Wing shape in waterbirds: morphometric patterns associated with behavior, habitat, migration, and phylogenetic convergence

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Abstract: Wing shape plays a critical role in flight function in birds and other powered fliers and has been shown to be correlated with flight performance, migratory distance, and the biomechanics of generating lift during flight. Avian wing shape and flight mechanics have also been shown to be associated with general foraging behavior and habitat choice. We aim to determine if wing shape in waterbirds, a functionally and ecologically diverse assemblage united by their coastal and aquatic habitats, is correlated with various functional and ecological traits. We applied geometric morphometric...
approaches to the spread wings of a selection of waterbirds to search for evolutionary patterns between wing shape and foraging behavior, habitat and migratory patterns. We found strong evidence of convergent evolution of high and low aspect ratio wing shapes in multiple clades. Foraging behavior also consistently exhibits strong evolutionary correlations with wing shape. Habitat, migration and flight style, in contrast, do not exhibit significant correlation with wing shape in waterbirds. Although wing shape is critical to aerial flight function, its relationship to habitat and periodic locomotor demands such as migration is complex.

Résumé

La forme de l’aile joue un rôle essentiel dans le vol chez les oiseaux et les autres animaux présentant un vol actif. Il a été démontré que cette dernière est corrélée aux performances de vol, à la distance de migration et à la biomécanique générant de la portance pendant le vol. La forme de l’aile et la mécanique du vol chez les oiseaux sont également associées au comportement alimentaire et au choix de l'habitat. Notre objectif est de déterminer si la forme de l’aile chez les oiseaux aquatiques, un assemblage fonctionnellement et écologiquement diversifié uni par leurs habitats côtiers, est corrélée à divers traits fonctionnels et écologiques. Nous nous sommes appuyés sur des techniques de morphométrie géométrique appliquées aux ailes déployées d'une sélection d'oiseaux aquatiques afin de mettre en évidence un lien évolutif entre la forme des ailes, le comportement alimentaire, l'habitat et les mouvements migratoires. Nous avons trouvé des preuves concrètes de l'évolution convergente des formes d'ailes à fort et faible allongements dans plusieurs clades. Le comportement alimentaire présente également de fortes corrélations évolutives avec la forme des ailes. L'habitat, la migration et le style de vol, en revanche, ne présentent pas de corrélation significative avec la forme de l'aile chez les oiseaux aquatiques. Bien que la forme de l'aile soit essentielle au vol, sa relation avec l'habitat et les exigences locomotrices périodiques telles que la migration reste complexe.
Resumen

La forma del ala tiene un papel crítico en el vuelo de las aves y otros voladores activos, y se ha comprobado que se correlaciona con la eficiencia del vuelo, la distancia migratoria y la biomecánica en la generación de sustentación durante el vuelo. La forma de las alas de las aves y la mecánica del vuelo también están relacionadas con las estrategias de búsqueda de alimento y elección de hábitat. Nuestro propósito es determinar si la forma del ala se correlaciona con varias características funcionales y ecológicas en aves acuáticas, un grupo funcional y ecológicamente diverso que comparten un hábito costero y acuático. Se utilizó morfometría geométrica en alas extendidas de una selección de aves acuáticas para buscar patrones evolutivos entre la morfología del ala y estrategia de alimentación, hábitat y patrones migratorios. Se ha encontrado evidencia robusta de evolución convergente de morfologías de ala con mayor o menor alargamiento en varios clados. El comportamiento de búsqueda de alimento también tiene correlaciones evolutivas consistentes con la morfología del ala. Sin embargo, el hábitat, tipo de migración y tipo de vuelo no muestran una correlación significativa con la morfología del ala en aves acuáticas. Aunque la forma del ala es crítica para la función del vuelo aéreo, su relación con el hábitat o demandas locomotoras periódicas como la migración son complejas.

Introduction

Wing shape has long been known to exhibit a strong correlation with a generalized description of aerodynamic performance: long, narrow wings (high aspect ratio) characterize large-bodied gliding and
soaring organisms, whereas short, broad wings (low aspect ratio) characterize smaller-bodied organisms with more maneuverable flight (Norberg 1990; Tobalske 2007; Alexander 2015). This general correlation between wing shape and aerodynamic function has also been found in every group of aerial or aquatic powered fliers, including cephalopods, insects, fishes, pterosaurs and bats, and has often been applied to airfoil design in mechanized flight (Da Vinci 1505; Norberg 1990; Norberg 1995; Hansen 2003; Lentink and Biewener 2010; Martin-Silverstone et al. 2020). Despite the extensive body of work on bird flight and wing shape, we are only beginning to understand the complexity of biological wings, the relationship between their form and their function, and their evolutionary history.

Previous work has shown a strong relationship between avian wing shape and various aspects of flight function. Aspect ratio has a significant relationship with maneuverability, rapid takeoff and efficient gliding (Hartman 1961; Greenewalt 1975; Norberg 1990). Wingtip shape has proven to be significant with regards to dispersal ability, takeoff and flight performance, and relative migration distance within species or between closely related species (Mulvihill and Chandler 1990; Lockwood et al. 1998; Combes and Daniel 2001; Swaddle and Lockwood 2003; Brewer and Hertel 2007; Claramunt et al. 2012; Minias et al. 2015). Wang and Clarke (2014; 2015) discovered that wing bone shape and wing outlines have a strong phylogenetic signal when examined in an evolutionary context; wing shape was more closely associated with clade membership than flight style. In addition, recent work across birds has linked wing length and beak morphology to feeding behaviors and ecological habitats (Pigot et al. 2020). These large-scale analyses show convergence as a common evolutionary pattern across birds, underscoring the need to carefully assess avian morphological traits against the phylogenetic and ecologic background of birds selected for study.

Waterbirds comprise a diverse assemblage for exploring patterns of morphological and ecological diversity. They include water-adapted species from three clades: Aequiornithines (diving
birds, wading birds, shorebirds), Gruiformes (containing rails and cranes) and Anseriformes (ducks and geese) (Prum et al. 2015). With sufficient ornithological interest for their own focus group (e.g., Waterbird Society), waterbirds have been subject to extensive research including recent exploration of the genetic basis underlying interdigital webbing in their feet (Tokita et al. 2020). Waterbirds, known conclusively now to be representatives of at least three phylogenetic assemblages, are nonetheless united ecologically by their proximity to, and dependence on, aquatic or nearshore habitats that has led to convergence in morphology, trophic strategy and locomotor behavior. Recent work shows that waterbird wing shapes are diverse, occupying roughly half of total avian wing shape space (Wang and Clarke 2014; 2015). These studies, among the first to analyze avian wing shape within phylogenetic context, demonstrated that some traditional functional and ecological variables showed little correlation with wing shape. This result runs counter to the idea that form and function are correlated. Thus, exploration of wing shape among the diversity of waterbirds may yield unexpected insights in the relationship between structure and function.

