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AQUATIC LOCOMOTION IN BIRDS – BIOMECHANICS, MORPHOMETRICS, AND EVOLUTION

By

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Aquatic locomotion in birds – biomechanics, morphometrics, and evolution

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The entire diversity of life on earth exists in air or water. Whether an organism lives in air or water provides the most fundamental description of its physical world and establishes an organism's ecological niche on the most essential level. Because these two fluids are vastly different from one another, they also dictate, via the process of natural selection, the morphology and physiology of the organisms which call them home. By studying how organisms interact with these fluids – to locomote or obtain food, for example – we have the ability to not only link organism form and function, but also to study the process of evolution itself. These two goals have been the focus of my dissertation, using diving birds as a model system.

Of the 40 extant orders of birds, 16 orders contain aquatic or semi-aquatic members – species which regularly locomote on or in water as part of their life-history. Birds constitute just over 30% of all terrestrial vertebrates; thus, the bird species which move in water are both substantial and diverse. Only 1 of 16 orders have lost the ability to fly. Species in the remaining 15 orders face simultaneous selection for effective and efficient locomotion in both air and water, despite the vast differences between these two fluids.

In Chapter 1 of this dissertation, I review the biomechanics of aquatic locomotion in birds and test existing hypotheses surrounding their morphologies. In Chapter 2, I use geometric morphometrics to determine how the multifunctionality of semi-aquatic birds – specifically, the wings of wing-propelled diving birds – has constrained or facilitated their morphological diversity. In Chapters 3 and 4, I use kinematic analysis to test whether the pressures of retaining aerial flight mean that species which use their wings for locomotion in both air and water are less effective and less efficient in water than lineages which have lost aerial flight. Finally, in Chapter 5, I document submerged aquatic locomotion in non-aquatic birds, despite a lack of selection or experience for this behavior, altering current understanding of the evolution of aquatic lifestyles in vertebrates.

Chapter 1

Diving in birds – biomechanics, morphometrics, and evolution

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Abstract:

This review is, first, a synthesis of existing knowledge about diving in birds and, second, an attempt to highlight the potential of this system to answer broad questions in evolutionary biology. I review the locomotor strategies of diving birds and examine the many hypotheses surrounding their morphology, physiology, and evolution. Based on new and previously published data, I find that specialization for diving by either foot-propulsion or wing-propulsion has not driven the enlargement of hindlimb or forelimb musculature. Furthermore, I find little evidence that wing-propelled diving has selected for small wings to reduce hydrodynamic drag. Excluding flightless birds, both wing-propelled and foot-propelled divers have equally small wings for their body sizes, likely driven by selection against buoyancy.

Introduction:

Charles Darwin, writing from the decks of the HMS Beagle, described the striking similarity between the diving petrels found in the icy waters around Tierra del Fuego and the auks from his homeland in the northern hemisphere (Darwin and Gould, 1838). Both diving petrels and auks have small wings attached to rotund bodies, fly with rapid wingbeats, and obtain their food from the sea by using their forelimbs for submerged swimming. But through correspondence with the prominent English ornithologist John

Gould, Darwin understood that these two birds are only distantly related. So struck by the convergence between diving petrels and auks was Darwin that, in writing *On the Origin of Species*, he would use these species as a prime example of the capacity for natural selection to shape the morphology of organisms to their ecology (Darwin and Gould, 1838). Thus, diving animals have long played a prominent role in evolutionary biology (also see Bock and von Wahlert, 1965; Simpson, 1946; Spring, 1971).

Diving poses significant challenges. Water is 800 times denser and 60 times more viscous than air (Denny, 1993; Vogel, 1994). Thus, for terrestrial lineages to develop diving habits requires modifications to the morphological and physiological systems responsible for locomotion. But despite these challenges, members of all major lineages of terrestrial animals have re-invaded water to some extent (Houssaye and Fish, 2016). Starting from the inception of evolutionary theory, studies of those lineages which have re-invaded water has deepened our understanding of the underlying principles of evolution. Still, there is much to be learned.

Gaps in our knowledge exist in part because much of the research on the anatomy, physiology, and evolution of diving animals has focused on mammals. Diving birds and diving mammals are different beasts. Extant diving birds almost certainly evolved from volant ancestors (Livezey, 1989b; Mayr et al., 2020; Simpson, 1946; Storer, 1971). Thus, in birds, adaptations for aquatic locomotion have been superimposed on a body plan already adept at fluid locomotion (Storer, 1960) – with streamlined bodies to reduce drag and forelimbs capable of producing thrust far from a substrate. This is not true, however, of the ancestors of diving mammals (Fish, 2016; Gingerich, 2015). In mammals, adaptations for aquatic locomotion have been superimposed on a body plan adapted for terrestrial locomotion. Terrestrial animals rarely reach speeds where drag is appreciable, meaning that streamlining in non-diving mammals is rare (Vogel, 1994). Furthermore, mammalian limbs have been shaped by selection for terrestrial locomotion and require significant modifications to function efficiently for fluid locomotion (Fish, 1996; Fish, 2016). Therefore, insights gained from diving mammals may not translate directly to birds, as the tradeoffs between life in air and life in water – which have dramatic consequences for the morphologies of mammals – may be of lesser import.

Recent advancements in the miniaturization of technology – including time-depth recorders, GPS trackers, and digital cameras – have aided a surge of research on diving birds. The diving petrels and auks discussed by Darwin are prominent examples of avian divers, but they are not alone. Of the 40 orders of birds, 16 contain semi-aquatic members – species which regularly locomote on or in water. Birds constitute just over 30% of all terrestrial vertebrates; thus, the number of semi-aquatic bird species is substantial. The exact number depends on one's definition of "semi-aquatic", as reliance on the aquatic environment for food and predator avoidance varies greatly both between and within orders. This variation in diving behavior, along with the multitude of comprehensive resources describing the ecologies of birds (Billerman et al., 2020; Hoyo et al., 1992; Marchant and Higgins, 1991), and their well-resolved phylogenetic relationships (Ericson et al., 2006; Hackett et al., 2008; Jetz et al., 2012; Jetz et al., 2014) makes diving birds a powerful study system in which to explore the evolution of form, function, and behavior.

Here, I review what is known about the morphology and biomechanics of aquatic locomotion in birds and provide new insights through phylogenetically-informed analyses. The aquatic behavior of birds has never been reviewed in full. Thus, scientists attempting a comparative study of the morphology of avian divers, for example, must comb through multiple databases, books, and papers – often with unique terminologies and classification schemes – to correctly categorize the species in their dataset. This has occasionally led to the misclassification of species in comparative studies or required ‘hopeful’ classifications based on anatomical features or taxonomic placement. But with the rise of video hosting and sharing platforms – including YouTube, Vimeo, and the Macaulay Library – along with the near-omnipresence of digital cameras, it is now possible to carefully classify the diving behavior of birds from across the globe through “direct” observation.

My goal for this chapter of my dissertation is to highlight the awesome potential of this study system, both to facilitate the study of diving birds and the use of diving birds as model systems for the study of evolution, more broadly. I do so by first reviewing the diversity of aquatic locomotor strategies utilized by birds; a topic which has never been reviewed in full. I then highlight the many hypotheses surrounding the morphology and behavior of diving birds which – with recent advancements in technology and phylogenomics – are now readily testable. I provide examples of such hypothesis tests with new data describing the wing shapes and sizes of nearly 1,000 species and previously published data describing avian muscular morphology.

Diversity of aquatic locomotor strategies in birds –

Any meaningful treatment of aquatic locomotion in birds must first review which birds dive and their mechanisms of propulsion. However, these questions are not as simple as they may first seem. Indeed, they have been, and continue to be, a topic of active discussion and research (e.g., Albores-Barajas et al., 2011; Blokhin, 2004; Bourget and Chapdelaine, 1975; Bried, 2005; Brooks, 1945; Forbush, 1922; Fournier and Krementz, 2018; Hayes and Bennett, 1985; Ingram and Salmon, 1941; Ingram and Salmon, 1942; Kelso, 1922; Kelso, 1926; Miller, 1983; Oldham, 1919; Sordahl, 1982; Sutton, 1925; Townsend, 1909; Townsend, 1924; Townsend, 1930).

