Integrative and Comparative Biology

Integrative and Comparative Biology, volume 62, number 4, pp. 878–889
https://doi.org/10.1093/icb/icac117

Society for Integrative and Comparative Biology

SYMPOSIUM

High Wing-Loading Correlates with Dive Performance in Birds, Suggesting a Strategy to Reduce Buoyancy

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From the symposium "Lesser known transitions: organismal form and function across abiotic gradients" presented at the annual meeting of the Society for Integrative and Comparative Biology virtual annual meeting, January 3–February 28, 2022.

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Synopsis Diving birds are regarded as a classic example of morphological convergence. Divers tend to have small wings extending from rotund bodies, requiring many volant species to fly with rapid wingbeats, and rendering others flightless. The high wing-loading of diving birds is frequently associated with the challenge of using forelimbs adapted for flight for locomotion in a "draggier" fluid, but this does not explain why species that rely exclusively on their feet to dive should have relatively small wings, as well. Therefore, others have hypothesized that ecological factors shared by wing-propelled and foot-propelled diving birds drive the evolution of high wing-loading. Following a reexamination of the aquatic habits of birds, we tested between hypotheses seeking to explain high wing-loading in divers using new comparative data and phylogenetically informed analyses. We found little evidence that wing-propelled diving selects for small wings, as wing-propelled and foot-propelled species share similar wing-loadings. Instead, our results suggest that selection to reduce buoyancy has driven high wing-loading in divers, offering insights for the development of bird-like aquatic robots.

Introduction

Diving, wherein air-breathing animals submerge in water, is a widespread and diverse strategy in birds. Diving birds occupy all continents and oceans, exploit marine, estuarine, and freshwater systems, and dive to forage on benthic, planktonic, and nektonic prey, as well as to escape predators (Simmons and Cramp 1977; Marchant and Higgins 1991; Billerman et al. 2020). Diving birds also vary markedly in their methods of hydrodynamic propulsion (Lovvorn 1991; Wilson et al. 1992; see also Supplementary Tables S3 and S4). The penguins (Sphenisciformes), diving petrels (Procellariiformes, *Pelecanoides* spp.), and alcids (Charadriiformes, Alcidae) rely on their wings to dive, as do a few Passeriformes (Cinclidae). Grebes (Podicipediformes, Podicipedidae), loons (Gaviiformes, Gaviidae), cormorants (Suliformes, Phalacrocoracidae), and others rely on their feet in water. And some groups—including many shearwaters (Procellariiformes, Procellaridae), sulids (Suliformes, Sulidae), and a subset of the ducks (Anseriformes, Anatidae)—adopt a mixed strategy, frequently using both the wings and feet to accomplish submerged aquatic locomotion.

Water is roughly 800 times more dense and 60 times more viscous than air (Denny 1993; Vogel 1994). Consequently, birds face distinct force systems depending on their fluid surroundings (Rayner 1986; Pennycuick 1987a; Ropert-Coudert et al. 2003). In air, the downward pull of gravity is ever-present and is responsible for a significant portion of the energy required for aerial and terrestrial locomotion (Kram and Taylor 1990; Tobalske 2007). In water, owing to its greater density, the upward pull of buoyancy experienced by a diving bird subjugates the downward pull of gravity at most depths they experience (Lovvorn and Jones 1991; Wilson et al. 1992; Ribak 2004), and the energy

Advance Access publication July 9, 2022

required to counteract buoyancy dominates total dive costs (Lovvorn et al. 1991; Stephenson 1994). Though volant diving birds swim slower than they fly in air (e.g., Kikuchi et al. 2015; Lapsansky et al. 2020), the resistance imposed by water, which must be counteracted by the wings and/or feet for locomotion to occur, is also substantially greater in water than in air (∼four-fold, assuming equivalent Reynolds numbers; Vogel 1994).

Among volant diving birds, wing-propelled divers (e.g., puffins, dippers) face the unique challenge of using the same locomotor system for locomotion in both air and water, despite the distinct properties of these two fluids (Rayner 1986; Pennycuick 1987a). Wing-propelled divers tend to have small wings for their body sizes (Greenewalt 1975; Warham 1977; Pennycuick 1987a, 1987b; Rayner 1988; Norberg 1990; Hertel and Ballance 1999; Elliott et al. 2013; Taylor and Thomas 2014). Accordingly, previous authors have hypothesized that the use of the wings for hydrodynamic propulsion specifically favors high wing-loading—defined as the ratio of body mass versus wing area—due to the greater resistance imposed by water relative to air on flapping wings (e.g., Pennycuick 1987b; Rayner 1988; Norberg 1990). In short, the fluid resistance on a wing is proportional to the size of that wing. Counteracting greater resistance during flapping requires greater forces and metabolic energy (Ellington 1984a). Thus, selection may favor relatively small wings in wing-propelled divers to reduce the forces and/or energy required to drive the wings and locomote in water (Rayner 1986; Pennycuick 1987b; Thaxter et al. 2010; Elliott et al. 2013). As low wing-loading affords more economical flight (Rayner 1988; Norberg 1990), especially at low speeds, selection for wing-propelled diving has been implicated in the high flight speeds and poor maneuverability in air of many wing-propelled divers (Cody 1973; Warham 1977; Pennycuick 1987a, 1987b; Rayner 1988; Norberg 1990), high energy costs of flight (Thaxter et al. 2010; Elliott et al. 2013), and the evolution of flightlessness (Simpson 1946; Storer 1960; Bock and von Wahlert 1965; Pennycuick 1987a, 1987b).