We began with the hypothesis that using landmark-based geometric, rather than simple linear, morphometrics to capture waterbird wing shape would yield clearer relationships to important ecological traits. And given that no single variable fully captures the complexity of avian lifestyle, we tested several: flight style, foraging behavior, habitat, migratory status, and migratory status categorized by geographic location. Flight style has previously been used to describe the wingbeat pattern used in horizontal flight, i.e., frequent flapping vs. gliding (Viscor and Fuster 1987). Foraging behavior better captures the range of different behaviors that may require more or less agility, for example plunge diving vs. dabbling. Habitat categories often reflect differences in air currents or foliage density, which again would draw upon wing function. Finally, migration variables are used here to capture how much a
bird requires long distance migratory flights, and determine whether long migratory distances over land rather than ocean results in any wing shape differences.

Our central aim is to explore the relation between wing metrics and a variety of ecological variables waterbirds, which exhibit diverse behaviors in a range of habitats. We test the hypothesis that wing shape and foraging behavior are strongly correlated (Higham 2007; Webb 1984) and the strength of the correlation between wing shape indices and migratory patterns. Using geometric morphometric data in the context of a well-resolved phylogeny (Hackett et al. 2008; Jetz et al. 2012), we also examine biomechanical traits such as the distribution of wing area, wing loading and wing aspect ratio. Finally, we look anew at phylogenetic convergence of wing shape in the light of an integrated phylomorphospace and comparative approach.

**Materials and Methods**

**Specimen selection, phylogeny and ecological data sources**

We analyzed wing images for 136 species of waterbirds from eight clades to search for correlation with ecological or behavioral traits (Suppl. Table 1). A diversity of wing shapes is represented (Fig. 1). Penguins are excluded, because their wing feather morphology is too divergent for many of the measurements in this study (e.g., no clear distinction between primary, secondary and covert feathers) and because previous work has shown their wing outlines differ markedly from that of other birds (Wang and Clarke 2015). Included species all are documented by an adult wing (dorsal view) in the Wing and Tail Image Collection of the University of Puget Sound's Slater Museum of Natural History (2011). All included wing images are preserved in the standard "spread wing" position.
**Fig. 1** Waterbird wing shapes across the phylogeny with color-labeled clades: A, Anseriformes; C, Charadriiformes; P, Podicipediformes; Gr, Gruiformes; G, Gaviiformes; Pr, Procellariiformes; S, Suliformes; Pe, Pelecaniformes. Images reproduced with permission from the Puget Sound Wing and Tail Image Collection and the Burke Museum of Natural History and Culture.

Our phylogeny follows Pigot et al. (2020) in the use of the avian molecular tree of Jetz et al. (2012), the latter based on the earlier phylogenetic tree of Hackett et al. (2008). One thousand full molecular trees from the Hackett Sequenced Series were downloaded from BirdTree.org. A maximum credibility tree was created from these 1000 trees with median node heights using TreeAnnotator from BEAST (Drummond and Rambaut 2007). The resulting tree contained a single negative branch length, which was converted to a branch length of 0.01. The tree was imported into R and pruned to our species with the `drop.tip()` function in the `ape` package (Paradis and Schliep 2019) for subsequent use in phylogenetic analyses.

We scored our sample of 136 waterbirds for body mass, phylogenetic relationships, and a suite of ecological traits including foraging behavior, habitat, and migration. For body mass we accessed data in Dunning Jr. (2007). We gathered ecological trait data from various traditional and recent compilations. “Flight style” came from Viscor and Fuster (1987) with species in our analysis coded according to their clade-level assignments. “Foraging behavior” was adapted from the “All About Birds” website (Cornell Lab of Ornithology 2015), *The Birder’s Handbook* (Ehrlich et al. 1988), and the Animal Diversity Web (Myers et al. 2020) (see “Terminology” in Suppl. text for list of terms). All terms were taken from the Cornell Lab of Ornithology, except "aerial hunter," which we use here to describe birds that hunt on the wing. Jaegers and frigatebirds, for example, prey on other birds in flight, and
petrels often catch food on the wing rather than diving (Cornell Lab of Ornithology 2015). In both of these cases, significant time is spent in the air to catch prey. “Foraging niche” was defined and logged following Pigot et al. (2020). As we found no substantive differences between foraging niche and foraging behavior (Suppl. Fig. 2), we used foraging behavior. “Habitat” data came from the Cornell Lab of Ornithology (2015), *The Birder’s Handbook* (Ehrlich et al. 1988), and the Animal Diversity Web (Myers et al. 2020).

“Migratory status” (full migrant, partial migrant, non-migrant) was obtained from *BirdLife International* (2020). Most species in this compilation were logged as full migrants or non-migrants. A single species, *Phalacrocorax carbo* (great cormorant), was registered as a third category, “partial migrant,” because only part of the population migrates. The majority of waterbirds have geographic ranges that were scored as either “continent-based” or “oceanic” using range maps from *BirdLife International* (2020). As a result, we scored our waterbirds for an additional variable that combines migratory status with geographic location. Only five species ranged across both continental and oceanic geography, and we scored these as “mixed range.” We combined these data with migratory status to generate our variable "Migration+Location” (i.e., continental migrant, continental non-migrant).

**Digitization**

To capture wing shape, wing images were digitized with a mixture of homologous and sliding semi-landmarks (Fig. 2A for wing anatomy; Fig. 2B for numbered landmarks). The trailing edge of the coverts was also included in wing shape, because overall covert shape was found to contribute significantly to wing shape disparity (Wang and Clarke 2015). The R package *StereoMorph* (Olsen and Westneat 2015; Olsen and Haber 2017) was used to digitize the images. Homologous landmarks (Fig 2B, larger red circles) include the anteroproximal point (approximate location of the humeral head), the
anteriormost part of the wrist, the distal tips of the first five primary flight feathers, the division between primary and secondary flight feathers, the last secondary flight feather, the distalmost primary greater covert tip, the division between the primary and secondary greater coverts, and the last secondary greater covert. Six curves of sliding semi-landmarks (Fig. 2B, smaller yellow circles) were created at the anterior edge of the wing (humeral head to wrist, wrist to distal tip of first primary flight feather), the posterior edge of the flight feathers (tip of fifth primary flight feather to tip of last primary flight feather, tip of last primary flight feather to tip of last secondary flight feather), and the posterior edge of the greater coverts (distalmost tip of primary coverts to tip of last primary covert, tip of last primary covert to tip of last secondary covert). These points create the dataset for the whole-wing morphospace, subsets of which were used to calculate additional variables and morphospaces.

Fig. 2 Landmark protocol for wings. A) Anatomy of a bird wing, handwing – grey portion, armwing – white portion; B) Numbered homologous landmarks (red) and sliding semi-landmarks (yellow); C) Subset of landmarks used for handwing morphospace, and measurements taken for hand-wing index calculations (purple, $l_{S1}$ and $l_{hw}$); D) Wingspan (blue, $l_w$) chords (red, $C_1$-$C_5$) for AR distribution analysis; E) Wing area segments: anterior armwing (light green, $S_{awA}$), posterior armwing (dark green, $S_{awP}$), anterior midwing (light purple, $S_{mwA}$), posterior midwing (dark purple, $S_{mwP}$), wingtip (light blue, $S_{wt}$); F) Calculating slope for AR distribution of a wing.
Wing shape measurements and functional metrics

Wingspan, wing length, aspect ratio, wing area, wing loading, and pointedness of the wingtip (for symbols, see Table 1) comprise the most commonly used wing metrics for comparative functional analysis (Ellington 1984; Norberg 1990).