In general, the literature and my personal observations indicate that any avian species can swim on and in water if compelled. It stands to reason that no animal is content to drown. Thus, if forced into water, birds will use their appendages to try to escape; albeit, with varying levels of success. In some species, including European starlings (*Sturnus vulgaris*), the effectiveness of their aquatic locomotion is only observable through forced submersion, as individuals are otherwise unwilling to take to water (Chapter 5). Other species will swim or dive on their own volition to avoid predators (Blokhin, 2004; Fournier and Krementz, 2018; Hayes and Bennett, 1985; Ingram and Salmon, 1942; Morgan, 1994; Riehl, 2020; Sordahl, 1982; Sutton, 1925; Willis, 1994), especially when injured (Forbush, 1922; Kelso, 1926; Townsend, 1909; Townsend, 1924). This includes those species which otherwise do not strongly associate with water, such as house sparrows (*Passer domesticus*) (Chapter 5). 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. All else being equal, the individual with greater escape dive performance – the one which dives more quickly and/or for longer – and the individual with the greater escape dive efficiency – the one which uses less metabolic energy to escape – should have an advantage over others. But for most species, escape dives are rare, and may be reserved to specific age classes [chicks or juveniles] (Hayes and Bennett, 1985; Ingram and

Salmon, 1942; Morgan, 1994; Sordahl, 1982; Sutton, 1925; Willis, 1994). Possessing traits which allow an individual to use less energy to escape dive will confer little selective advantage if some individuals never dive in their lifetime. Thus, these traits will be susceptible to drift. In addition, the act of submerging, even momentarily, can be an effective method of avoiding predators. This is true for dabbling ducks, which will avoid assaults by aerial predators by quickly dipping underwater just before the predator can make contact (AB Lapsansky, personal observation).

More restrictive is the category of birds which dive for food. For these species, dive efficiency – defined as the metabolic energy required to dive per unit time or distance – and dive performance – defined as the speed and/or acceleration attainable underwater – are likely important factors in determining fitness. More efficient underwater locomotion allows for longer dive times (via more efficient consumption of stored oxygen) and, therefore, a greater ratio of resources acquired to energy invested. As well, more efficient underwater locomotion allows deeper dives, afforded by the ability to dive for longer periods of time, which can provide access to food sources only available in deep water. Thus, all species which regularly dive for food are expected to possess adaptations for improved dive efficiency. The ability to achieve high underwater swim speeds and accelerations – i.e., high dive performance – should be especially important for birds which feed on motile prey (e.g., fish, squid, etc.) but not necessarily for those which feed on sedentary food sources (e.g., plants, mollusks, etc.), unless these animals must also avoid motile aquatic predators or feed in flowing water. Studies of species which differ in the mobility of their food sources might reveal traits which are adaptive for high dive speeds and accelerations.

Of those birds which dive for food, significant variation exists both among and within orders, families, and even genera. Some species are reliant on diving to acquire a significant portion of their food – hereafter, **obligate divers** – whereas others dive for food only on rare occasions – hereafter, **facultative divers**. In both cases, selection should favor morphological traits and locomotor patterns which increase aquatic efficiency, but the strength of selection on facultative divers is especially difficult to estimate. On one extreme, facultative diving may provide individuals with the resources necessary to survive harsh conditions (Bourget and Chapdelaine, 1975; Brodsky, 1985; Cottam, 1945), while on the other, diving may be one of many ways in which to acquire the same resource (Miller, 1983). As well, facultative diving may be specific to populations or even individuals. Intraspecific variation within facultative diving species complicates comparative studies attempting to identify adaptations for increased dive efficiency and performance.

The mechanisms of propulsion by diving birds have also been the matter of significant debate. Birds produce force underwater using their hindlimbs (i.e., feet), their forelimbs (i.e., wings), or a combination of both pairs of appendages, but how each species fits within these three categories was an active topic of discussion for the first half of the 20th century (Bent, 1919; Dewar, 1938; Forbush, 1922; Ingram and Salmon, 1941; Kelso, 1922; Kelso, 1926; Townsend, 1909; Townsend, 1924; Townsend, 1930). Much of the confusion appears to have stemmed from the fact that many records of aquatic locomotor behavior were based on observations of injured or frightened animals (discussed by Townsend, 1924). As with non-aquatic birds forced into water, it seems that injured or frightened animals will make use of all four appendages (hindlimbs and forelimbs) to avoid capture (Townsend, 1924). As well, species which typically rely on only one pair of appendages for steady-state locomotion will make use of the other pair to maneuver (Clifton and Biewener, 2018; Hui, 1985; Spring, 1971), including to escape curious ornithologists (Forbush, 1922; Morgan, 1994; Townsend, 1924).

Diving birds occupy all continents and inhabit a vast range of environments (Billerman et al., 2020). It would be unreasonable to expect any single group of authors to possess complete knowledge of the habits of all birds. Combined with the diversity and ambiguity of diving behaviors discussed above, it is no surprise that species are sometimes misclassified.

To facilitate efforts to study diving birds and efforts to use diving birds as a study system, I have conducted an exhaustive summary of the aquatic habits of all birds (Table 1). Ashmole (1971) was likely the first to publish such a summary – describing the feeding strategies of some 71 groups of primarily pelagic birds – in what is now a landmark of seabird ecology research. In the 50 years since its publication, this effort has been repeated for specific seabird communities and expanded by numerous authors (Ainley et al., 1984; Croxall and Prince, 1980; Harper, 1987; Harper et al., 1985; Harrison et al., 1991; Prince and Morgan, 1987). Additionally, Lovvorn (1991) summarized locomotor habits for foot-propelled diving birds, and Wilson et al. (1992b) for 38 species of penguins, loons, grebes, petrels, and alcids (Lovvorn, 1991; Wilson et al., 1992b). However, no single effort has covered all avian orders or even all orders with diving members.

To accomplish this task, I relied on two multi-volume handbooks recently converted into digital forms (*Handbook of Australian, New Zealand and Antarctic Birds* and *Birds of the World*). These references were use as "starting points", but I traced references to the original source of information wherever possible so as not to perpetuate incorrect or "hopeful" classifications. In addition to references of dive behavior, I provide video or photographic references for diving behavior for nearly all diving groups. Both forms of reference are available as a supplementary file [Appendix 1]. These references are not exhaustive. Instead, they are meant to serve as verification of diving behavior and as launchpads for further inquiry.

Because my primary goal for this effort is to facilitate research on and using diving birds, and because evidence in the literature and my own observations indicate that all birds will exhibit aquatic locomotion if forced, I focus only on those species which dive as part of their foraging strategy. Thus, **diving is defined here as the complete submergence in water with the goal of acquiring food**. All orders are included, allowing researchers to confidently categorize species as "non-diving" (for food, at least). Families, genera, and species are treated separately if clear variation in diving behavior exists within those groupings. Diving groups are categorized based on their method of thrust production in water (foot-propelled [FP] and/or wing-propelled [WP]) during steady-state swimming (i.e., not during maneuvers, escapes, or when injured). Importantly, FP and WP are categorized 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 (Order: *Anseriformes*, Family: *Anatidae,* Genera: *Polysticta* & *Somateria*) and scoters (Order: *Anseriformes*, Family: *Anatidae,* Genus: *Melanitta*) regularly dive both by wing + foot-propulsion and by exclusively foot-propulsion (Heath et al., 2006; Richman and Lovvorn, 2008). However, these species and others with similarly flexible locomotor habits receive “1s” for both FP and WP, as both pairs of appendages may show signs of selection for aquatic locomotion.

Groups are also categorized based on their entry method into the water (*EM*) as surface diving (*S*) – meaning they enter the water after floating on the water’s surface – and/or plunge diving (*P*) – meaning they enter the water directly from the air and without first resting on the surface (Ashmole, 1971; Chang et al., 2016; Ropert-Coudert et al., 2003). I have also noted the location of food taken as Benthic and/or Pelagic. These terms are often indicative of whether species feed on sedentary or motile prey, respectively, though not always. For example, Little auks (Order: *Charadriiformes*, Family: *Alcidae,* Genera: *Alle)* feed on suspended zooplankton, which are essentially sedentary from the perspective of the bird (Enstipp et al., 2018). I have included the surface habits of each group to give the reader a sense of those groups which regularly transit on water for reasons other than rare instances of predator evasion, but which may or may not dive for food. For both surface and submerged swimming (i.e., diving) categories, I note the reliance (Rel.) of said group on each form of aquatic locomotion as either obligate (*O*) or facultative (*F*). Groups are categorized as obligate divers if diving is considered to constitute 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 and likely exerts strong selective pressure. Groups are classed as facultative divers if documentation of diving for food is broadly considered rare (e.g., Briggs, 1978; Brodsky, 1985; Oldham, 1919; Taylor, 2008). Finally, I have included columns for both terrestrial and aerial habits, though it should be noted that considerable variation may exist within groups (Bruderer et al., 2010) which is outside the scope of the present analysis. Taxonomic organization follows that of *Birds of the World* (Billerman et al., 2020).

As illustrated in Table 1, the following orders contain diving members: *Anseriformes*, *Podecipidiformes*, *Gruiformes*, *Charadriiformes*, *Phaethontiformes*, *Gaviiformes*, *Sphenisciformes*, *Procellariformes*, *Suliformes*, *Pelecaniformes* *Accipitriformes*, *Coraciiformes*, and *Passeriformes*.