However, contrary to this line of reasoning, murres and puffins do not exhibit improved dive performance during their simultaneous molt, when they have significantly reduced wing areas (Bridge 2004). Further, many exclusively foot-propelled divers also have relatively high wing-loading (Rayner 1988; Norberg 1990), despite not using their wings for hydrodynamic propulsion except in rare circumstances (Townsend 1924; Clifton and Biewener 2018; Lapsansky and Armstrong 2022). Rayner (1988) suggested that, because wing- and foot-propelled divers share aquatic habits, some common feature of this environment may drive selection for their proportionally small wings, but also that high wing-loading in some foot-propelled species could be due to selection favoring fast flight. Alternatively, Lovvorn and Jones (1994) proposed that high wing-loading in foot-propelled divers could be the result of relaxed selection for slow flight or maneuvering performance. Life on water provides a "runway" for landings and take-offs, with few obstacles, reducing the time spent at low flight speeds and the importance of maneuverability during these phases of flight (Norberg 1990). Likewise, while most birds must outfly their aerial predators to escape, divers can submerge to avoid capture. Thus, relaxed selection for slow flight and high aerial maneuverability would allow foot-propelled divers to exhibit low-area, pointed wings for fast flight (Lovvorn and Jones 1994). As these life-history features are shared by wing-propelled divers, this hypothesis was later extended as an explanation for high wing-loading across diving methods (Kovacs and Meyers 2000; Bridge 2004). Finally, Wilson et al. (1992) and Taylor and Thomas (2014) suggested that high wing-loading may have co-evolved with diving because the air trapped among and within the wing feathers adds buoyancy (Stephenson et al. 1989). As the energy required to counteract buoyancy during diving is substantial (Lovvorn et al. 1991; Stephenson 1994), a reliance on diving may favor proportionally small wings as a means to lower buoyancy costs, analogous to the reduction of bone pneumaticity frequently documented in divers (O'Connor 2004; Smith 2012; Smith et al. 2021).

Of course, species-specific life-history traits may cause deviations from general trends. For example, species which nest in trees (e.g., Marbled murrelets [*Brachyramphus marmoratus*]) may have relatively low wing-loadings to enable greater maneuverability in slow flight. Similarly, species that rapidly migrate may have more pointed wings for fast flight. However, elucidating general trends has the potential to expand the understanding of the factors behind the repeated evolution of flightlessness in diving birds (Thaxter et al. 2010; Elliott et al. 2013) and inform the development of dual-medium engineered systems (Lock et al. 2013; Siddall and Kovač 2014; Low et al. 2015).

Previous comparative studies have noted higher wing-loadings in wing-propelled divers than in other birds, often including foot-propelled divers, implicating hydrodynamic drag on the flapping wing as a driver of high wing-loading. However, these studies considered only a subset of extant diving groups (Raikow 1973; Greenewalt 1975; Warham 1977; Pennycuick 1987a, 1987b) or did not account for phylogenetic effects (Rayner 1988; Norberg 1990; Elliott et al. 2013).

Our goal herein is to test among the multiple hypotheses seeking to identify the evolutionary pressures driving high wing-loading in diving birds. We used phylogenetic comparative methods to analyze newly collected data describing the shape and size of 2,324 wings from 951 species of birds. If hydrodynamic resistance has driven relatively small wings in wing-propelled divers, then we would predict wing-propelled divers to have higher wing-loadings than both non-diving and exclusively foot-propelled divers (Pennycuick 1987a, 1987b; Rayner 1988; Elliott et al. 2013). Instead, if some common feature of the aquatic environment drives relatively small wings (Rayner 1988), then divers are predicted to share similar wing-loadings regardless of their method of propulsion. Pointed wings across divers would support the hypotheses introduced by Rayner (1988) and Lovvorn and Jones (1994) that the wings of divers are shaped by selection for high flight speeds or relaxed selection for slow flight performance, respectively. Diversity in wing pointedness among divers would suggest an alternative explanation—potentially selection to reduce buoyancy (Wilson et al. 1992; Taylor and Thomas 2014)—for high wing-loading in diving birds.

Previous comparative studies attempting to link morphological traits to diving behavior vary widely in their behavioral classifications. Moreover, the questions of which birds dive and how they propel themselves in water are themselves the topics of historical and active discussion (Townsend 1909, 1924; Forbush 1922; Kelso 1922, 1926; Albores-Barajas et al. 2011; Fournier and Krementz 2018; Abourachid et al. 2019), and previous reviews of aquatic locomotor behavior include only subsets of avian species (Ashmole 1971; Lovvorn 1991; Wilson et al. 1992). To avoid misclassifying species, and to facilitate future research, we reevaluated the aquatic habits of all avian groups through an exhaustive survey of published literature and video evidence in addition to hypothesis testing.

Methods

Data collection

We measured wing shape and size of 2,324 wings from 951 species from specimens in four museum collections: the Burke Museum of Natural History and Culture, the Slater Museum of Natural History, the Museum of Vertebrate Zoology at the University of California, Berkley, and the Beaty Biodiversity Museum. Only wings of females were used in this study, both to reduce intraspecific variation, and because sexual dimorphism may co-vary with diving behavior among species.