Table 1 Variables and abbreviations for wing and aerodynamic metrics (adapted from Norberg 1990).

We followed the terminology used in Norberg (1990): wingspan, $b$, is the distance between wingtips; wing length, $l_w$, is the distance from the shoulder joint to wingtip; armwing length, $l_{aw}$, is the distance between the shoulder and wrist joints; and handwing length, $l_{hw}$, is the distance between wrist joint and wingtip (Fig. 2A). It is worth noting that ornithologists have often used 'wing length' as the measure from the wrist joint to the wingtip (equivalent to $l_{hw}$), because that has been the easiest measure to get from a museum specimen with a folded wing (Greenewalt 1962). Because we used spread wings, we can distinguish between the different regions of the wing.

Fig. 3 Wing measurements associated with flight performance. (A) Based on definitions in Norberg and Rayner (1987) and Norberg (1990). (B) Measurements on folded wings for Kipp's index (Lockwood et al. 1998), illustration adapted from Sibley (2018). Abbreviations: $b$, wingspan; $l$, length; $S$, area; $\Delta S_1$, distance between longest primary and first secondary flight feathers.

Traditionally, aspect ratio is wingspan divided by mean chord, because the chord of a bird wing changes significantly over its length. However, most recent studies measure single-wing aspect ratio, as wing length squared divided by wing area (Norberg 1990). We followed that convention here as $AR = \ldots$
We also developed an aspect ratio slope metric ("AR slope") using wing length and a series of five incrementally more distal chords to calculate an aspect ratio series along the wing. These points generated a linear regression (Fig. 2F), from which was derived the AR slope. This metric measures the degree that aspect ratio changes along the length of the wing.

Airfoil area ($S$) refers to the lift-generating surface of an object (Table 1) (Norberg 1990). Single-wing area ($S_w$) refers solely to the area of one wing (Norberg 1990). Armwing area ($S_{aw}$) is the area of the wing between the shoulder and wrist joints, which extends across the secondary feathers (Fig. 3A), and handwing area ($S_{hw}$) is the area of the wing between the wrist joint and the wingtip, which extends across the primary feathers (Fig. 3A) (Norberg 1990). Wing loading ($\frac{Mg}{S}$) is a measure of the force of body weight placed per unit of wing area (Norberg 1990). Pennycuick (2008) noted that wing loading needs to be calculated using total airfoil area ($S$), which includes the area of both wings and the body. This area represents the portion of the bird that is contributing to lift while gliding. Norberg and Rayner (1987) examined data from many birds and bats and found that the body area is approximately 20% of combined wing area. Because our dataset is composed of single wings, we approximated wing loading as $WL = \frac{Mg}{2S_w + (2S_w \times 0.2)} \text{N} \cdot \text{m}^{-2}$.

Handwing pointedness has been linked to flight performance and dispersal ability (Lockwood et al. 1998; Claramunt et al. 2012). “Kipp’s distance” ($\Delta S_1$) has been defined as the distance between the longest primary and secondary flight feathers, though has since changed to being the distance between the longest primary flight feather and first secondary flight feather: $l_w - l_{s1}$ (Kipp 1959; Lockwood et al. 1998; Claramunt et al. 2012; Sheard et al. 2020; Pigot et al. 2020), which is readily measured on the folded wings of museum specimens (Fig. 3B). “Kipp’s index” ($I_K$), or the “handwing index” (HWI), is a commonly used metric for wingtip shape. This index is often calculated as a proportion of Kipp’s
distance against the traditional wing length measurement: $I_K = \frac{l_{w}-l_{S1}}{l_{w}} \times 100$ (Fig. 3BC) (Lockwood et al. 1998; Baldwin et al. 2010).

**WingMorph app for calculating functional metrics**

We developed a Mac Xcode app called *WingMorph* (free for download; http://www.github.com/mwestneat/WingMorph) to calculate functional metrics for bird wings. The app imports the two-dimensional wing landmarks, from which it computes functional metrics (wing spans, chords, aspect ratios, handwing index, regional wing areas, total wing area; Fig. 2C-E) that are output as a trait matrix (.csv) file. The full set of wing metrics calculated for our waterbird dataset are available (Suppl. Table 2).

**Morphometric analysis and phylogenetic comparative methods**

The functional metric morphospace was calculated using aspect ratio, AR slope, wing area, wing loading, and handwing index. This data was size corrected by calculating the log shape ratios for wing area and wing loading, two variables strongly affected by body size. A single geometric mean was calculated between wing area and wing loading. Each of those variables was divided by that geometric mean, and those values were log$_{10}$-transformed (Mosimann 1970; Price et al. 2019). Because each of the variables in morphospace use dramatically different ranges, each set of variables were z-scored for standardization before running the principal component analysis (PCA).

Geometric morphometric analysis was performed using the R packages *geomorph* (Adams et al. 2020) and *RRPP* (Collyer and Adams 2018; Collyer and Adams 2020), which included a General Procrustes analysis of coordinate data (used for standardizing landmark data in whole-wing and handwing data) and PCA to generate whole-wing and handwing morphospaces. The whole-wing morphospace was represented by the landmarks in Fig. 2B, and the handwing morphospace was
represented by a subset of those landmarks outlining the handwing, from the wrist, around the wingtip, to the last primary flight feathers (circles in Fig. 2C). Wing area distribution data (calculated from polygons as presented in Fig. 2E) were analyzed using PCA using the base `prcomp()` function (R Core Team 2020). *Phytools* (Revell 2012) was used for discerning phylogenetic signal (`phylo.sig()`, Pagel’s lambda) and ancestral state estimation (discrete character: `reRootingMethod()`; continuous character: `contMap()`). The equal rates (ER) and symmetric rates (SYM) models were recommended for `reRootingMethod()` (Revell 2012), and they had an equivalent log likelihood for this dataset, so the ER model was used in this analysis. *Ape* (Paradis and Schliep 2019) was used for setting up the phylogenetic tree, and *geiger* (Harmon et al. 2008) was used for phylogenetic analysis of covariance (`aov.phylo()`, 1000 simulations, Wilks test). Phylogenetic analysis of covariance was done with the first six PCs for whole-wing morphospace data (90.9% total variance) and with the first three PCs for handwing morphospace data (91.3% total variance). Data were plotted with ggplot2 (Wickham 2016) and plotly (Sievert 2020), and phylomorphospaces were plotted using ggphylomorpho (Barr 2017). A few non-waterbird clades among our waterbird clades (Galliformes, Strisores, Columbaves, Inopinaves (=landbirds); following nomenclature of Prum et al. 2015) are either arboreal or ground-dwelling. These birds were excluded so they would not introduce non-waterbird behaviors to the analyses.

Convergence in whole-wing shape among waterbirds was tested by using the R package *convevol* (Stayton 2015). We used the function `convratsig()` to test whether identified sets of tip species have converged more strongly on a region of morphospace than would be expected from that of a simulated null distribution. We used convergence measure C1, representing the proportion of the maximum distance between focal taxa that has been closed by evolution. For several larger groups of species, we also used the function `convnumsig()` to test whether the frequency of lineages independently evolving into a certain region of morphospace is significantly different from a simulated null distribution.
(convergence measure C5). Both tests were run with 1000 simulations. The `convnumsig()` function requires the number of species selected for comparison within a given group to be larger than the number of variables, in this case, PCs. As such, only the first five PCs were used for `convnumsig()` to enable tests for clusters with six species or more. The `convratsig()` function does not have this restriction, allowing us to use ten PCs (~90% total variance) for clusters with 2-10 species and increase the robustness of the convergence analysis.