In the order *Anseriformes* (ducks, geese, and swans), divers rely on either their hindlimbs or both their hindlimbs and forelimbs for aquatic propulsion. This order contains non-diving species, as well as obligate and facultative divers. All members of the order *Podecipidiformes* (grebes) are diving and are exclusively foot-propelled during steady-state aquatic locomotion. Though many members of the *Gruiformes* will dive to avoid predators (Fournier and Krementz, 2018; Wintle and Taylor, 1993), only those in the genus *Fulica* (coots), are obligate divers. However, given their strong association with water and the difficulty of studying rails and finfoots, it is conceivable that most species in the order *Gruiformes* are facultative divers (Alvarez del Toro, 1971; Taylor, 1998). All members of the family *Alcidae* (auks) dive with their wings, and species in the genus *Cepphus* (guillemots) will also use their feet to hover while feeding on benthic prey. They do not, however, use their feet during steady-state locomotion in open water. The few species in the order *Phaethontiformes* (tropicbirds) apparently dive to considerable depths after entering the water from a plunge (Corre, 1997; Sommerfeld and Hennicke, 2010), but their mechanism of propulsion underwater is unknown. The five species in the order *Gaviiformes* (loons, sometimes referred to as “divers”) are foot-propelled, obligate divers. All members of *Sphenisciformes* (penguins) are non-volant and forage exclusively through wing-propelled diving. As with *Anseriformes*, a great deal of variation exists within the *Procellariformes* (albatrosses, shearwaters, and allies), with all families containing either facultative or obligate divers. Most seem to use both the feet and wings for aquatic propulsion, but species in the genus *Pelecanoides* (diving petrels) apparently use only their wings, though I am unable to find any visual evidence to support this widespread view. In the order *Suliformes*, species in the order *Sulidae* (gannets and boobies) use both the feet and wings for aquatic propulsion, whereas those in *Anhingidae* and *Phalacrocoraxidae* (anhingas and cormorants, respectively) are exclusively foot propelled. Finally, the order *Passeriformes* contains three wing-propelled divers in the family *Cinclidae*, genus *Cinclus* (White-throated, Brown, and American dippers). Again, these categories apply only to healthy birds during steady-state aquatic locomotion.

Plunge divers in the orders *Accipitriformes*, *Pelecaniformes*, and *Coraciiformes*, and in the family *Laridae* (Order: *Charadriiformes*) illustrate the limitations of our definition of "diving". At least some species in all four groups plunge into water as a critical component of their foraging strategy, but none descend in water using their appendages. Instead, they rely on momentum gained in the air to overcome the drag and buoyancy of water (Ashmole, 1971; Chang et al., 2016; Ropert-Coudert et al., 2003). However, diving species within these groups may use their appendages to ascend in water following a plunge, thereby exhibiting aquatic locomotion and, potentially, associated morphological modifications. Ospreys (Order: *Accipitriformes*, Family: *Pandionidae*, Genus: *Pandion*) forage almost exclusively by plunging into water, but rarely submerge. Still, they use their wings (and, perhaps, their feet when not holding prey) to launch themselves out of the water following a plunge. Gulls and terns (Family: *Laridae*) also plunge dive, submerging on occasion, but do not contact the water with their wings to ascend. The same is true of pelicans (Order: *Pelecaniformes*, Family: *Pelecanidae*), though submergence by these species is apparently exceedingly rare (Hall, 1925; Skinner, 1925). Finally, kingfishers (Order: *Coraciiformes,* Family: *Alcedinidae*) exhibit dramatic interspecific variation in foraging behavior (Woodall, 1991). Some species reach multiple body-lengths below the surface through plunge diving and use their wings to ascend; others feed entirely on terrestrial fauna. Others, still, are presumed to eat fish and other aquatic prey (Barker and Vestjens, 1989), but their foraging behavior is poorly documented. Species in this final group might take aquatic prey by skimming the surface of the water or, perhaps, through plunges which may or may not result in complete submergence.

Researchers should consider their specific questions when classifying species in these latter four groups. For example, if the goal is to explore the effects of aquatic locomotion on the osteology of the bones in the wing, then it might be most appropriate to classify terns as non-diving, as the wings occupy a passive role in plunging and submergence is rare. However, if the investigation instead focuses on the osteology of the cervical vertebrae, then terns might be better classed as divers, as they experience similar force regimes as other plunge divers even though submergence is rare.

In addition, researchers should carefully consider classifications of species in the *Procellariformes*, as our knowledge of diving in this group is incomplete (Dunphy et al., 2015; Shoji et al., 2016). This is especially true of the species in the genus *Pterodroma*, the gadfly petrels. Traditionally, gadfly petrels have been considered either non-diving or rarely-diving (Ashmole, 1971; Harper et al., 1985; Prince and Morgan, 1987), but recent studies utilizing capillary tube depth gauges have documented dive depths of greater than 20 meters in some species (Rayner et al., 2008; Taylor, 2008). Still, the frequency of these dives relative to other foraging methods is largely unknown. Dive behavior may vary considerably between *Pterodroma* species, or depend on food availability or locality (Warham, 1996). Hopefully, new technologies and methods of analysis (e.g., Cianchetti-Benedetti et al., 2017) will reveal the diving habits of these species.

For the sake of brevity, I will not go through each group in Table 1 further, but I will comment on three interesting cases of interspecific variation which warrant more focused study.

First, the family *Cinclidae* contains five species, only three of which dive. These three species use their wings to dive in fast-flowing streams to feed on macroinvertebrates, fish, and other animal prey; *Cinclus cinclus* in Eurasia, *Cinclus pallasii* in Asia, and *Cinclus mexicanus* in North and Central America (Winkler et al., 2020a). The other two species, *Cinclus leucocephalus* and *Cinclus schulzii*, reside in South America but forage in similar environments and for similar prey as their relatives (Winkler et al., 2020a). For unknown reasons, the South American dippers do not dive, instead remaining firmly attached to the substrate while foraging (Tyler and Ormerod, 1994). Whether this variation in behavior is reflected in the morphology of these species is largely unknown, though there does appear to be variation in feather microstructure which may be adaptive for submerged swimming (Rijke and Jesser, 2010).

Second, the genus *Melanitta* (scoters) contains two species which are exclusively foot-propelled divers – *Melanitta nigra* and *Melanitta americana*– and three species –

Melanitta perspecillata, *Melanitta fusca*, & *Melanitta deglandi* – which will also use their wings for a proportion of their dives (Mullarney, 1983). The diving strategy in the sixth species in the genus, *Melanitta stejnegeri*, is apparently unknown. All six species occupy similar habitats, are of similar sizes, and dive to forage on benthic invertebrates (Winkler et al., 2020b). Again, whether this variation in behavior is reflected in the morphology of these species is unknown.

Finally, as noted above, the family Alcedinidae exhibits dramatic interspecific variation in foraging behavior (Woodall, 1991). This variation has already proved fruitful for research (e.g., Crandell et al., 2019; Eliason et al., 2020), but many questions remain unanswered. Research on the foraging behavior and morphology of species in the genera *Ceyx*, *Halcyon*, *Todiramphus*, and *Caridonax* would be especially valuable.

Foot-propelled vs. Wing-propelled aquatic propulsion –

The data presented in Table 1 illustrate that aquatic locomotor strategy – i.e., whether a species uses their hindlimbs, forelimbs, or both for propulsion underwater – varies both between and among diving groups. Why variation exists across birds has long been a topic of debate, with numerous authors offering explanations for this variation based on the hypothesized advantages and disadvantages of foot- and wing-propulsion (e.g., Kuroda, 1967; Lovvorn and Jones, 1994; Mayr et al., 2021; Richman and Lovvorn, 2008; Storer, 1960). Table 2 summarizes the relative advantages and disadvantages of bird’s aquatic locomotor strategies, as discussed by the literature, and will serve to organize much of the remaining discussion.

Four factors in Table 2 [*FP A1, FP D1, WP A1, and WP A2*] are based on the physical principles of drag- vs. lift-based aquatic propulsion. These principles may not be clear to the reader; thus, I review them here.

Birds are thought to produce hydrodynamic force by drag-based or lift-based mechanisms, or a combination of the two. Drag is defined as a force which acts parallel to the direction of fluid flow about a propulsor (e.g. the feet or wings), whereas lift is defined as a force which acts perpendicular to the direction of fluid flow about a propulsor (Denny, 1993; Vogel, 1994). No bird has yet stumbled upon jet propulsion, although the opposite mechanism, suction, is used for feeding in at least one species (Enstipp et al., 2018).

Lift-based aquatic propulsion is more efficient than drag-based aquatic propulsion from both theoretical (Daniel and Webb, 1987; Vogel, 1994; Webb and Weihs, 1983) and empirical perspectives (Baudinette and Gill, 1985; Davenport et al., 1984; Fish, 1996; Jackson et al., 1992; Richman and Lovvorn, 2008; Schmid et al., 1995; Williams, 1999). If we assume that drag-based propulsion is synonymous with "rowing" and lift-based propulsion with "flapping", which is a coarse but reasonable approximation at the Reynolds numbers characteristic of swimming birds (Walker, 2002), then this relationship holds across all speeds (Walker and Westneat, 2000). At high speeds, drag-based mechanisms are especially ineffective and inefficient, because they require the appendage to move faster than the speed of translation (Daniel and Webb, 1987; Johansson and Norberg, 2001; Vogel, 1994).