The bulk of the wing data (>95%) are from the spread wing collection at the Burke Museum. At the Burke Museum, spread wings were photographed using a Canon EOS Rebel T2i digital camera (Canon Inc., Tokyo, Japan) attached to a Beleser CS-20 Copystand (Charles Beseler Company, Stroudsburg, Pennsylvania, USA). At the start of each data collection period (day start and between height adjustments), the camera was set to a fixed height, leveled using a circular plastic spirit level, and a photograph of a stainless-steel ruler (Westcott R590-12, Acme United Corporation, Naugatuck, Connecticut, USA) was taken to determine the scale for all following photographs. We obtained data for additional volant species from the Slater Museum of Natural History's digital wing and tail image collection. Photographs from the Slater Museums digital collection are cropped according to the size of the wing, but a standard scale bar is included within all wing photographs, allowing us to determine the scale for each wing individually. In addition to data from three species of penguins prepared as spread wings, data for seven penguin species are from study skins at the Beaty Biodiversity Museum and the Museum of Vertebrate Morphology. In both cases, the animals were positioned horizontally and photographed by museum staff via tripod-mounted and leveled cameras. A ruler was placed along the wing, allowing us to determine the scale for each wing individually.

Wing photographs were aligned to a consistent orientation in Adobe Photoshop CC (Adobe Inc., San Jose, California, USA). We first reflected left wings using the "Flip" tool and then rotated all photographs such that the leading edge and root of each wing were on the left and bottom of each image, respectively. We then adjusted each wing such that the anterior-most point of the wrist joint was aligned over the presumed position of the humeral head by drawing a line between these two points with the "Straighten" tool. We then cropped each photograph to remove pixels lower than the presumed position of the humeral head.

The wing area (S, cm^2), second moment of area (S_2, cm^4), and dimensionless second moment of area ($\widehat{S_2}$, Ellington 1984b) were calculated from aligned photographs of each wing using a custom MATLAB script. The script isolated the wing from the background via K-means clustering implemented using the MATLAB function "imsegkmeans." Wing area (S, cm^2) was calculated as total area filled by the wing, not including the area between emarginate feathers. To assess wing pointedness, we segmented the wing into strips 1 pixel in height and calculated second moment of area (cm^4) and dimensionless second moment of area from the wing root. Following Ellington (1984b), second moment of wing area is defined as:

$$S_2 = \sum_{r=0}^{R} cr^2 \Delta r, \tag{1}$$

where R = wing length, r = radial position along the wing, and c = wing chord at r, and dimensionless second moment of area is defined as:

$$\widehat{S_2} = \frac{S_2}{SR^2}. \quad (2)$$

Species averages were used in all analyses. Many specimens lacked body mass data, and specimens in museum collections may be emaciated. Thus, we used body masses from Dunning (2008).

We used species mean dive duration as a metric of dive performance (Watanuki and Burger 1999; Halsey et al. 2006). We collated mean dive durations for 124 species from the literature and measured mean dive duration for 3 species of dippers (*Cinclus*) from videos available in the Macaulay Library at the Cornell Lab of Ornithology (Supplementary Fig. S1). For dippers, we determined the duration of all dives as the number of frames between submergence and emergence of the head divided by the frame rate of the video, using Adobe Premiere Pro (Adobe Inc., San Jose, CA, USA) to scrub through each video frame-by-frame.

Phylogenetic comparative methods

Statistical analyses were performed in R version 4.1.3 (R Foundation for Statistical Computing, Vienna, Austria). We used the R package *evomap* for testing among hypotheses (Smaers and Rohlf 2016). This package provides a method to test for statistical differences in both the scaling coefficient (Y-intercept of a log-linear scaling regression) and scaling exponent (slope in a log-linear scaling regression) of an allometric relationship among groups (Glazier 2021). Using *evomap*, we first tested for differences in the scaling coefficients among groups while assuming that groups share the same scaling exponent. For example, we tested whether there was statistical support for unique scaling coefficients in the relationship of wing area versus body mass between wing-propelled divers and all other volant birds while assuming the two groups share the same scaling exponent, estimated by *evomap* for a given phylogenetic tree. In other words, assuming wing area scales in wing-propelled divers as it does in other volant birds, we tested if wing-propelled divers have relatively small wings. Finding a significant difference in scaling coefficients among groups, we then explored whether there was also statistical support for unique scaling exponents among groups, which would indicate unique relationships between body mass and a given wing parameter among groups. All morphological data were log-transformed prior to hypothesis testing to linearize the data (Glazier 2021).

To account for the relationships among species and phylogenetic uncertainty, all tests were conducted across 200 phylogenetic trees downloaded from birdtree.org (Jetz et al. 2012; Jetz et al. 2014), with 100 trees based on the Hackett backbone (Hackett et al. 2008) and 100 trees based on the Ericson backbone (Ericson et al. 2006). Rabosky (2015) highlighted issues with birdtree.org's method of obtaining "complete species trees," wherein species without genetic data are stochastically added to each tree (Rabosky 2015). At the same time, to exclude species without genetic data could potentially bias results, as species may be sampled non-randomly for DNA (Upham et al. 2019). Thus, we followed the recommendation of Upham et al. (2019) by also computing statistical tests using the subset of species with genetic data (again across 200 trees) (Upham et al. 2019). We report average test statistics and P-values for statistical tests from these 400 comparisons in the "Results" section of the main text, but results for each backbone (Ericson and Hackett) and species set (*All species* & *Species with genetic data*) are reported separately within the Supplementary Materials (Supplementary Tables S1, S2, and S5–S11).