**Results**

Our geometric morphometric analysis provided new information on wing shape and wing functional metrics in waterbirds. We found that whole-wing aspect ratio, wing area, wing loading, and body mass, are all significantly influenced by phylogenetic relationships (Suppl. Table 3). Our phylogenetic comparative analyses showed that wing shape in waterbirds is significantly associated with ecological traits, such as foraging behavior and habitat, but not with migratory behaviors. Phylomorphospace analysis revealed a strong phylogenetic pattern of repeated convergence in wing shape across waterbird clades.

**Wing shape correlations with ecology and migration.**

Results show a wide range of wing shapes in waterbirds, from short, broad low aspect ratio wings in the rail *Rallus limicola* (*AR* = 1.8) to long, slender, high aspect ratio wings in the albatross *Phoebastria immutabilis* (*AR* = 5.8) (Figs. 4-8). Results show strong patterns of correlation between multiple wing metrics and ecological traits such as foraging behavior and habitat across the phylogeny of waterbirds. Some significant differences were found to be associated with taxonomic grouping as
well, but there was no significant association of waterbird wing shape functional metrics with migratory status. Below is a summary of the functional metrics and discussion of key variables. We present the complete analysis of functional metrics and their ecological and migratory associations in the supplemental materials.

Both low and high aspect ratio wings appear to have evolved at least five times independently (Fig 4B). The waterbirds with higher aspect ratio wings tend to be plunge divers and aerial hunters (Fig. 4, Suppl. Fig. 3C), although albatrosses with very high aspect ratio wings dabble (surface skim or head submerged tipping downward) when they forage (Fig. 4). Birds with lower aspect ratio wings tend to be probers and stalkers (Fig. 4, Suppl. Fig. 3C). Surface divers, ground foragers, and dabblers tend to have medium aspect ratio wings (Fig. 4, Suppl. Fig. 3C).

**Fig. 4 (A) Ancestral state estimation of waterbird foraging behavior. (B) Wing aspect ratio.**

Abbreviations: H, evolution of high aspect ratio wings, L, evolution of low aspect ratio wings.

Functional metrics plotted in morphospace suggest there exists significant overlap between major groups for foraging behavior and migration+location variables (Fig 5). The loadings in Fig. 5A and Suppl. Table 4 shows that AR, AR slope, and HWI are positively correlated and provide most of the influence for PC1. Wing area and wing loading are also positively correlated and mostly influence PC2. The top left (low on PC1 and high on PC2) has birds with low aspect ratio wings and a low HWI. Moving towards the higher PC1 are birds with high aspect ratio wings and a high HWI. Birds with low PC2 values do not have a notably different AR than the birds with higher PCs, but it seems there is a complex interaction with wing area and/or wing loading to bring the species to the lower PC 2 values.
Fig. 5 Morphospace of functional metrics: aspect ratio, AR slope, wing area (WA), wing loading (WL), and handwing index (HWI). A) colored by taxonomy and includes loading plot, B) colored by foraging behavior, C) colored by migration+location. Wing area and wing loading were corrected for size using Mosimann shape ratios, then all the variable distributions were standardized using z-scores before running the PCA. PCs 1-2 represent 91.9% of the total variance. Size of points indicates relative wing loading. Interactive plot in Suppl. Fig. 4.

Landmark-based morphospaces of waterbird wings

Whole-wing morphospace.—Whole-wing morphospace shows some clustering by clade, whereas ecological specializations distinguish species from a central cluster that includes species with various behaviors in various habitats (Fig. 6C-E). PC 1 and whole-wing aspect ratio are closely associated, boxplots following very similar trends for all phylogenetic and ecological categories (Suppl. Fig 3A-E, and Suppl. Fig. 5 A-E respectively; also Suppl. Fig 6A). This trend suggests that PC1 is driven largely by whole-wing aspect ratio, rather than body mass and wing loading traits (Suppl. Fig. 5F-J). PC2 is an axis influenced strongly by the relative size of the armwing to the handwing, curvature of the leading edge of the wing (straight or curved), pointedness of the wingtip (rounded or pointed), and coverage of the primary coverts (more proximal or more distal) (Suppl. Fig. 6B). The PC3 axis is influenced by coverage of the secondary coverts (anterior wing or extending to the trailing edge; Suppl. Fig. 6C) and the curvature of the leading edge.

Considering whole-wing phylomorphospace by taxonomic group, Anseriformes, Gaviiformes, Pelecaniformes, Podicipediformes, and Suliformes score low and Charadriiformes high on PC 2 (Fig. 6A-B). Gruiformes and Charadriiformes extend into lower PC 1 and PC 2 values, and Procellariiformes and Charadriiformes score high on PC 1 and PC 2 (Fig. 6A-B). Different flight styles feature major overlap, with only gliding/soaring birds limited to high PC 1 values (Fig. 6C). Foraging behavior is
significantly correlated with whole-wing shape space (phylo-MANOVA: Wilks statistic = 0.178, p-value = 0.0170, Suppl. Table 8). Aerial hunters and plunge divers are limited to higher PC 1 values, probing birds extend to lower PC 1 values, and the other foraging behaviors are more central (Fig. 6D). The major habitat groups also feature a lot of overlap in the central region of wing morphospace (Fig. 6E), with ocean, shoreline and a few marsh birds exhibiting higher PC 1 values. Marsh-dwelling birds also extend to lower PC 1 values. Migratory and continental birds occupy a huge range of wing morphospace (Fig. 6F, G), whereas oceanic birds (migratory and non-migratory) are limited to higher PC 1 values (Fig. 6G).

**Fig. 6** Whole-wing morphospace based on principal components (PC) 1 and 2, 71.7% of total variance. (A) Phylomorphospace with warp grids depicting wing shape at extremes of axes and wing shapes of selected specimens. Subsequent morphospaces are colored for (B) major clades, (C) flight style, (D) foraging behavior, (E) habitat, (F) migration, and (G) migration + location. Abbreviations: FF, forward/bounding flight, GS, gliding/soaring flight, HF, high-frequency flapping flight, UF, undulating flapping flight. PC scores in Suppl. Table 7. Interactive plot in Suppl. Fig. 7.
Wing area morphospace.—Like whole-wing morphospace, wing area morphospace shows a central cluster with some peripheral extensions. This analysis compares the distribution of the handwing to armwing areas, as well as the extent to which the dorsal greater coverts cover the wing surface. PC 1 (53.3%) represents the ratio between anterior and posterior armwing areas, with posterior armwing areas generating higher PC 1 values. PC 2 (34.4%) represents the change in relative wingtip area, with smaller wingtip areas generating higher PC 2 values.