But then why don't all animals use lift to swim? Lift requires circulation around a foil and is, therefore, only effective for force production at relatively high Reynolds numbers (i.e. high speeds) (Daniel and Webb, 1987; Norberg, 1990; Rayner, 1995; Vogel, 1994; Webb, 1988). Thus, at low Reynolds numbers (i.e. low speeds) drag can generate greater thrust than can lift (Vogel, 1994; Walker and Westneat, 2000), and can therefore aid animals to accelerate from rest, perform powerful maneuvers, and hold station under external forces (Chin and Lentink, 2019; Godoy-Diana and Thiria, 2018).

In air, birds rely on the lift force created by their wings to power forward flight, and the same appears to be true when the wings are used for diving (Bannasch, 1995; Clark and Bemis, 1979; Hamilton, 2006; Hui, 1988; Johansson, 2003; Johansson and Aldrin, 2002; Lovvorn, 2001; Richman and Lovvorn, 2008). Foot-propelled aquatic locomotion in birds, on the other hand, has largely been considered drag-based (Johansson and Norberg, 2000; Vogel, 1994). Thus, the distribution of foot-propelled and wing-propelled diving in birds has been explained based on the relative advantages of lift- vs. drag-based mechanisms of thrust production. For example, it would behoove birds which “hover” while foraging on benthic prey to use drag-based mechanisms of thrust production, as they must create considerable forces to counteract buoyancy while moving at nominal speeds. Thus, species like alcids in the genus *Cepphus* use their feet while hovering underwater (Table 1).

However, several recent studies have challenged the long-held view that foot-propelled aquatic locomotion in birds is purely drag-based. Grebes (Johansson and Norberg, 2000; Johansson and Norberg, 2001), loons (Clifton and Biewener, 2018), and cormorants (Ribak, 2004), can likely produce substantial lift forces with their hindlimbs. Moreover, Johansson and Norberg (2003) demonstrated that the webbed feet of surface swimming birds are capable of producing lift forces thanks to unsteady fluid interactions (Johansson and Norberg, 2003).

Thus, the view that wing-propelled diving is purely lift-based, and that foot-propelled diving is purely drag-based, is oversimplified. In fact, animals routinely utilize both mechanisms of force production, even using the same appendage, depending on the speed of their translational movement (Chin and Lentink, 2019; Feldkamp, 1987; Vogel, 1994; Westneat, 1996). However, as noted by Lovvorn and Liggins (2002), the relative contributions of lift- vs. drag-based mechanisms in producing thrust in swimming birds has not yet been thoroughly explored (but see Clifton, 2017). This could be accomplished via traditional analytical analysis (*sensu* Ribak et al., 2010; Walker and Westneat, 2000), through computational fluid dynamics [CFD], or, and perhaps most promising, by measuring forces on robotically driven appendages (Clifton, 2017; Izraelevitz et al., 2018; Lock et al., 2012). Using these methods, one could tease out the details of thrust production in diving birds and uncover potential trade-offs governing propulsor design in diving birds, including the contribution of the acceleration reaction to diving (Daniel, 1984); a phenomenon which is largely unappreciated (but see Ribak et al. 2010).

As highlighted by Vogel (1994), lift-based systems must be precisely shaped to generate force, whereas almost any structure can be used to generate drag. Thus, Vogel states that “multifunctional appendages ought to be more likely to use the drag-based system” (Vogel, 1994). This might explain in part why grebes and loons – which have feet shaped for lift-production – are nearly incapable of locomoting on land (Shufeldt, 1898; Wilcox, 1952), and likely explains why obligate diving mammals struggle to walk (Fish, 1996; Fish, 2016).

Two more factors in the above table [*FP D2, WP A2*] indicate a cost of foot-propulsion and, therefore, suggest a relative advantage of wing-propulsion. In foot-propelled diving birds, thrust is generated primarily as the leg is extended [power phase], with negligible to negative thrust produced as the leg is retracted [recovery phase] (Aigeldinger and Fish, 1995; Clifton and Biewener, 2018; Davenport et al., 1984; Lovvorn and Liggins, 2002; Ribak, 2004; Ribak et al., 2010). Wing-propelled diving birds, on the other hand, can produce thrust during both the upstroke and downstroke of their wings, thereby eliminating the need for a recovery stroke (Bannasch, 1995; Clark and Bemis, 1979; Hui, 1988; Johansson and Aldrin, 2002; Lapsansky and Tobalske, 2019; Lovvorn, 2004; Watanuki, 2006; Watanuki et al., 2003). Consequently, a bird swimming with their hindlimbs must generate higher instantaneous velocities during the power phase to achieve the same average speed as a bird swimming with its forelimbs, as no force is produced during a considerable portion of the foot-propelled kinematic cycle. In other words, foot-propulsion, at least as it is accomplished by extant species, is inherently unsteady. Because drag on the body (parasite drag) increases non-linearly with speed, and because energy must be used to accelerate the body and surrounding fluid during the power phase [i.e., acceleration reaction], this unsteadiness should significantly increase the cost of locomotion (Daniel, 1984; Lovvorn, 1991; Lovvorn, 2001).

Though the hydrodynamic principles discussed above are well-supported by both theoretical (Daniel and Webb, 1987; Vogel, 1994; Webb and Weihs, 1983) and empirical research (Baudinette and Gill, 1985; Fish, 1996; Jackson et al., 1992; Richman and Lovvorn, 2008; Schmid et al., 1995; Williams, 1999), the relative efficiency of diving by foot- versus wing-propulsion has only been directly tested once (Richman and Lovvorn, 2008). Richman and Lovvorn (2008) compared the costs of foot-propelled vs. foot- + wing-propelled dives by white-winged scoters (*Melanitta fusca*) in at 2 m tank via respirometry. While the use of the wings reduced the energetic costs of diving by an estimated average of 34%, variation in metabolic costs between and within individuals meant that there was no significant difference between dive types (Richman and Lovvorn, 2008).

In summation, the hydrodynamic principles surrounding wing- and foot-propelled diving, as they are presently understood, do little to explain why a diving bird of today might use its wings underwater, its feet, or a combination of the two. Thus, functional tradeoffs, ecological factors, and historical context, are likely important in explaining the distribution of wing-propelled and foot-propelled diving in birds (Mayr et al., 2021).

For example, Storer (1960), noted that birds which forage in open water (pelagic environments) tend to be wing-propelled whereas those which forage in freshwater and littoral environments tend to be foot-propelled. He suggested that "upright aquatic vegetation, such as is commonly found in fresh-water habitats, must impede wing-propelled divers to a much greater extent than foot-propelled ones," thereby determining the distribution of foot-propelled and wing-propelled diving [*WP D2*]. Richman and Lovvorn (2008) expanded this hypothesis with specific reference to diving in white-winged scoters and their relatives. These species occupy shallow environments with dense vegetation during the breeding period, but winter in more open water. Thus, vegetation may enforce foot-propelled diving in some environments but permit the use of wings in others (Richman and Lovvorn, 2008).

The ancestral foraging habits of each diving lineage may also play an important role in determining the distribution of hindlimb and forelimb propulsion across the avian phylogeny. Extant diving birds almost certainly evolved from volant ancestors (Livezey, 1989b; Mayr et al., 2020; Simpson, 1946); thus, the relatives of modern diving birds had forelimbs capable of generating hydrodynamic lift. Their feet would likely be relatively ineffective at creating lift (but see Johansson and Norberg, 2003), but would be capable of powering diving through drag (Vogel, 1994). Under this scenario, early diving birds would have faced the choice of using their forelimbs *and* lift-based mechanisms *or* their hindlimbs *and* drag-based mechanisms to power their aquatic locomotion, despite the fact that this dichotomy has now been circumvented. Where sustained speeds were required, wing-propulsion would have a clear advantage, being both more efficient and effective at producing thrust. This would seemingly drive species which forage in pelagic environments and those which dive at high speeds – including plunge divers and those entering moving water (i.e., dippers) – to become wing-propelled divers. Those feeding on sessile, benthic prey could effectively forage underwater using their hindlimbs. Early foot-propelled divers might, thereafter, face selection for hindlimb morphologies capable of producing lift, as this would facilitate access to novel food sources, resulting in the specialized feet of birds like loons and grebes (Clifton and Biewener, 2018; Johansson and Norberg, 2000; Johansson and Norberg, 2001). This hypothesized scenario could be supported or invalidated by examining the foraging ecology of ancestral diving birds based on analyses of beak shape (*sensu* Olsen, 2017), for example.