Presently, the methods in *evomap* assume a Brownian motion (BM) model of evolution (Smaers and Rohlf 2016). Thus, we used the function "phylosig" available in *phytools* to calculate Blomberg's K (Blomberg et al. 2003) and Pagel's λ (Pagel 1999) for all morphological parameters to assess the degree of phylogenetic signal and the validity of this assumption (Revell 2012). A Blomberg's $K < 1$ indicates that relatives resemble each other less than expected under BM, while Blomberg's $K > 1$ indicate that relatives resemble each other more than expected under BM (Kamilar and Cooper 2013). Pagel's λ varies from 0 to 1, with Pagel's $\lambda = 0$ indicating that values of traits are unrelated to the relationships between species and Pagel's $\lambda = 1$ indicating that traits have evolved consistent with BM (Kamilar and Cooper 2013). In all cases, values of phylogenetic signal were close to 1 (Supplementary Tables S1 and S2), indicating that an assumption of BM is reasonable.

Both wing area and dive duration scale with body mass (Norberg 1990; Halsey et al. 2006). To test for a relationship between wing area and dive duration, we first used the "lm" function in base R to determine the relationship between each of these parameters and body mass. We then used the "pgls" function in *caper* to test for a significant correlation between the residuals of these relationships across our 400 phylogenetic trees (Orme et al. 2018). Residuals of the wing area versus body mass relationship were inverted for visualization purposes (Supplementary Fig. S1).

Behavioral classification

To classify the aquatic habits of birds, we started by examining two multi-volume handbooks (Marchant and Higgins 1991; Billerman et al. 2020) and reviews of seabird foraging ecology (e.g., Ashmole 1971; Ainley et al. 1984; Harper et al. 1985; Croxall 1987; Lovvorn 1991; Wilson et al. 1992). All references to aquatic locomotor behavior were traced to primary sources wherever possible so as not to perpetuate incorrect or "hopeful" classifications. In addition to literature references, we reviewed videos and photographs for all groups through publicly available repositories (Macaulay Library at the Cornell Lab of Ornithology, YouTube, Vimeo, etc.), and provide references to recorded evidence of diving behavior for nearly all diving groups. Both forms of reference are available as Supplementary Material (Supplementary Table S4). These literature and visual references are not exhaustive. Instead, they are meant to serve as verification of diving behavior and as launchpads for further inquiry.

For hypothesis testing, we defined diving as the complete submergence in water with the goal of acquiring food. We chose this definition because our literature review and personal observations indicate that any avian species can swim on and in water if compelled (Lapsansky and Tobalske 2021). Some species, including those species that otherwise do not strongly associate with water (e.g., *Passer domesticus*), will swim or dive on their own volition to escape predators (Sutton 1925; Ingram and Salmon 1942; Sordahl 1982; Hayes and Bennett 1985; Morgan 1994; Willis 1994; Blokhin 2004; Lapsansky and Tobalske 2021), especially when injured (Townsend 1909, 1924; Forbush 1922; Kelso 1926). Whether selection for improved performance and/or efficiency of escape diving has had an appreciable impact on the morphology and/or physiology of bird populations is unknown, as these behaviors are likely rare and may be reserved to specific age classes (Sutton 1925; Ingram and Salmon 1942; Sordahl 1982; Hayes and Bennett 1985; Morgan 1994; Willis 1994).

For species that dive for food, however, dive efficiency—the metabolic energy required to dive per unit time or distance—is likely important in determining fitness. More efficient underwater locomotion not only results in a greater ratio of energy gained to energy invested, but also slows the use of limited oxygen stores, allowing deeper dives to access to greater food resources, and longer dive durations, which will minimize accumulated transit time (non-feeding diving and ascending). Thus, all species which regularly dive for food are expected to possess adaptations for improved dive efficiency.

Of those birds that dive for food, significant variation exists among and within orders, families, and genera. We classified species reliant on diving to acquire food as *obligate divers*, whereas we classified species that dive for food only on rare occasions as *facultative submergers*. Groups are categorized as obligate divers if diving constitutes a major foraging mode and can therefore be readily documented or observed. Thus, this category should be viewed as exclusive to those species for which diving is of major importance. Groups are classed as facultative submergers if documentation of diving for food is broadly considered rare and documented dives are infrequent and shallow (e.g., Briggs 1978; Brodsky and Weatherhead 1985; Oldham 1919; Taylor 2008). For both groups, selection should favor morphological traits and locomotor patterns that increase dive efficiency, but the strength of selection on facultative submergers is especially difficult to estimate. On one extreme, facultative submerging may provide individuals with the resources necessary to survive harsh conditions (Cottam 1945; Bourget and Chapdelaine 1975; Brodsky and Weatherhead 1985), while, on the other, submerging may be one of many ways in which to acquire the same resource (Miller 1983). As well, facultative submerging may be specific to populations or even individuals, which will complicate comparative studies attempting to identify adaptations for increased dive efficiency and performance, as the behavior of most museum specimens is unknown.