Taxonomy provides the strongest separation between groups within wing area morphospace. Anseriformes, Gruiformes, Pelecaniformes and Podicipediformes compose the central cluster (Fig. 7A, B). Charadriiformes are present in the central cluster but also extend into areas of higher (gulls and terns) and lower (a couple jacanas) PC 1 values. Suliformes are split between average and low PC 1 values. Procellariiformes and Gaviiformes tend to have high PC1 values. There is no major pattern in shape space with regard to flight style, although undulating flappers expand to fill the morphospace (Fig. 7C). Considering foraging, aerial hunters have larger anterior than posterior wings with a range of wingtip sizes (Fig. 7D). Some surface divers and a few probers have large posterior wing areas, a wing shape feature not observed in birds characterized by other foraging behaviors. Ocean-dwelling birds tend to have the widest range in morphospace (Fig. 7E). The wing areas of other habitats largely overlap, although marsh-dwelling birds with small anterior and large posterior wing areas cluster together. Full migrants tend to have greater coverage of morphospace than non-migrants (Fig. 7F). Oceanic migrants tend to have larger anterior than posterior wings and exhibit a range of wingtip sizes (Fig. 7G). Most categories (except mixed migrant) have representatives with larger posterior than anterior wing areas.

Fig. 7 Wing-area morphospace based on principal components (PC) 1 and 2. (A)
Phylomorphospace with icons depicting extremes of morphospace and wing area distributions
of selected specimens. Subsequent morphospaces are colored for (B) major clades, (C) flight style, (D) foraging behavior, (E) habitat, (F) migration, and (G) migration + location.

Abbreviations: FF, forward/bounding flight, GS, gliding/soaring flight, HF, high-frequency flapping flight, UF, undulating flapping flight. PC scores available in Suppl. Table 9. Interactive plot in Suppl. Fig. 8.

Handwing morphospace.—Handwing morphospace shows some clustering among the variables (Fig. 8). PC 1 (69.0% of the variation) represents wing tip shape, and PC 2 (15.7% of the variation) records the location of the tip of the first secondary flight feather in relation to the wrist (inclined distally or proximally) and the curvature of the primary flight feathers (straight or curved trailing edge).

Phylogenetically, many of the same trends in the whole-wing morphospace are repeated in handwing morphospace (Fig. 8A, B). Gruiformes and Pelecaniformes tend to have lower PC 1 values, Anseriformes average, and Procellariiformes high PC 1 values. Charadriiformes shows the greatest range in handwing morphospace, and two suliform clusters are on either side of the plot with both high and low PC 1 values. For flight style, forward/bounding flapping flight and gliding/soaring birds overlap very little, though they overlap with the high-frequency flapping and undulating flapping birds (Fig. 8C). There is a lot of overlap within foraging behavior, aerial hunters and plunge divers tend towards the right and probing birds occupy the largest area of morphospace, and are the only ones expanding into the area with low PC 1 and PC 2 values (Fig. 8D). Foraging behavior has a significant relationship with handwing morphospace (phylo-MANOVA: Wilks statistic = 0.369, corrected p-value = 0.032, Suppl. Table 11). Habitat morphospace does not differentiate clusters. Unlike the other habitats, marsh-dwelling birds expand toward low PC 1 and PC 2 values. Habitat also shows a weakly significant relationship with handwing morphospace (phylo-MANOVA: Wilks statistic = 0.571, corrected p-value
There is little difference in migratory versus non-migratory birds in wing morphospace (Fig. 8F). Oceanic birds tend to have more pointed handwings than continental birds, which occupy a greater range in morphospace (Fig. 8G).

**Fig. 8** Handwing morphospace based on principal components (PC) 1 and 2. (A) Phylomorphospace with warp grids depicting extremes of axes and handwing outlines from selected specimens. Subsequent morphospaces are colored for (B) major clades, (C) flight style, (D) foraging behavior, (E) habitat, (F) migration, and (G) migration + location.

Abbreviations: FF, forward/bounding flight, GS, gliding/soaring flight, HF, high-frequency flapping flight, UF, undulating flapping flight. PC scores available in Suppl. Table 10. Interactive plot in Suppl. Fig. 9.

**Convergence in waterbird wing shape**

When tested with a phylogenetic framework, wing shapes in waterbirds converged at statistically significant levels multiple times. We found significant convergence in whole-wing phylomorphospace among groups of waterbirds with high and with low wing ARs, among clusters of waterbirds with similar foraging behaviors and habitats as well as clusters with a variety of foraging behaviors and habitats (Table 2).

**Table 2** Convergence testing in the eleven groups of waterbirds circled in Fig. 9. C1 represents the amount of convergence in wing shape within a given area of morphospace (1 = high, 0 = low) and whether this value is significant given the phylogenetic relationships of the group. C5 was restricted to clusters of more than 5 species and calculates the number of times lineages represented by the selected cluster invaded the area of morphospace and whether that number is significant with relation to the group’s phylogenetic relationships.
**Group 1:** Aramus guarauna, Jacana jacana, Jacana spinosa, Rallus elegans, Rallus limicola, Rallus longirostris; **Group 2:** Alca torda, Brachyramphus marmoratus, Cerorhinca monacera, Fulmarus glacialis, Gavia immer, Gavia pacifica, Gavia stellata, Larus marinus, Sula dactylatra, Sula leucogaster, Sula sula; **Group 3:** Aechmophorus clarkia, Dendrocygna bicolor, Egretta rufescens, Phalacrocorax auritus, Phalacrocorax carbo, Podilymbus podiceps; **Group 4:** Aechmophorus occidentalis, Branta bernicla, Pelecanus erythrorhynchos, Pelecanus occidentalis, Podiceps grisegena; **Group 5:** Aethia cristatella, Cygnus buccinator, Cygnus columbianus, Podiceps auritus, Podiceps nigricollis; **Group 6:** Fregata minor, Pterodroma externa, Puffinus pacificus, Sterna elegans; **Group 7:** Aythya valisineria, Bucephala clangula, Pelecanoides urinatrix; **Group 8:** Charadrius vociferus, Oceanodroma furcata; **Group 9:** Arenaria melanocephala, Clangula hyemalis; **Group 10:** Anhinga anhinga, Bubulcus ibis; **Group 11:** Aethia psittacula, Branta canadensis **Group 12:** Cerorhinca monacera, Sula sula.

Most of the groups in Table 2 (circled in Fig. 9) had significant C1 convergence in wing shape, indicating that the maximum phylogenetic distance represented by the clusters was greater than expected under the Brownian motion model of evolution. The larger groups (1-3) also featured highly significant C5 values, a statistic indicating that the selected organisms invaded that area of morphospace a greater number of times than would be expected under the Brownian motion model of evolution.

**Fig. 9** Testing wing shape convergence within whole-wing morphospace. Colored numbers refer to index of bird species in Suppl. Table 1. Large black numbers refer to group number in Table 2. Black lines indicate larger clusters for convergence testing with C1 and C5, magenta...
lines indicate smaller clusters for convergence testing with C1. Solid lines indicate significant results, dotted lines indicate insignificant results.