Importantly, though, neither Storer's conjecture or the hydrodynamic principles surrounding wing- and foot-propelled diving explain why many modern divers rely exclusively on their hindlimbs for thrust even while foraging in open water and at high speeds. For example, cormorants and shags (*Phalacrocoraxidae*) reach depths of upwards of 100 m and sustain speeds from 1.5-1.7 m s^{-1} in open water (Ribak, 2005; Watanabe et al., 2011) – conditions in which the wings would clearly be effective. These species, and others capable of producing lift forces via their hindlimbs (Clifton and Biewener, 2018; Johansson and Norberg, 2003), still experience inefficiencies due to the unsteadiness of foot-propulsion (Daniel, 1984; Lovvorn, 2001; Richman and Lovvorn, 2008), and yet do not use their wings even during deep, open-water dives. This suggests that there may be an advantage to specialization – that using either the hindlimbs or the forelimbs has advantages over a mixed-strategy – perhaps due to morphological tradeoffs associated with foot-propelled and wing-propelled diving.

This topic, and the remaining hypotheses in Table 2, will serve as the scaffold for the remaining discussion.

Hypothesis testing:

In addition to reviewing their behavior and biomechanics, I used new and previously published data, analyzed via phylogenetic comparative methods, to test two widespread hypotheses surrounding diving birds and illustrate the potential of this system for scientific inquiry.

1) **Aquatic locomotion requires an enlargement of the pelvic** [*FP D3*] **or pectoral musculature [***WP D3***], together favoring specialization toward either foot-propelled or wing-propelled diving** (Gadow, 1902; Kovacs and Meyers, 2000; Storer, 1960; Watanabe et al., 2011; Wilson et al., 2008)**.**

2) **Selection for wing-propelled diving favors reduced wing sizes** [*WP D4*] (Bock and von Wahlert, 1965; Cody, 1973; Elliott et al., 2013; Kuroda, 1954; Pennycuick, 1987; Pennycuick, 2008; Rayner, 1988; Storer, 1960; Thaxter et al., 2010; Thompson et al., 1998), which might prevent foot-propelled species from using their wings underwater.

To test these hypotheses, I digitized or collected data describing the muscle masses in the pelvic girdle of 404 species, the muscle masses in the pectoral girdle of 1,116 species, and the wing shape and size of 951 species of birds.

First, by comparing the muscle masses of diving and non-diving species, I tested whether aquatic locomotion has resulted in an enlargement of either the hindlimb musculature [*FP D3*] for foot-propelled diving (Gadow, 1902; Storer, 1960; Watanabe et al., 2011), or forelimb musculature [*WP D3*] for wing-propelled diving (Kovacs and Meyers, 2000; Storer, 1960). Together, this would favor specialization toward a single locomotor strategy, as the added mass used for aquatic locomotion would increase flight costs (Ellington, 1984a; Gadow, 1902; Rayner, 1988; Watanabe et al., 2011). As well, the muscles in the pectoral girdle – necessary for wing-propelled diving and flight – might increase the cross-sectional area of a diving bird, thereby increasing drag (Wilson et al., 2008).

Second, by comparing the wing size and shape of diving and non-diving species, I tested whether selection for wing-propelled diving has favored small wings in species which use their wings for aquatic propulsion [*WP D4*] (Bock and von Wahlert, 1965; Cody, 1973; Elliott et al., 2013; Kuroda, 1954; Pennycuick, 1987; Pennycuick, 2008; Rayner, 1988; Storer, 1960; Thaxter et al., 2010; Thompson et al., 1998), which might thereby limit the usefulness of wing-propulsion in otherwise foot-propelled species even under seemingly favorable conditions.

The idea that wing-propelled diving favors small wings is widespread in both the scientific (above citations) and public communities (Reilly, 2013; Seabird, 2021), yet the rationale for this view is rarely been stated explicitly. Most explanations allude to a small wing being more efficient for aquatic locomotion due to profile drag (Ashmole, 1971; Rayner, 1988; Storer, 1960), thereby predicting that species which use their wings for aquatic propulsion will have smaller wings than exclusively foot-propelled species. Alternatively, however, high wing-loading may be the result of relaxed selection *against* high flight speeds (Kovacs and Meyers, 2000; Lovvorn and Jones, 1994) or selection to reduce buoyancy (Wilson et al., 1992a), both of which would favor small wings across aquatic locomotor strategies. Of course, "small" is a relative term. In this case, wing size is expressed relative to body mass –using a term called *wing-loading* – which is calculated as the ratio of body mass to wing area. Thus, to say that wing-propelled diving selects for "small wings" is to say that wing-propelled diving selects for "small wings for a given body mass" or for "high wing-loading" (Pennycuick, 1987; Rayner, 1988).

Methods:

To test Hypothesis 1, I digitized the mass of the muscles in the extremities for 404 species of volant birds included in Hartman (1961). Unfortunately, although this dataset includes the mass of the muscles in the upper extremities for 375 species, no obligate wing-propelled divers are included (Hartman, 1961). While it is tempting to include masses for diving species from other studies, what constitutes muscles of the lower and upper extremities is likely subjective. Thus, to test Hypothesis 1 with regards to wing-propelled diving, I assembled masses of the pectoralis and supracoracoideus for 1,116 species of volant birds from various sources (Bethke and Thomas, 1988; Greenewalt, 1962; Hartman, 1961; Kovacs and Meyers, 2000; Kuroda, 1960; Kuroda, 1967; Livezey and Humphrey, 1986; Wright et al., 2016), including for 44 obligate foot-propelled divers and 26 obligate wing-propelled divers. Hartman (1961) expressed muscle masses as percentages relative to total body mass. For consistency with other references, those percentages were back calculated to units of grams. If data for a given species was present across multiple sources, preference was given to the more recent study.

To test whether selection for decreased hydrodynamic drag, high flight speeds, or reduced buoyancy has resulted in high wing-loading for wing-propelled diving, I collected data describing the wing shape and size of 2,324 wings and 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.

The bulk of the wing data (>90%) 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 attached to a Beleser CS-20 Copystand and leveled via a bubble-type level. To facilitate digitization, wings were placed on a green “chromakey” background and illuminated via two Britek photo lights. I obtained data for additional volant species from the Slater Museum of Natural History digital collections.

Because of their unique anatomy, spread wings of penguins are rare. However, the stiffness of penguin wings (Raikow et al., 1988) means that wing shape is preserved when specimens are prepared as study skins. Thus, 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 via tripod-mounted and leveled cameras, with a ruler placed at the height of the wing for scale. Because penguins are the only flightless group for which I have wing size and shape data, analyses comparing diving groups (Wing-propelled vs. Exclusively Foot-propelled and non-diving vs. diving) were conducted with flightless species excluded.

The wing area and second moment of area were calculated for images of each wing using a custom MATLAB script. Species averages were used in all analyses. Because specimens donated to museum collections are often emaciated, body masses for the wing dataset are from Dunning (2008).

Species were categorized based on their diving behavior according to Table 1. Only obligate divers were categorized as “diving”, with facultative divers and species with unknown diving frequency considered “non-diving”. This is because facultative diving may be specific to populations and/or individuals, and the dive behavior of individual specimens in my dataset is unknown. Species which plunge dive, but which do not use their appendages to descend further in the water column, were also considered “non-diving” for these analyses, as they likely do not face the selective pressures shared by other divers (e.g., buoyancy minimization, hydrodynamic drag minimization, etc).

Phylogenetic Comparative Methods

The hypotheses tested here concern group deviations from allometric predictions. Thus, I used the R package *evomap* to test for differences in the intercept describing those allometric relationships between groups while first holding the slope of the allometric relationship constant (Smaers and Rohlf, 2016). Finding a significant difference in intercept, I then tested whether both intercept and slope of the allometric relationship differed significantly between groups to detect unique allometries. All data were log-transformed prior to hypothesis testing.

To account for 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). Thus, I followed Rubin's rule (Nakagawa and De Villemereuil, 2019) by also testing hypotheses using the subset of species with genetic data (again, across 200 trees) (Upham et al., 2019).

Presently, the methods in *evomap* assume a Brownian motion model of evolution (Smaers and Rohlf, 2016). Thus, I used the function "phylosig" available in *phytools* to calculate Blomberg's K (Blomberg et al., 2003) and Pagel's λ (Pagel, 1999) for all data types to estimate the phylogenetic signal (Revell, 2012). In all cases, values of phylogenetic signal were consistent with a Brownian motion model of trait diversification.

Results:

Muscle mass

To test whether foot-propelled aquatic locomotion selects for enlarged hindlimb muscle masses, I compared the mass of the muscles in the hindlimb of 8 species of obligate foot-propelled divers to 396 non-diving species using data from Hartman (1960). I found no difference between obligate foot-propelled diving birds and non-diving birds in the mass of the hindlimb (Table 4; Figure 1), though this may be due to low sample size. To test whether wing-propelled diving selects for enlarged forelimb muscle masses, I compared birds which use their wings for aquatic propulsion to the combined group of non-diving and exclusively foot-propelled divers. I found no difference in the mass of the pectoralis (Table 5; Figure 2) or consistent difference in the mass of the supracoracoideus (Table 6; Figure 3). However, a significant difference for the supracoracoideus was found for 55 of 400 total phylogenetic trees.