Thus, for the statistical analyses conducted here, only obligate divers (Supplementary Table S3) were categorized as "diving." Species that plunge dive, but do not use their appendages to descend further in the water column (e.g., kingfishers, ospreys), were also categorized as "non-diving" for our statistical analyses, as these species may not face the selective pressures shared by species which use their limbs to descend in water (e.g., buoyancy minimization, wing-drag minimization, etc.). Thus, our statistical analyses consider divers as a conservative group, which should increase the likelihood of identifying traits linked to aquatic locomotor behavior.

Based on literature and visual evidence, we categorized groups in Supplementary Table S3 according to their method of thrust production on and in water (foot-propelled [FP] and/or wing-propelled [WP]) during steady-state swimming (i.e., not during turning, escapes, or when injured). Importantly, we considered FP and WP as separate binary states, and species which use both the wings and feet for aquatic locomotion may not do so for all dives. For example, eiders (genera *Polysticta* and *Somateria*) and scoters (genus *Melanitta*) regularly dive both by wing + foot-propulsion and by foot-propulsion alone (Heath et al. 2006; Richman and

Table 1 Example species, method of thrust production in water during steady-state swimming, reliance on diving as a foraging technique, and categorization for statistical testing.

Species	Foot-propelled (FP)	Wing-propelled (FP)	Reliance	Statistical Categorization
Surf Scoter (*M. perspicillata*)	1	1	Obligate	Wing-propelled
Pied-billed Grebe (*P. podiceps*)	1	0	Obligate	Foot-propelled (Exc.)
Common Murre (*U. aalge*)	0	1	Obligate	Wing-propelled (Exc.)
Southern Giant Petrel (*M. giganteus*)	1	1	Facultative	Non-diving
Cooper’s Hawk (*A. cooperii*)	0	0	NA	Non-diving

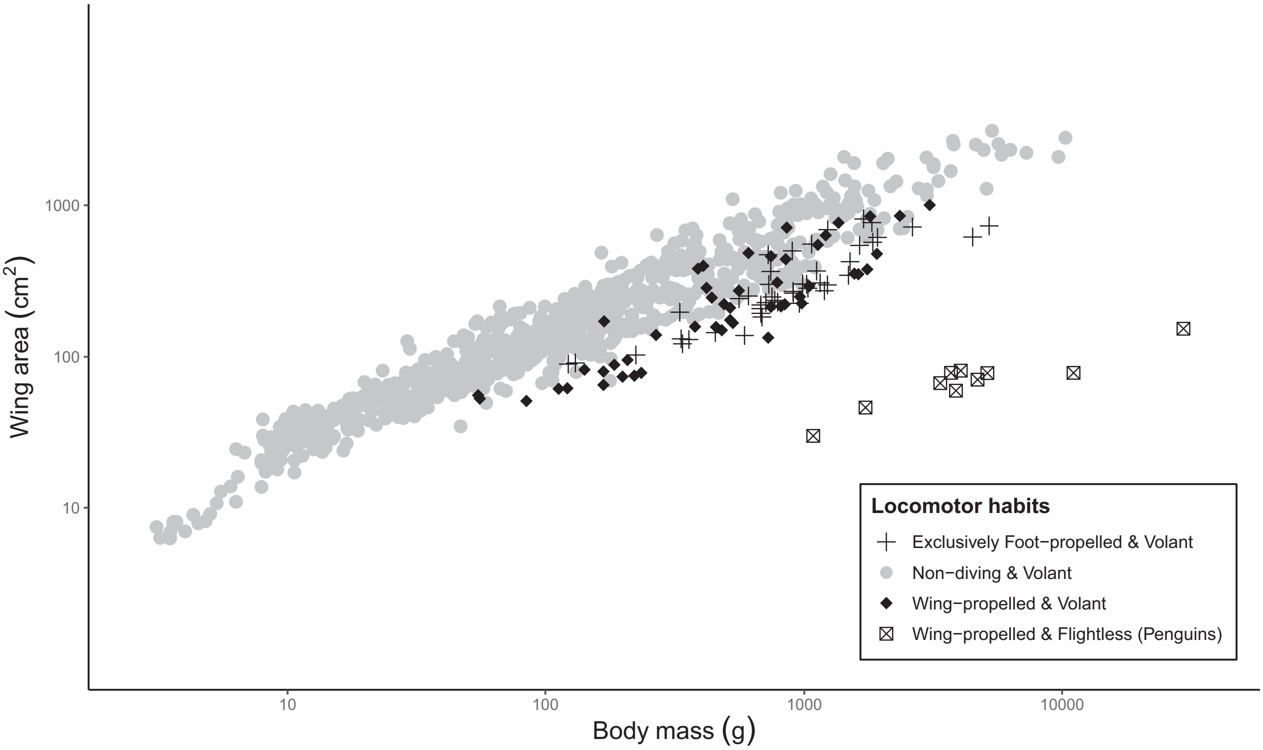

Fig. 1 Wing area (cm^2) versus body mass (g) for 951 species of birds.

Lovvorn 2008). However, these species and others with similarly flexible locomotor habits received TRUE’s for both FP and WP, as both pairs of appendages are expected to show signs of selection for aquatic locomotion.