Overall, most groups tested here resulted in significant convergence in wing shape in multiple regions of morphospace. Clusters of species that occupied the regions of morphospace and share similar foraging behaviors and/or habitats had significant convergence (Groups 1, 2, 3, 6, 12). Regions with clusters of species featuring different foraging behaviors and habitats were also significantly convergent (Groups 4, 5, 7, 8, 11). We also located a few pairs that were close in morphospace, but were phylogenetically close enough such that they were not significant in terms of evolutionary convergence (Groups 9, 10): a ground-foraging turnstone and a surface-diving duck have 34.0% convergence on medium aspect ratio wings with a curved leading edge and pointed wings (Group 9: C1 p = 0.053, Table 2; Fig 9), and a surface-diving darter and a ground-foraging egret have 8.0% convergence on medium aspect ratio wings with pointed wingtips and a curved leading edge (Group 10: C1 p = 0.385, Table 2; Fig 9).

**Discussion**

The wings of waterbirds are highly diverse in size and shape. They show a broad range when scored for important functional metrics that characterize their functional diversity and evolutionary history. The central conclusion of this study is that important wing metrics such as aspect ratio, wing areas and wing loading are significantly associated with the trophic ecology and specific habitat traits in waterbird taxa. We also conclude that migratory behavior is not strongly correlated with wing shape in waterbirds from three major avian clades, despite a general correlation between handwing index and migratory behavior among birds (Dawideit et al. 2009; Sheard et al. 2020). Finally, we have identified
multiple regions of phylomorphospace showing convergence in waterbird wing shape. Thus, particular wing shapes appear to be well-suited for survival and reproduction in coastal and aquatic birds.

**Trends in waterbird wing shape and ecology**

Aspect ratio, a frequently used functional metric when studying flight function (Greenewalt 1962; Norberg 1990), is measured as a single- or double-wing variable, the latter two times the value of the former metric and calculated from the square of total wingspan tip-to-tip divided by sum of the area of both wings (Walker and Westneat 2002). The single-wing AR range among waterbirds (1.8-5.8) is similar to that in other broad-based avian datasets, such as Baliga et al. (2019; AR 1.7-5.4) and Wang and Clarke (2014; AR 2.5-8.1) for wider phylogenetic samples of birds, and those of bats (AR 2.2-4.3; Luo et al. 2019), insects (2.3-8.0; Bhat et al. 2019) and even fishes with flapping underwater flight (AR 1.9-4.3; Thorsen and Westneat 2005). The waterbird ecotypes with the highest aspect ratios are aerial hunters and plunge divers, while those with the lowest AR are the probers. Both procellariiforms and suliforms exhibit a wide range of aspect ratios for a wide range of ecological strategies. Most procellariiforms are ocean-dwelling aerial hunters. They are characterized by a broad range in aspect ratio and whole-wing shape space to accommodate a range of locomotor demands on the wing. Suliformes, in contrast, is divided into two distinct clusters, one with wings of medium aspect ratio (surface-diving cormorants) and another with wings of high aspect ratio (plunge-diving gannets). Procellariiforms exhibit a variety of wing shapes for a given foraging behavior, whereas suliforms have two distinct foraging behaviors and two disparate and extreme areas of wing shape space.

AR slope identifies procellariiforms as having the greatest range in wing shape change along the length of the wing. Some procellariiform wings (petrels) taper much faster than others (albatrosses), which may be related to the specific aerodynamic requirements for different foraging behaviors (aerial
hunting versus dabbling). Most other waterbird clades have a small range of AR slope (excluding charadriiform outliers), suggesting that wing taper is a relatively conservative trait in most birds.

Although the denominator in calculating aspect ratio, wing area can be plotted separately. Waterbirds that spend a lot of time flapping (either forward/bounding or high-frequency) have a narrow range of lesser wing area, suggesting that smaller wings may be an adaptation for less stressful, repetitive movement. Gliding/soaring birds and undulating flappers have a higher average and range of wing areas, underscoring the importance in higher wing area and its variation. Wing area did not differ significantly between gliding/soaring waterbirds and those with undulating flight, and so wingbeat frequency may have less influence over the wing area. No specific wing area seems optimal for any particular variable, as wing area morphospace overlap among variables is substantial. As an example, procellariiforms occupy a very localized region of wing area space, which may be the result of the constraints from aerial hunting or from the long bouts of flight required by their oceanic habitat (Warham 1977). On the other hand, the brent goose (Anseriformes: Branta bernicla) and sandhill crane (Gruiformes: Grus canadensis), which are relatively large birds with long necks that remain extended in flight and travel long distances during migration (Cornell Lab of Ornithology 2015), seem to converge on wing area distributions at the top of the wing area morphospace (Fig 7).

Wing loading is another key parameter yielding insight into the structure and function of wings for flight (Vágási et al. 2016). Wing loading is not tied to a particular wing shape (Suppl. Fig 10), but rather to the functional demands of the bird. Within a study examining European species, some birds are found to have a low wing loading that optimizes cost of transport for long distances, whereas other birds have high wing loading that optimizes speed at the cost of energy efficiency (Vágási et al. 2016). The birds with the highest wing loadings in our waterbird dataset are ducks, loons, and grebes, birds that forage by dabbling and surface diving in lakes/ponds and use high-frequency flapping to get aloft. Loons
and grebes are diving birds that have reduced skeletal pneumaticity to increase skeletal density (O’Connor 2009), which in turn increases wing loading during flight. In contrast, birds that glide and soar have greater skeletal pneumaticity (O’Connor 2009; Smith 2012), reducing body mass and thus wing loading.

Wing kinematics and wing morphing during flight affects wing loading (Taylor et al. 2012; Harvey et al. 2019), an important frontier in flight biomechanics. Although presented for uniformity in a single outstretched pose, avian wings have a number of components that may be adjusted during flight. Wing shape changes at different flight speeds (Lentink et al. 2007; Tobalske 2007). Feathers spread farther apart at slower flight speeds, increasing wing area and vice versa (Tobalske 2007). If one assumes a given bird has a constant body mass, the foregoing necessarily means that wing loading must vary with flight speed. In our study wing shape is static as in the studies we have extensively cited (Lockwood et al. 1998; Wang and Clarke 2015; Pigot et al. 2020). How wing shape varies during flight across birds is an intriguing question for future research.

**Wing shape and migration**

Most of the birds we sampled (120 species, 88%) are regarded as full migrants; only 15 species are logged as non-migrants and 1 as a partial migrant. We could not distinguish any patterns in wing shape that would distinguish migratory versus non-migratory waterbirds at this scale. The combination variable migration+location, however, shows weak significance with respect to handwing index (HWI), which is commonly used for wingtip shape (Wilks statistic = 7.278, p = 0.0510). The relationship between migratory behavior, morphology and physiology is complex (Piersma et al. 2005). Migratory patterns are known to vary within genera and sometimes within species (Berthold and Terrill 1991; Lockwood et al. 1998; Fernández and Lank 2007). For example, the rail genus *Rallus* includes the non-
migrant *Rallus longirostris* as well as the full migrants *R. elegans* and *R. limicola*. Likewise, the cormorant genus *Phalacrocorax* includes the non-migrants *P. brasili anus* and *P. urile*, the partial migrant (some populations migrate, some do not) *P. carbo*, and the full migrants *P. auritus* and *P. pelagicus*. Despite stark differences in migratory behavior, these birds occupy the same region of morphospace (Fig. 6).