To test whether foot-propelled diving selects for decreased pectoral mass to limit overall body mass and facilitate aerial flight (Gadow, 1902; Storer, 1960; Watanabe et al., 2011) or to reduce parasite drag (Wilson et al., 2008), I compared the combined mass of the pectoralis and supracoracoideus versus body mass of exclusively foot-propelled species to all other species and (separately) wing-propelled divers. There was no support for unique intercepts between species which dive exclusively via foot-propulsion and all other birds [Table 7]. There was also no difference in the combined mass of the pectoralis and supracoracoideus between species which utilize aquatic wing propulsion and exclusively foot-propelled species (Table 8).

Wing area versus body mass

Assuming neutral (or near-neutral) buoyancy, the power required for horizontal swimming is determined by drag and therefore proportional to the cross-sectional area of an animal [L^2] (Lovvorn et al., 2001). Alternatively, the power required for aerial flight is determined by lift and is proportional to body mass [L^3] (Ellington, 1984a). To test whether these unique constraints have resulted in different scaling relationships between flightless divers and other birds (Ashmole, 1971; Storer, 1960; Thompson et al., 1998), I compared the relationship of wing area versus body mass between penguins and volant species. I found strong and consistent support for unique intercepts in the relationship of wing area versus body mass between volant and flightless species (Table 9). In other words, penguins, the only flightless species included in the wing dataset, have significantly higher wing-loadings than volant species (Figure 4). However – allowing unique intercepts – there was little consistent support for unique allometries (slopes) between volant and flightless species (Table 9), though the result was significant for 14 of 400 total phylogenetic trees.

To test whether wing-propelled diving selects for small wings due to hydrodynamic drag incurred during wing flapping, I compared the wing areas of species which utilize wing-propelled diving to diving species which are exclusively foot-propelled. I found no support for unique intercepts between wing-propelled divers and exclusively foot-propelled divers (Table 10). However, there was consistent support for unique intercepts between non-diving and pooled divers (Table 11). In other words, diving species have higher wing-loading than do non-divers (Figure 4), perhaps due to selective pressure shared by wing-propelled and foot-propelled divers. Allowing unique intercepts, I found no consistent support for unique allometries (slopes) between diving and non-diving species (Table 11), though the result was significant for 31.5% of the total trees (126 of 400 phylogenetic trees). Thus, while diving birds have smaller wings than non-diving birds for their mass, wing area scales similarly in both groups.

To determine whether divers have wings selected for high speed flight, I tested for the presence of unique intercepts between divers and non-divers in the relationship of second moment of area of the wing (as measured from the proximal edge) versus wing area (Ellington, 1984b; Lovvorn and Jones, 1994). This constitutes a test of whether groups differ in the distribution of the area of their wing. There was no consistent support for unique intercepts between divers and non-divers (Table 12). Furthermore, plotting the dimensionless version of second moment of area (Ellington, 1984b) versus body mass further indicates that the wings of diving species are no more pointed that non-diving species (Figure 5).

Discussion:

Foot-propelled and wing-propelled diving in birds have not co-evolved with the enlargement of muscle masses for aquatic locomotion. Previous authors have argued that foot-propelled diving has co-evolved with enlarged hindlimb muscles to power swimming (Gadow, 1902; Storer, 1960; Watanabe et al., 2011), and that wing-propelled diving has co-evolved with enlarged forelimb muscles (Kovacs and Meyers, 2000; Storer, 1960), particularly the supracoracoideus, to power the upstroke of the wing in a denser fluid. Together, this would seem to favor specialization toward either exclusively foot-propelled or wing-propelled aquatic locomotion in volant species, as an enlargement of both locomotor modules would increase body mass and thereby limit flight performance (Ellington, 1984a; Watanabe et al., 2011). As well, increased pectoral muscle mass might increase the width of the body (but see Stettenheim, 1959), thereby increasing hydrodynamic drag (Wilson et al., 2008). However, the comparative data analyzed here indicate that aquatic locomotion has not favored the enlargement of muscle masses in either the hindlimbs of foot-propelled divers (Figure 1) or the forelimbs of wing-propelled divers (Figures 2 & 3). While the supracoracoideus is enlarged relative to the pectoralis in four groups of wing-propelled divers [penguins, alcids, diving petrels, and dippers] according to the literature (Baldwin, 1988; Goodge, 1957; Hartman, 1961; Kuroda, 1967), this trend is not diagnostic of birds which use their wings underwater.

Furthermore, despite the widespread view that exclusively foot-propelled divers have smaller flight muscle masses (pectoralis + supracoracoideus) than do other species (Storer, 1960; Watanabe et al., 2011; Wilson et al., 2008), they are not significantly different from the flight muscle masses of other birds (Table 7), including species which utilize wing-propelled diving (Table 8).

I found no evidence that wing-propelled diving has selected for small wings to reduce hydrodynamic drag during wing-flapping. While species which utilize wing-propelled diving do have higher wing-loadings than non-diving species (Figure 4), this pattern is shared with exclusively foot-propelled divers (Table 10). This suggests that diving has selected for small wings irrespective of whether they are used for thrust production, indicating that this pattern is driven either by relaxed selection against high flight speeds (Bridge, 2004; Kovacs and Meyers, 2000; Lovvorn and Jones, 1994) or selection for reduced buoyancy (Wilson et al., 1992a). This result is in contrast with those of Elliot et al. (2013), either because these authors did not account for phylogenetic effects in their analyses, or because they did not consider shearwaters to be wing-propelled divers (Elliott et al., 2013).

Lovvorn and Jones (1994) first argued that high wing-loading in foot-propelled divers might be the result of a relaxed selection *against* fast flight, as diving birds may not benefit significantly from the rapid takeoffs, maneuverability, and slow flight performance afforded by low wing-loading (Norberg, 1990; Rayner, 1988). Diving species can submerge to avoid predators, eliminating the requirement to escape through aerial flight. As well, life on water provides a "runway" for landings and take-offs, reducing the need for maneuverability in slow flight (Kovacs and Meyers, 2000; Lovvorn and Jones, 1994). Kovacs and Meyers (2000) [citing Lovvorn and Jones (1994)] later extended this hypothesis to wing-propelled divers. Comparative data analyzed here do not support this hypothesis, however. Importantly, Lovvorn and Jones (1994) state that relaxed selection against high-speed flight would favor "…low-area, pointed wings for fast flight…". However, I found that the wings of diving birds are no more pointed, in terms of second moment of area (Ellington, 1984b), than other birds (Table 12), including birds of similar masses (Figure 5).

The 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 (Wilson et al., 1992a). Wilson et al., (1992) predicted that high wing-loading in foot-propelled species is the result of selection for reduced buoyancy, given that wings trap air both between and within the feathers (i.e., within the rachis). Indeed, the considerable amount of air entrapped between feathers is readily visible in videos of birds diving (https://www.youtube.com/watch?v=nbnJsc-GPaA). While some of the air trapped between feathers can be shed in the early stages of the dive, air volumes in the rachis cannot. Because counteracting buoyancy constitutes a major component of the total energy required to dive (Lovvorn and Jones, 1991; Stephenson, 1994), selection for diving seems to have favored high wing-loading as a means to reduce buoyancy. Although diving birds do not have wings selected for high-speed flight, the fact that diving birds can avoid predators and slow flight using water has likely been important in facilitating this pattern.

Alternatively, Wilson et al., (2008) also suggested that high wing-loading in foot-propelled species could be the result of selection to reduce drag. Foot-propelled divers hold their wings close to the body while diving. Still, large wings may increase hydrodynamic drag by expanding a bird's wake or via feather vibration (Lovvorn et al., 2001; Wilson et al., 2008). In wing-propelled divers, the wings are held out from the body and do not contribute to parasite drag. However, smaller wings may still experience lower profile drag due to reduce vibration. Thus, my results could also indicate that hydrodynamic drag has selected for small wings in diving birds, including wing-propelled divers, driven by the effects of hydro-elastic flutter. However, wing-propelled divers flex their wings during diving, which appears to increase the stiffness of the feathers beyond the point at which substantial vibrations can manifest during wing-flapping. In addition, cormorants and anhingas, which have wettable feathers, have exceptionally large wings relative to other divers, suggesting that the buoyancy is the driving force behind high wing-loading in diving birds.

It is not obvious how one might test between these two possible explanations given comparative data. Comparing the length of the primary feathers to the length of the wing of diving and non-diving birds – or, alternatively, the length of the wing to the length of the wing bones (Lapsansky, in prep) – might be illustrative. As primary feathers add to buoyancy, this may also explain why diving birds appear to have elongated covert feathers relative to non-diving species (Wang and Clarke, 2015). In other words, it might not be that diving birds have longer coverts, but shorter primaries, to reduce buoyancy. However, possessing shorter primaries might also act to reduce hydro-elastic flutter of the feathers, which would likely decrease drag to some degree. Thus, the benefits of high wing-loading for diving may be two-fold. Empirical testing, using 3D printed models of birds with varied primary lengths and flexibilities, would be one mechanism through which to explore these questions.

