations outside the bounds of extant organisms, and perhaps even feasibility (Koehl 2003; Waldrop et al. 2020). When coupled with a taxonomically broad morphological survey, a performance landscape can illuminate evolutionary exploration of topographic features (Keren et al. 2017; Olsson et al. 2020). The ability to map performance directly onto morphospaces defined by individual traits, as we have done here in the bivariate \( AR \) and \( \tilde{Q} \) morphospaces (also see Tseng 2013) facilitates easier interpretability of results than morphospaces defined by composite variables, such as those produced by principal components analysis and similar dimensional reduction techniques.

In the current work, we use a performance landscapes generated by a simple model of gliding flight to estimate performance of real birds in flight. These landscapes are estimates of performance only, and come with a variety of caveats discussed in Waldrop et al. (2020). While we feel that the model matches other estimates and measurements of extant birds in gliding flight, it should be noted that neglected aspects of flight (e.g. body interactions) may affect the values and their relationships within performance landscapes.

**Considering the third dimension**

Bird wings are inherently 3-dimensional structures, but shape analysis has historically focused largely on 2d attributes (for example, Mönkkönen 1995; Lockwood et al. 1998; Taylor and Thomas 2014). Three-dimensional attributes of wing morphology, such as camber also influence the aerodynamics of the wing (Brown 2001; Null and Shkarayev 2005; Waldrop et al. 2020). Indeed, the performance differences that we describe here are a function of an interaction between aspect ratio and camber, so restricting our consideration to traditional planform metrics would have limited our ability to describe functional divergence between gliding and non-gliding birds. With increasing capacity to collect and analyze 3-dimensional data, our results highlight the necessity of doing so.
**Acknowledgements**

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References


Beaulieu JM, O’Meara B. 2012. OUwie: analysis of evolutionary rates in an OU framework (R package).


Table Captions

Table 1. Phylogenetic signal of body mass ($M_b$) camber ($\bar{Q}$), aspect ratio ($AR$), non-dimensional wing length ($r_{ND}$), and non-dimensional wing chord ($\bar{C}_{ND}$).

Table 2. Model outputs from the top performing OUwie fit for camber ($\bar{Q}$), aspect ratio ($AR$), non-dimensional wing length ($r_{ND}$), and non-dimensional wing chord ($\bar{C}_{ND}$). Wing length and chord were non-dimensionalized by dividing the linear measurements by body mass$^{0.33}$. In all cases, dual optimum and dual rate models were preferred, as demonstrated by the high AICc weights. Optima are presented $\pm$ SE.
Figure Captions

Figure 1. Morphological configurations and relevant metrics. Aspect ratio \( (AR) \) varied from < 5.0 to > 11.0 in our sample; examples of different \( AR \) are depicted in panel A. showing two gliders (blue-green color): \( \text{Diomedia exulans} \) (i.), \( \text{Buteo jamaicensis} \) (ii.), and a non-glider (tan color): \( \text{Junco hyemalis} \) (iii.). Wing length \( (r) \), chord \( (C) \) and section thickness \( (t) \) were measured as indicated (panels B. and C.) on 3-dimensionally scanned wings. Camber \( (Q) \) was calculated as the ratio of \( t/C \) and ranged in our sample from 0.07 to 0.16.

Figure 2. Phylogenetic distribution of aspect ratio \( (AR) \), camber \( (Q) \) and non-dimensional wing length \( (r_{ND}) \). The tree was pruned from the Jetz et al. (2012) supertree, and stochastic character mapping (Huelsenbeck et al. 2003; Bollback 2006) was used to map gliding (blue-green) vs. non-gliding (tan) flight behavior. Vertical ticks in \( AR \), \( Q \) and \( r_{ND} \) panes represent individual measurements, circles denote the species median, and horizontal bars reflect one median absolute deviation (MAD) on either side of the medians.

Figure 3. Gliding flight performance landscapes with distribution of measured bird species. Coefficient of lift measured at minimum sinking speed \( (V_{z,\text{min}}; \) panel A.) and maximum lift to drag ratio \( (C_L/C_D; \) panel B.) surrogate functions are shown at Reynolds number \( (Re) = 105,000 \). Black circles in both panes represent non-gliding taxa, and light gray squares show species that glide regularly. White ellipses show 95% confidence regions (Jackson et al. 2011) for non-gliders (i.) and gliders (ii.), and black ellipses show the same for non-gliders (iii.), and two putative gliding strategies: aerial perching (iv.) and aerial searching (v.). See main text for descriptions of gliding strategies.
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<table>
<thead>
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<th>Shape Trait</th>
<th>Pagel’s $\lambda$</th>
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<td>Shape Trait</td>
<td>AICc Weight</td>
<td>Estimated Glider Optimum</td>
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Supplemental figure 1. Workflow for extracting data from 3D scanned bird wings. A. Wings were scanned using a NextEngine 3D Scanner Ultra HD laser scanner (NextEngine, Inc., Santa Monica, CA). Wings were scanned at a minimum of 200 dpi to provide adequate shape information, including surface characteristics (B., in this case, a peregrine falcon, *Falco peregrinus*). The scanned wings were then stripped to their vertices (C.) and segmented into slices (D.) for further measurement, including section thickness and chords, from which our proxy of wing camber was calculated (E.).