Many aspects of avian biology and behavior influence wing shape, introducing some plasticity in shape at all taxonomic levels. For example, the wing shape of western sandpipers (*Calidris mauri*) varies depending on sex and maturity (Fernández and Lank 2007). Females migrate longer distances than males, and males have to perform aerial displays to attract the females. Therefore, the female wing is longer and more pointed than the wing in males. For rapid escape, immature sandpipers require shorter, rounder wings than adults. Two species of the finch genus *Carduelis* exhibit different wing shapes, the insular non-migrant Corsican finch (*C. corsicanus = C. citrinella corsicanus*) with more rounded wings than the migrant citril finch (*C. citrinella = C. citrinella citrinella*) from the mainland (Förschler et al. 2008; Gill et al. 2020). Although the wing shape differences between these finches match expectations given their migratory patterns, their daily locomotor needs may also explain this difference; the insular *C. corsicanus* must navigate dense foliage compared to its mainland counterpart (Förschler et al. 2008). Among our rail species in the genus *Rallus*, *R. longirostris* and *R. elegans* are similar in size and wing shape, but the former is non-migratory and the latter migratory (Cornell Lab of Ornithology 2015; BirdLife International 2020). Some birds alter migratory habits over the course of a few generations (Berthold and Terrill 1991). Our results suggest that migratory behavior is one factor among many that influence wing shape as shown in previous studies (Mönkkönen 1995; Baldwin et al. 2010; Huber et al. 2017).
**Evolutionary convergence across phylomorphospace**

Four general patterns emerge from our metric consideration of wing form across birds. First, phylomorphospace plots indicate the presence of a significant phylogenetic component to many aspects of avian wing morphology (Wang and Clarke 2015; Pigot et al. 2020). Thus, clade membership has some predictive value with regard to wing morphology.

Second, most sampled waterbirds cluster in the centroid of distribution for a range of wing metrics. These waterbirds are characterized by a wide range of locomotor, foraging and migratory behaviors and ecological habitats. Thus, the sweet spot of wing morphospace among waterbirds is occupied by distantly related taxa with disparate functional, behavioral and ecological traits. Similar to limb morphospace for disparate clades among rodents, outliers in morphospace are limited to extreme morphologies, such as the limbs of fossorial taxa (Hedrick et al. 2020).

Third, a few avian subgroups did plot in relatively extreme wing morphospace, such as the low aspect ratio wings of the probing jacanas and rails and the high aspect ratio wings of aerial and plunge diving specialists (terns, gannets and petrels). In these cases, therefore, wing morphology seems strongly linked to their specialized lifestyles, unlike the vast majority of birds occupying the center of morphospace where aerodynamic factors rather than disparate functional and ecological traits govern wing morphology.

Collectively, these conclusions highlight the prevalence of convergence in wing shape phylomorphospace across waterbirds. We identified and tested 12 likely instances of wing shape convergence. The selected clusters included areas with high and low AR wings in pairs and larger groups of taxa and sampled the majority of waterbird phylomorphospace. Ten out of twelve of these groups were highly significant examples of convergence on similar wing shape from distant ancestral starting points (Table 2). Convergence in form among flapping appendages is a major evolutionary
pattern in organisms as diverse as birds (Norberg 1986; Norberg 1990), bats (Norberg 1986), insects (Strauss 1990) and bony fish (Aiello et al. 2017).

Several of the convergent clusters share foraging behavior or habitat, supporting the hypothesis that there is an optimal wing shape for a given behavior or habitat. Jacanas (Charadriiformes), rails and the limpkin (Gruiformes) show an average of 62.5% convergence on very low aspect ratio wings with rounded wingtips and a slightly larger handwing than armwing (Group 1: C1 p = 0; Fig. 9, Table 2). The species in this cluster transitioned into this space six times, significantly more than would be expected by chance (C5 p = 0, Table 2). Loons (Gaviiformes) also appear to converge in wing shape with gannets and boobies (Suliformes: Sulidae) (Group 2: Fig. 9, Table 2) in a region of morphospace shared with a procellariiform (Fulmarus glacialis) and a few charadriiforms (Brachyramphus marmoratus, Cerorhinca monocerata, Larus marinus). This group averages 45.8% convergence on high aspect ratio wings with somewhat pointy wingtips, a relatively straight edge and a relatively larger armwing than handwing (C1 p = 0). The species in this cluster transitioned into this morphospace 10 times, significantly more than would be expected by chance (C5 p = 0.009, Table 2). Within this cluster, the charadriiform, the rhinoceros auklet (Cerorhinca monocerata), and red-footed booby (Sula sula) share 39.1% convergence (Group 12: C1 p = 0.047, Table 2; Fig. 9). Another cluster of waterbirds with high aspect ratio wings (Group 6: frigatebird, petrel, shearwater, tern) averaged 55.4% convergence (C1 p = 0, Fig. 9).

Other convergent clusters are composed of waterbirds with a range of behaviors and habitats, suggesting wing shapes may be employed in multiple behaviors and habitats with only extreme wing shapes tied to extreme behaviors and habitats. For example, two pelecaniforms (Pelecanus erythrorhynchos, Pelecanus occidentalis), an anseriform (Branta bernicla), and two podicipediforms (Aechmophorus occidentalis, Podiceps grisegena) averaged 45.8% convergence on medium aspect ratio
wings with rounded wingtips and a much larger armwing than handwing (Group 4: C1 p = 0, Table 2; Fig 9). Swans, an auklet, and grebes averaged 50.1% convergence on medium aspect ratio wings with a straighter leading edge, a slightly rounded wingtip, and slightly larger armwings than handwings (Group 5: C1 p = 0, Table 2; Fig 9). Two anseriforms (Aythya valisineria and Bucephala clangula) and a procellariiform (Pelecanoides urinatrix) averaged 33.5% convergence on medium aspect ratio wings with slightly pointed wingtips and a comparatively similar handwing to armwing (Group 7: C1 p = 0.018, Table 2; Fig 9). A ground-foraging charadiiform (Charadrius vociferus) and an aerial-hunting procellariiform (Oceanodroma furcata) averaged 49.5% convergence on medium aspect ratio wings with very pointed tips and a much larger handwing than armwing (Group 8: C1 p = 0.011, Table 2; Fig 9).

Table 3 'Group 4' waterbirds showing convergence in wing morphospace.

| Group 4 Waterbirds | Convergence |
|-------------------|-------------|
| Pelicans (Pelecanus) | 49.5% convergence |
| Grebes (Aechmophorus occidentalis, Podiceps grisegena) | 49.5% convergence |
| Brent goose (Branta bernicla) | 49.5% convergence |

Abbreviations: **Taxonomy** Pod., Podicipediformes, Ans., Anseriformes, Pel., Pelecaniformes. **Flight Style** HF, High-frequency flapping, FF, forward/bounding flight, GS, gliding/soaring flight.

Group 4 waterbirds (Table 3), which include two pelicans (Pelecanus), two grebes (Aechmophorus occidentalis, Podiceps grisegena) and the brent goose (Branta bernicla), differ markedly in behavior, habitat and overall morphology. This disparate cluster of species is an example of convergence with no basis in the ecological or functional variables examined in this study. The pelicans glide and soar, the grebes use high-frequency flapping, and the brent goose employs forward/bounding flapping flight. Regarding foraging behaviors, the pelicans plunge (P. occidentalis) and surface dive (P. erythrorhynchos), the grebes surface dive, and the brent goose dabbles. Regarding habitats, pelicans live
near lakes and ponds (*P. erythrorhynchos*) and oceans (*P. occidentalis*), the grebes live near lakes and ponds, and the brent goose prefers marshes. In size they range from medium to the high end of body mass range (1-5 kg). Birds with similar wing loading are present across wing morphospace (Suppl. Fig. 8).