Low mass-specific wing area – i.e., high wing-loading – is a pattern shared by both wing-propelled and foot-propelled divers. Thus, it is surprising that the view that "wing-propelled diving favors small wings" is especially pervasive throughout scientific literature (Bock and von Wahlert, 1965; Cody, 1973; Elliott et al., 2013; Kuroda, 1954; Pennycuick, 1987; Pennycuick, 2008; Rayner, 1988; Storer, 1960; Thaxter et al., 2010; Thompson et al., 1998). Though diving seems to select for smaller wings, traditional explanations fail to explain this pattern in wing-propelled divers. Assuming neutral buoyancy, the power required for horizontal swimming is determined by drag and proportional to the area of an animal [L^2] (Lovvorn et al., 2001), while the power required for aerial flight is determined by lift and is proportional to body mass [L^3] (Ellington, 1984a). Many explanations for high wing-loading in wing-propelled divers rest on the disparity between these allometric relationships. However, these arguments do not explain why the wing area of a given wing-propelled diver cannot be larger than the scaling relationship between drag and body area, and pertain only to the scaling exponent, but not the intercept of said scaling relationship. Assuming continuity of

Reynolds number, forces are ~3.5 times greater in water than in air. Thus, propulsors *can* be smaller in water and still produce their requisite force (Denny, 1993), but they do not *need* to be smaller.

While flightless wing-propelled divers [penguins] do have high wing-loading, there is little evidence of that wing area scales differently in flightless wing-propelled divers than in other birds (Table 9, Figure 4). However, this might be due to low sample size or because all flightless wing-propelled divers are from a single clade. Finally, all groups which use their wings underwater except penguins (Order: *Sphenisciformes*) fold their wing during aquatic use; therefore, if a small wing is detrimental to aerial flight capabilities (Ellington, 1984a), it is unclear why wing-propelled divers would not simply fold their wing to a greater extent underwater and retain a large wing. Further, if wing-propelled divers are constrained by available muscle power, they can (and do) flap their wings more slowly in water (Lapsansky et al., 2020).

It is important to remember that the wings of wing-propelled divers generate thrust as well as suffering drag. While a smaller wing experiences lower drag, it also produces less useful force and is less efficient. This conclusion stems from the equations for lift and drag (Denny, 1993; Vogel, 1994) as well as from experiments with engineered, dual-medium wings (Izraelevitz et al., 2018; Lock et al., 2010; Lock et al., 2012; Lock et al., 2013; Lock et al., 2014). In fact, all else being equal, a larger wing will provide greater Froude propulsion efficiency – defined as the ratio of energy required to drive a propulsor to the power imparted to the fluid – than a smaller wing. This is because a larger wing can generate the same thrust while imparting a smaller acceleration to the fluid by interacting with a larger fluid volume (Vogel, 1994).

Still, there is good reason to expect that wing-propelled diving would favor a shorter wing. If birds are constrained by the stress experienced at the shoulder (which must be countered by the force of muscle contractions), then a shorter wing could produce similar forces while experiencing lower torques, as the center of that force is experienced closer to the shoulder (i.e., with a shorter moment arm) (Fish, 2016). However, I found little evidence that this pressure has shaped the wing sizes of wing-propelled diving birds to be different from those of foot-propelled divers (Figure 4). Additionally, it is unclear why wing-propelled diving would favor short wings in the face of decreasing aerial flight performance when the wing could simply be folded more to reduce the torque on the shoulder.

Classifying diving species based on their apparent morphological specialization for diving is common. Implicit in this practice is the idea that diving performance and efficiency are negatively correlated with performance and efficiency in air. This tradeoff is evident in mammals (Fish, 1996; Fish, 2016) [streamlined bodies and lift-producing appendages constrain the performance and efficiency of walking] but is less extreme in birds, especially with regards to flight (Lapsansky and Tobalske, 2019; Lapsansky et al., 2020; but see Elliott et al., 2013, Lovvorn and Jones, 1994, Prange and Schmidt-Nielsen, 1970, Thaxter et al., 2010, and Watanabe et al. 2011). New technologies have revealed that even seemingly unspecialized diving birds can dive for far longer and far deeper than their outward appearances would suggest (Chastel and Bried, 1996; Rayner et al., 2008; Taylor, 2008).

It is important to recognize that diving has evolved independently multiple times. Each lineage occupies a morpho-space surrounding a “local optimum” of trait values, given their reliance on aquatic locomotion and phylogenetic history. For example, cormorants and shags have retained wings large enough to glide and soar despite their reliance on diving – reducing the costs of buoyancy through partially wettable plumage (Grémillet et al., 2005; Wilson et al., 1992a). Obligate plunge divers like gannets and boobies have relatively large wings and similarly reduce buoyancy costs by using momentum to carry themselves through the early stages of their dives, wherein buoyancy is greatest. Thus, it is not appropriate to classify species based on their morphological specialization for diving and then assume that the traits of those species improve diving performance. Indeed, comparing the dive depth and durations of species indicates that less-specialized groups often have greater dive performance for their size (Halsey et al., 2006; Watanuki and Burger, 1999).

To better illustrate this point, I curated data describing the mean dive durations of 127 species from 9 orders from the literature and by timing dives from videos available from the Macaulay Library's digital collection. As demonstrated by previous studies (Halsey et al., 2006; Watanuki and Burger, 1999), alcids have greater dive performance for their body sizes than do penguins, despite retaining aerial flight. Furthermore, dippers, which look not unlike their non-aquatic relatives, fall well-within the trend for morphologically specialized diving birds (Figure 6). If future authors deem the binary categories used here insufficient, they should use the residuals of this or other allometric relationships of dive performance, rather than perceived morphological specialization.

Diving does not require enlarged muscle masses and wing-propelled diving does not require higher wing-loading than possessed by foot-propelled divers. Thus, it is unclear why exclusively foot-propelled species do not use their wings even during deep dives in open-water, but the efficiency of muscle contractions may be important.

The stroke velocities of wing-propelled divers are substantially lower in water than in air (Kikuchi et al., 2015; Lapsansky et al., 2020). This parameter is likely important in determining the cost of locomotion given that it should be proportional to the contractile velocity of the pectoralis and the supracoracoideus. Muscle fibers of a given fiber type and myosin isoform are most efficient at converting metabolic energy into mechanical power over a narrow range of contractile velocities (Goldspink, 1977; He et al., 2000; Reggiani et al., 1997; Rome et al., 1988). Thus, volant wing-propelled diving birds might maintain two populations of muscle fibers (Kovacs and Meyers, 2000; Meyers et al., 1992) or contract their muscles at inefficient speeds in air or water (Lapsansky et al., 2020), but this is likely not the case for exclusively foot-propelled species, as the maintenance of muscle represents a substantial energetic cost (Wilson et al., 2008). Therefore, the metabolic costs of contracting the pectoralis and supracoracoideus at inefficient velocities might negate any hydrodynamic benefits, thus inhibiting exclusively foot-propelled species from using their wings underwater even during deep dives in open water.

In conclusion, owing to the clear and distinct differences between life in air and life in water, as well as the considerable variation in locomotor habits within and between species, diving birds remain a powerful system in which to study the evolution of form, function, and behavior. Here, I review what is known about the biomechanics of foot-propelled and wing-propelled aquatic locomotion in birds to facilitate future research and test hypotheses using new and published data. Much remains to be learned about the evolution and functional morphology of these charismatic animals.

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Table 1: Aquatic locomotor habits of birds. All orders of birds are considered with increased resolution to family, genera, and species levels where variation exists. The terrestrial (Terr.) habits of each group are categorized as either WR (walking/running) or IL (infrequent/labored). The aerial (Aerial) habits of each group are categorized as NV (non-volant), IF (infrequent flight), GS (gliding/soaring + flapping), CF (continuous flapping), or FB (flap-bounding). For both surface and submerged aquatic habits, the use of an appendage pair (FP – foot-propelled, WP – wing-propelled) for steady-state aquatic propulsion is indicated by a filled rectangle corresponding to that group, and all diving and swimming groups are categorized as either obligate (O) or facultative (F) divers.