Of the total 951 species for which we collected morphological data, 104 species were categorized as obligate divers, 59 and 45 species were categorized as wing-propelled and foot-propelled divers, respectively, and 31 and 45 species were categorized as exclusively wing-propelled and exclusively foot-propelled divers, respectively, based on Supplementary Table S3. Because penguins are the only flightless group for which we have wing size and shape data, statistical tests comparing diving groups (wing-propelled versus foot-propelled and non-diving versus diving) were conducted with these flightless species excluded. Table 1 includes example species, their method of submerged aquatic locomotion, and categorizations for statistical analyses. Categorizations for all 951 species are available as Supplementary Material.

Results

Flightless versus volant birds

Comparing penguins to volant birds, we found consistent statistical support for unique scaling coefficients for the relationship between wing area (S) and body mass ($F = 30$, $P = 0.012$; Supplementary Table S5). In other words, penguins, the only flightless species included in our dataset, have significantly higher wing-loadings than volant birds (Fig. 1). However, there was

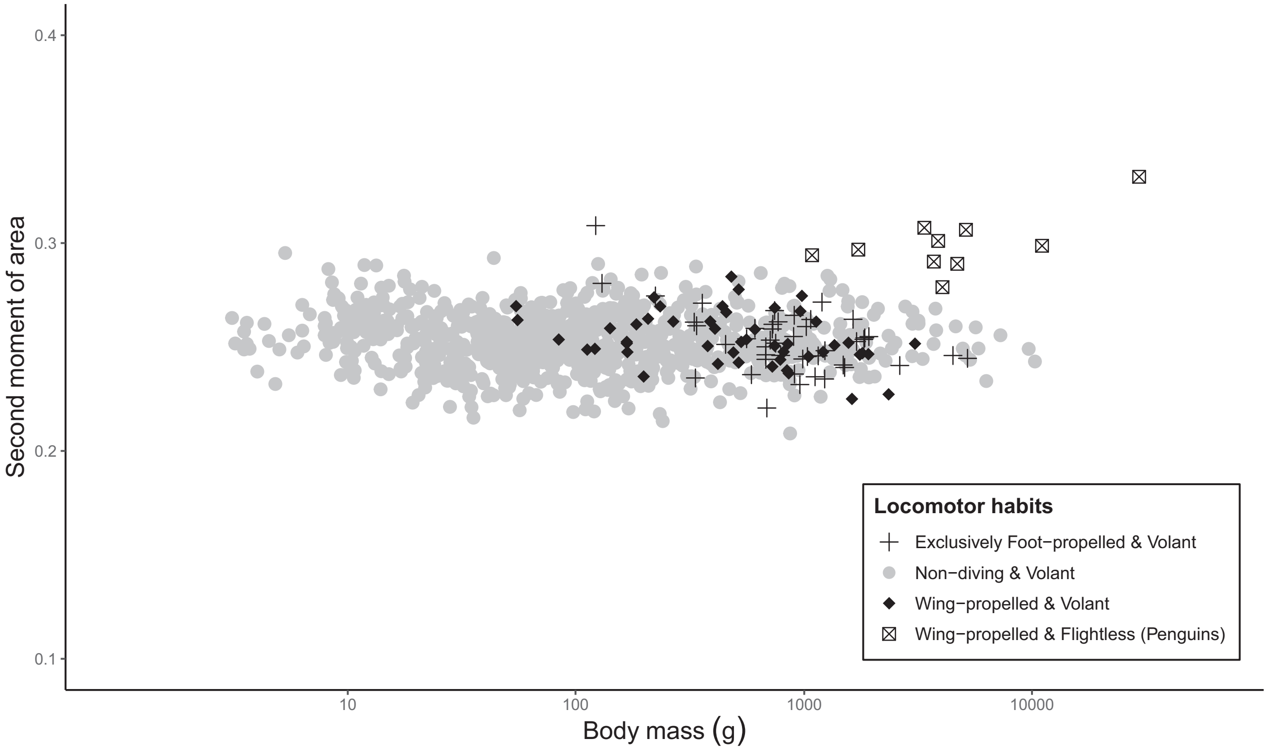

Fig. 2 Second moment of wing area (dimensionless; $\widehat{S_2}$) versus body mass (g) for 951 species of birds.

no consistent support for unique scaling exponents (slopes) for penguins and volant species ($F = 0.58$, $P = 0.70$; Supplementary Table S5), though the result was significant for 14 of 400 total phylogenetic trees.

Wing-propelled versus foot-propelled divers

Comparing species that use their wings to dive to exclusively foot-propelled divers, we found no support for unique scaling coefficients in the relationship between wing area and body mass ($F = 0.18$, $P = 0.70$; Supplementary Table S6). We also found no support for unique scaling coefficients when comparing exclusively wing-propelled and exclusively foot-propelled divers (i.e., excluding species that use wings + feet from consideration) ($F = 0.54$, $P = 0.49$; Supplementary Table S7).

Divers versus non-divers

There was, however, consistent support for unique scaling coefficients for non-diving and pooled volant divers (penguins excluded) in the relationship of wing area versus body mass ($F = 34$, $P = 0.0019$; Supplementary Table S8). In other words, divers have higher wing-loadings than do non-divers (Fig. 1), presumably due to a selective pressure shared across methods of hydrodynamic propulsion. We found no consistent support for unique scaling exponents for diving and non-diving species ($F = 5.3$, $P = 0.28$; Supplementary Table S8), though the difference was significant for 29% of the total trees. Thus, while diving birds have smaller wings than non-diving birds for their mass, wing area scales at similar rates in both groups.