Very few regions of whole-wing morphospace are truly dominated by a specific behavior or habitat. The highest aspect ratio wings characterize oceanic birds that glide and soar, and the lowest aspect ratio wings are found in birds that hunt from the ground in more enclosed habitats. In between these extremes, wing shapes have evolved convergently and are used in a variety of behaviors and habitats. It appears waterbirds are broadly adapted to more open habitats with wing shapes that serve multiple lifestyles and at least partially overlap in morphospace with birds in terrestrial habitats (Wang and Clarke 2015).

**Conclusions**

Avian wings are appendages of great functional importance to birds and show great shape diversity, ranging from those of high to low aspect ratio and those with rounded or pointed wingtips. Yet it has proved challenging to find significant and regular correlation across birds between wing shape and flight style or various ecological traits. In this study, we examined multiple functional and ecological variables, determining that wing shape and foraging behavior are significantly correlated in waterbirds. In contrast, flight style, habitat and migratory status are not correlated, although combining migratory status and location (continental vs. oceanic) shows weak correlation. Phylogenetic signal, as shown in previous studies, is prevalent, such that wing shape within clades exhibited similarity. Nevertheless, the central morphospace for most traits shows broad overlap of unrelated taxa. This work highlights the complexity in correlating wing shape to aerodynamic performance as well as a number of non-aerodynamic variables. The current study and its forerunners are based on static (spread) wing shape,
leaving open for future research considering wing shape as a dynamic variable that changes with flight speed.

**Data Availability Statement**

The wing image data underlying this article were provided by the Wing and Tail Image Collection hosted by University of Puget Sound's Slater Museum of Natural History at https://digitalcollections.pugetsound.edu/digital/collection/slaterwing, and the derived data is available in the article and in its online supplementary material.

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Declaration of Competing Interest

The authors declare no competing interests.

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| Symbol | Definition                        | Symbol | Definition                        |
|--------|----------------------------------|--------|----------------------------------|
| $AR$   | aspect ratio                     | $l$    | length                           |
| $b$    | wingspan, wingspread             | $l_{aw}$| armwing length                   |
| $c$    | wing chord                       | $l_{hw}$| handwing length                  |
| $\overline{c}$ | mean wing chord                     | $l_w$  | wing length                      |
| $g$    | acceleration of gravity          | $M$    | body mass                        |
| $Mg$   | body weight                      | $m_w$  | mass of one wing                 |
| $S_w$  | area of one wing                 | $T_i$  | wingtip-shape index              |
| $\overline{c}l_w$ | mean wing chord                  | $S$    | airfoil or wing area             |
| $S_{aw}$ | armwing area                     | $S_{hw}$| handwing area                    |
| $WCL$  | wing loading                     | $T_l$  | wingtip-length ratio             |
| $T_s$  | wingtip-area ratio               |        |                                  |

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Table 2 Convergence testing in the eleven groups of waterbirds circled in Fig. 9. C1 represents the amount of convergence in wing shape within a given area of morphospace (1 = high, 0 = low) and whether this value is significant given the phylogenetic relationships of the group. C5 was restricted to clusters of more than 5 species and calculates the number of times lineages represented by the selected cluster invaded the area of morphospace and whether that number is significant with relation to the group’s phylogenetic relationships.

| Group No. | C1 Obs. C | P-value | C5 Obs. C | P-value |
|-----------|-----------|---------|-----------|---------|
| 1         | 0.625     | < 0.001 | 6         | < 0.001 |
| 2         | 0.458     | < 0.001 | 10        | 0.009   |
| 3         | 0.625     | < 0.001 | 6         | < 0.001 |
| 4         | 0.489     | < 0.001 | ---       | ---     |
| 5         | 0.501     | < 0.001 | ---       | ---     |
| 6         | 0.554     | < 0.001 | ---       | ---     |
| 7         | 0.335     | 0.018   | ---       | ---     |
| 8         | 0.495     | 0.011   | ---       | ---     |
| 9         | 0.340     | 0.053   | ---       | ---     |
| 10        | 0.080     | 0.385   | ---       | ---     |
| 11        | 0.458     | 0.011   | ---       | ---     |
| 12        | 0.391     | 0.047   | ---       | ---     |

**Group 1:** Aramus guarauna, Jacana jacana, Jacana spinosa, Rallus elegans, Rallus limicola, Rallus longirostris; **Group 2:** Alca torda, Brachyramphus marmoratus, Cerorhinca monocerata, Fulmarus glacialis, Gavia immer, Gavia pacifica, Gavia stellata, Larus marinus, Sula dactylatra, Sula leucogaster, Sula sula; **Group 3:** Aechmophorus clarkia, Dendrocygna bicolor, Egretta rufescens, Phalacrocorax auritus, Phalacrocorax carbo, Podilymbus podiceps; **Group 4:** Aechmophorus occidentalis, Branta bernicla, Pelecanus erythrorhynchos, Pelecanus occidentalis, Podiceps grisegena; **Group 5:** Aethia cristatella, Cygnus buccinator, Cygnus columbianus, Podiceps auritus, Podiceps nigricollis; **Group 6:** Fregata minor, Pterodroma externa, Puffinus pacificus, Sterna
elegans; **Group 7:** *Aythya valisineria, Bucephala clangula, Pelecanoides urinatrix;*

**Group 8:** *Charadrius vociferus, Oceanodroma furcata; Group 9:** *Arenaria melanocephala, Clangula hyemalis; Group 10:** *Anhinga anhinga, Bubulcus ibis; Group 11:** *Aethia psittacula, Branta canadensis* **Group 12:** *Cerorhinca monocerata, Sula sula.*
Table 3 'Group 4' waterbirds showing convergence in wing morphospace.

| Species                     | Taxonomy | Flight Style | Foraging Behavior | Habitat     | Body Mass (kg) | Aspect Ratio | Wing loading (N m⁻²) |
|-----------------------------|----------|--------------|-------------------|-------------|----------------|--------------|---------------------|
| *Pelecanus erythrorhynchos* | Pel.     | GS           | Surface dive      | Lake/Pond   | 4.970          | 2.1          | 87.4                |
| *Pelecanus occidentalis*    | Pel.     | GS           | Plunge dive       | Ocean       | 3.702          | 2.4          | 81.8                |
| *Aechmophorus occidentalis* | Pod.     | HF           | Surface dive      | Lake/Pond   | 1.429          | 1.6          | 203.5               |
| *Podiceps grisegena*        | Pod.     | HF           | Surface dive      | Lake/Pond   | 1.023          | 3.3          | 167.2               |
| *Branta bernicla*           | Ans.     | FF           | Dabble            | Marsh       | 1.370          | 1.7          | 153.7               |

Abbreviations: **Taxonomy**: Pod., Podicipediformes, Ans., Anseriformes, Pel.,

**Pelecaniformes**. **Flight Style**: HF, High-frequency flapping, FF, forward/bounding flight, GS, gliding/soaring flight.