We assessed the pointedness of a species' wing by calculating the second moment of wing area (cm^4; S_2) as measured from the wing root. This measurement quantifies the distribution of wing area, with larger values indicating a larger distribution of area far from the wing root (Ellington 1984b). We then tested whether divers and non-divers differed in the relationship between second moment of wing area (S_2) versus wing area. We found no consistent support for unique scaling coefficients for divers and non-divers ($F = 0.45$, $P = 0.59$; Supplementary Table S9). Plotting the dimensionless version of second moment of area $\widehat{S_2}$ —in which the second moment of area is normalized to absolute wing size, allowing a more-direct comparison of disparately-sized species (Ellington 1984b)—versus body mass further indicates that the wings of diving species are no more pointed than non-diving species (Fig. 2).

To assess the relationship between wing size and dive performance, we tested whether wing-loading could explain among-species variation in mean dive duration (Fig. 3). Specifically, we tested whether propulsion method (wing-propelled versus not) and wing area

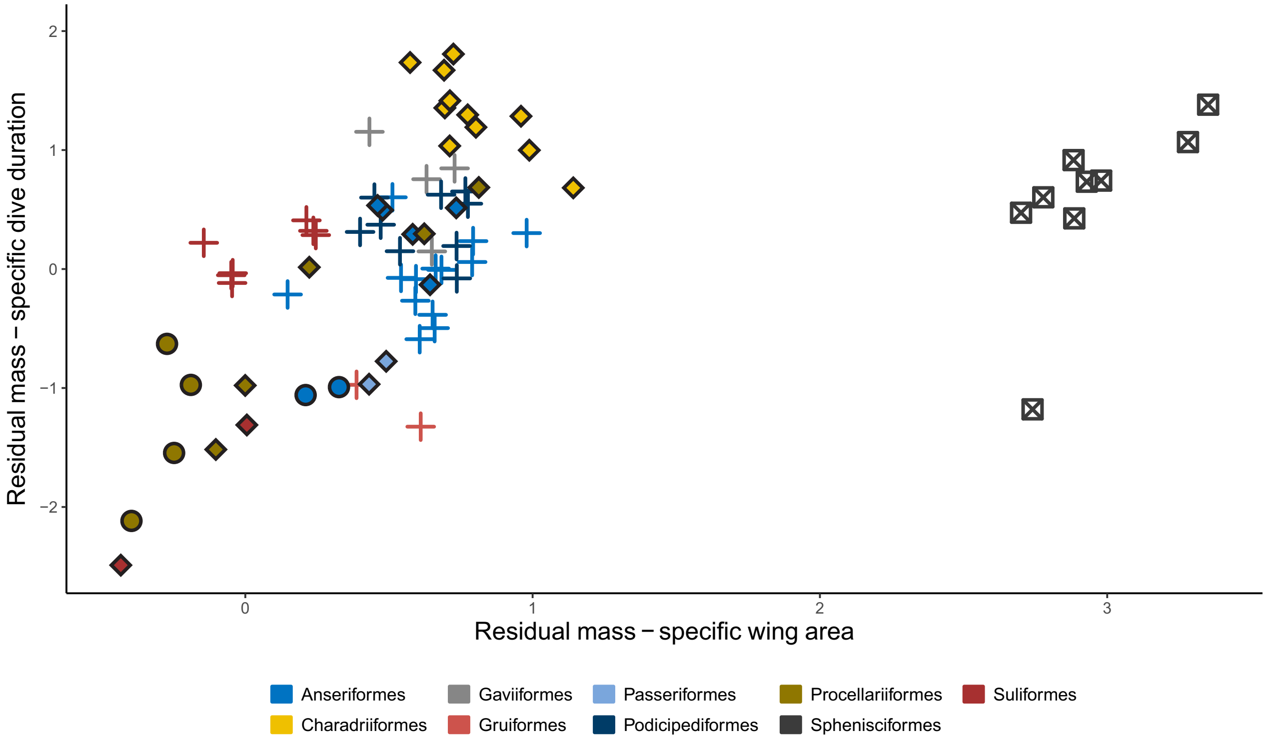

Fig. 3 Relationship between residual mass-specific wing area and residual mass-specific dive duration for 75 species. Color corresponds to taxonomic order. Circles indicate facultative submergers ("non-divers"), squares indicate non-volant species (penguins), crosses indicate exclusively foot-propelled divers, and diamonds indicate wing-propelled divers.

were significant predictors of mean dive duration across volant diving species, after removing the effects of body mass (see *Methods* for details). We found a strong and consistent relationship between residual dive duration and residual wing area (*tStat* = 5.7, $P = 0.0005$; Supplementary Table S10). Propulsion method, on the other hand, was not a significant predictor of dive performance (*tStat* = -0.38, $P = 0.49$; Supplementary Table S10). Models with propulsion method removed had an average $R^2 = 0.36$ (*tStat* = 6.0, $P = 0.0002$; Supplementary Table S11). In other words, for volant diving birds, wing-loading explains more than a third of the interspecific variation in mass-specific dive duration.

Discussion

We found little evidence that the use of the wings for propulsion in water favors high wing-loading in birds. While species that utilize their wings to dive do have higher wing-loadings than non-diving birds, this pattern is shared with exclusively foot-propelled divers, such that the wing-loadings of these two groups are statistically indistinguishable from one another (Fig. 1). Thus, diving has co-evolved with relatively small wings irrespective of whether those wings are used for hydrodynamic propulsion, presumably due to some shared feature of their ecologies (Rayner 1988).

In volant divers, wing-loading explains more than a third of the interspecific variation in mean dive duration (Fig. 3)—a common metric of dive performance (Watanuki and Burger 1999; Halsey et al. 2006). The duration that an air-breathing animal can dive is strongly correlated with the volume of stored oxygen within that animal and its rate of oxygen consumption (Halsey and Butler 2006; Halsey et al. 2006). Thus, the dive duration of a species should be correlated with its efficiency when diving—measured as the rate at which oxygen stores are consumed. Our data, therefore, suggest a trade-off between relative wing size and the efficiency of diving. This result is consistent with previous studies of activity (Thaxter et al. 2010; Orben et al. 2015; *but see* Shoji et al. 2015) and energy costs (Elliott et al. 2013) among divers with different wing-loadings.

Rayner (1988) suggested that high wing-loading in some foot-propelled species could be due to selection favoring fast flight, which is perhaps especially important for long distance migrants. Alternatively, Lovvorn and Jones (1994) proposed that high wing-loading in divers might be the result of relaxed selection for slow flight performance, as the rapid take-offs, maneuverability, and soft landings afforded by low wing-loading may be of lesser importance to divers. Thus, both suggest that divers should possess "low-area, pointed wings for fast flight" (Lovvorn and Jones 1994). Our analyses lend little support to these hypotheses, however. The wings of diving birds are not especially pointed, and exhibit substantial variation in pointedness (Fig. 2). Therefore, it seems unlikely that selection for high flight speeds is the primary driver behind high wing-loading in divers.

Instead, our data are most consistent with the hypothesis that high wing-loading in diving birds, including wing-propelled divers, is the result of selection for reduced buoyancy. In birds, counteracting buoyancy constitutes a major portion of the total energy required to dive (Lovvorn et al. 1991; Stephenson 1994). Wilson et al. (1992) and Taylor and Thomas (2014) hypothesized that selection for reduced buoyancy might favor relatively small wings, given that wings trap air both among and within the feathers. Thus, relatively small wings, by limiting buoyancy, might save substantial energy. Moreover, high wing-loading may be especially attainable for volant divers given their life-histories, as discussed by Lovvorn and Jones (1994). Selection favoring relatively small wings might explain why diving birds tend to have covert feathers which extend over much of the wing (Wang and Clarke 2015; Smith et al. 2021). It might not be that divers have more extensive covert feathers, but rather, relatively short primary and secondary feathers (Moloto 2019; see also Pap et al. 2017). Selection to limit buoyancy of the wings would also help explain the frequency with which diving groups—both wing-propelled and exclusively foot-propelled—have evolved flightlessness (Livezey 1989, 1992).

One limitation of our study is the low number of flightless species in our dataset. Previous authors have suggested that wing area should scale with body surface area in flightless, wing-propelled divers, given that the power required for horizontal swimming is largely determined by drag and, therefore, in proportion to surface area (Storer 1960; Thompson et al. 1998). This, in contrast to the power required for aerial flight, which is expected to scale with the required lift force and, therefore, in proportion to body mass (Ellington 1984b). Our results do not support this hypothesis but are based on data for only ten species and one taxonomic group. Unfortunately, it is rare to find spread wings of flightless species, and only penguins have wings stiff enough to allow measurements from study skins without some form of estimation (e.g., Livezey 1988). We have similarly excluded the estimated wing parameters from extinct species and data from previous studies to ensure a consistent methodology, which has clear drawbacks (Smith 2016).

In conclusion, we found that diving in birds has coevolved with relatively high wing-loading, potentially as a means to limit the buoyancy of the wings. We encourage others to directly test the wing-buoyancy hypothesis by measuring the anatomy and buoyancy of wing feathers across species. Our results offer insights to those interested in developing bird-like robots—a topic of intense interest due to the plethora of potential applications (Zufferey et al. 2022). Diving bird-like robots are typically designed with small, penguin- or alcid-like wings (Lock et al. 2014; Shen et al. 2021). But engineers can utilize non-buoyant materials for these wings, and so are not constrained to relatively small wings except by mechanical power limitations, which can be overcome by reducing flapping frequency (Pennycuick 1987b). Though a smaller wing incurs lower drag, which is especially high in water, it also produces less propulsive force and is likely less efficient (Vogel 1994; Lock et al. 2012; Izraelevitz et al. 2018). Thus, given our results, we recommend that engineered systems maximize wing size for increased propulsive efficiency across air and water.

Acknowledgments

We thank museum staff for their assistance with this project, especially Rob Faucett, Ildiko Szabo, and Phred Benham. We thank Vivian Maxwell and Anne-Renee Van Der Vuurst de Vries for logistical support. We thank The Macaulay Library at the Cornell Lab of Ornithology for access to their media collection. Finally, we thank two anonymous reviewers, whose comments greatly improved the quality of this manuscript.

Competing Interest

The authors declare that they have no competing or financial interests.

Funding

This work was supported in part by grants from the National Science Foundation [grant number EFRI 1935216 to B.W.T.] and the NSF Postdoctoral Research Fellowships in Biology Program [grant number 2109873 to A.B.L.].

Supplementary Data

Supplementary data available at *ICB* online.

Data Availability

The data underlying this article are available in the article and in its online supplementary material.

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