							Aquatic								
							Surface			Submerged					
	Order	***Family***	***Genus***	***Species***	**Terr.**	**Aerial**	FP	WP	Rel.	FP	WP	*EM*	Bent	Pela	Rel.
1	Struthioniformes	Struthionidae	-	-	*WR*	*NV*	▨	▨	▨	▨	▨	▨	▨	▨	▨
2	Rheiformes	Rheidae	-	-	*WR*	*NV*	▨	▨	▨	▨	▨	▨	▨	▨	▨
3	Tinamiformes	Tinamidae	-	-	*WR*	*IF*	▨	▨	▨	▨	▨	▨	▨	▨	▨
4	Casuariiformes	Casuariidae	-	-	*WR*	*NV*	▨	▨	▨	▨	▨	▨	▨	▨	▨
5	Apterygiformes	Apterygidae	-	-	*WR*	*NV*	▨	▨	▨	▨	▨	▨	▨	▨	▨
6	Anseriformes	Anhimidae	-	-	*WR*	*GS*	🟨		*F*	▨	▨	▨	▨	▨	▨
7		Anseranatidae	Anseranas	semipalmata	*WR*	*CF*	🟨		*O*	▨	▨	▨	▨	▨	▨
8		Anatidae	Dendrocygna	-	*WR*	*CF*	🟨		*O*	🟩		*S*	🟪		*O*
9			Thalassornis	leuconotus	*IL*	*CF*	🟨		*O*	🟩		*S*	🟪		*O*
10			Anser	-	*WR*	*CF*	🟨		*O*	▨	▨	▨	▨	▨	▨
11			Branta	-	*WR*	*CF*	🟨		*O*	▨	▨	▨	▨	▨	▨
12			Cereopsis	novaehollandiae	*WR*	*CF*	🟨		*F*	▨	▨	▨	▨	▨	▨
13			Stictonetta	naevosa	*WR*	*CF*	🟨		*O*	▨	▨	▨	▨	▨	▨
14			Cyanochen	cyanoptera	*WR*	*CF*	🟨		*F*	▨	▨	▨	▨	▨	▨
15			Cygnus	-	*WR*	*CF*	🟨		*O*	▨	▨	▨	▨	▨	▨
16			Coscoroba	coscoroba	*WR*	*CF*	🟨		*O*	▨	▨	▨	▨	▨	▨
17			Sarkidiornis	-	*WR*	*CF*	🟨		*O*	▨	▨	▨	▨	▨	▨
18			Pteronetta	hartlaubii	*WR*	*CF*	🟨		*O*	▨	▨	▨	▨	▨	▨
19			Oressochen	-	*WR*	*CF*	🟨		*F*	▨	▨	▨	▨	▨	▨
20			Chloephaga	-	*WR*	*CF*	🟨		*F*	▨	▨	▨	▨	▨	▨
21			Radjah	radjah	*WR*	*CF*	🟨		*O*	▨	▨	▨	▨	▨	▨
22			Alopochen	aegyptiaca	*WR*	*CF*	🟨		*O*	▨	▨	▨	▨	▨	▨
23			Tadorna	-	*WR*	*CF*	🟨		*O*	▨	▨	▨	▨	▨	▨
24			Plectropterus	gambensis	*WR*	*CF*	🟨		*O*	▨	▨	▨	▨	▨	▨
25			Tachyeres	patachonicus	*WR*	*IF*	🟨	🟨	*O*	🟩	🟩	*S*	🟪		*O*
26				pteneres	*WR*	*NV*	🟨	🟨	*O*	🟩	🟩	*S*	🟪		*O*
27				brachypterus	*WR*	*NV*	🟨	🟨	*O*	🟩	🟩	*S*	🟪		*O*
28				leucocephalus	*WR*	*NV*	🟨	🟨	*O*	🟩	🟩	*S*	🟪		*O*
29			Lophonetta	specularioides	*WR*	*CF*	🟨		*O*	▨	▨	▨	▨	▨	▨
30			Speculanas	specularis	*WR*	*CF*	🟨		*O*	▨	▨	▨	▨	▨	▨
31			Cairina	moschata	*WR*	*CF*	🟨		*O*	▨	▨	▨	▨	▨	▨
32			Nettapus	pulchellus	*IL*	*CF*	🟨		*O*	*?*	*?*	*S*	🟪		*F*
33				coromandelianus	*IL*	*CF*	🟨		*O*	*?*	*?*	*S*	🟪		*F*
34				auritus	*IL*	*CF*	🟨		*O*	*?*	*?*	*S*	🟪		*F*
35			Callonetta	leucophrys	*WR*	*CF*	🟨		*O*	▨	▨	▨	▨	▨	▨
36			Aix	-	*WR*	*CF*	🟨		*O*	🟩	🟩	*S*	🟪		*F*
37			Chenonetta	-	*WR*	*CF*	🟨		*O*	▨	▨	▨	▨	▨	▨
38			Amazonetta	brasilensis	*WR*	*CF*	🟨		*O*	▨	▨	▨	▨	▨	▨
39			Hymenolaimus	malacorhynchos	*WR*	*CF*	🟨		*O*	🟩	🟩	*S*	🟪		*O*
40			Merganetta	armata	*WR*	*CF*	🟨		*O*	🟩		*S*	🟪		*O*
41			Salvadorina	waigiuensis	*WR*	*CF*	🟨		*O*	🟩		*S*	🟪		*O*
42			Sibirionetta	formosa	*WR*	*CF*	🟨		*O*	▨	▨	▨	▨	▨	▨
43			Spatula	-	*WR*	*CF*	🟨		*O*	🟩	🟩	*S*	🟪		*F*
44			Mareca	-	*WR*	*CF*	🟨		*O*	🟩	🟩	*S*	🟪		*F*
45			Anas	-	*WR*	*CF*	🟨		*O*	🟩	🟩	*S*	🟪		*F*
46				capensis	*WR*	*CF*	🟨		*O*	*?*	*?*	*S*	🟪		*?*
47				aucklandica	*WR*	*NV*	🟨		*O*	🟩	🟩	*S*	🟪		*O*
48				nesiotis	*WR*	*NV*	🟨		*O*	*?*	*?*	*S*	🟪		*?*
49				chlorotis	*WR*	*CF*	🟨		*O*	🟩	🟩	*S*	🟪		*O*
50			Malacorhynchus	membranaceus	*WR*	*CF*	🟨		*O*	▨	▨	▨	▨	▨	▨
51			Marmaronetta	angustirostris	*WR*	*CF*	🟨		*O*	*?*	*?*	*S*	🟪		*?*
52			Rhodonessa	caryophyllacea	*WR*	*CF*	🟨		*O*	*?*	*?*	*S*	🟪		*?*
53			Asarcornis	scutulata	*WR*	*CF*	🟨		*O*	*?*	*?*	*S*	🟪		*F*
54			Netta	-	*WR*	*CF*	🟨		*O*	🟩		*S*	🟪		*O*
55			Aythya	-	*IL*	*CF*	🟨		*O*	🟩		*S*	🟪		*O*
56			Polysticta	stelleri	*WR*	*CF*	🟨		*O*	🟩	🟩	*S*	🟪		*O*
57			Somateria	-	*WR*	*CF*	🟨	🟨	*O*	🟩	🟩	*S*	🟪		*O*
58			Histrionicus	histrionicus	*WR*	*CF*	🟨		*O*	🟩	🟩	*S*	🟪		*O*
59			Melanitta	perspicillata	*IL*	*CF*	🟨		*O*	🟩	🟩	*S*	🟪		*O*
60				fusca	*IL*	*CF*	🟨		*O*	🟩	🟩	*S*	🟪		*O*
61				deglandi	*IL*	*CF*	🟨		*O*	🟩	🟩	*S*	🟪		*O*
62				stejnegeri	*IL*	*CF*	🟨		*O*	🟩	🟩	*S*	🟪		*O*
63				nigra	*IL*	*CF*	🟨		*O*	🟩		*S*	🟪		*O*
64				americana	*IL*	*CF*	🟨		*O*	🟩		*S*	🟪		*O*
65			Clangula	hyemalis	*IL*	*CF*	🟨		*O*	🟩	🟩	*S*	🟪	🟪	*O*
66			Bucephala	-	*IL*	*CF*	🟨		*O*	🟩		*S*	🟪		*O*
67			Mergellus	albellus	*IL*	*CF*	🟨		*O*	🟩		*S*	🟪	🟪	*O*
68			Lophodytes	cucullatus	*IL*	*CF*	🟨		*O*	🟩		*S*	🟪	🟪	*O*
69			Mergus	-	*IL*	*CF*	🟨		*O*	🟩		*S*	🟪	🟪	*O*
70			Heteronetta	atricapilla	*WR*	*CF*	🟨		*O*	🟩		*S*	🟪		*O*
71			Nomonyx	dominicus	*IL*	*CF*	🟨		*O*	🟩		*S*	🟪		*O*
72			Oxyura	-	*IL*	*CF*	🟨		*O*	🟩		*S*	🟪		*O*
73			Biziura	lobata	*IL*	*CF*	🟨		*O*	🟩		*S*	🟪		*O*
74	Galliformes	-	-	-	*WR*	*IF*	▨	▨	▨	▨	▨	▨	▨	▨	▨
75	Phoenicopteriformes	-	-	-	*WR*	*GS*	🟨		*O*	▨	▨	▨	▨	▨	▨

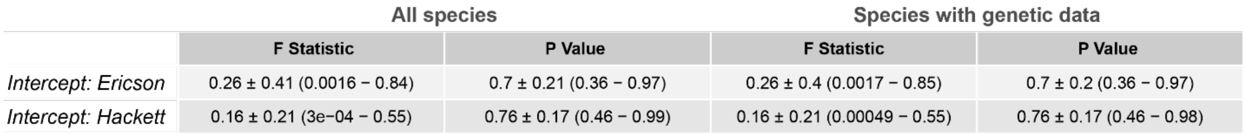
76	Podecipidiformes	Podicepidae	Rollandia	rolland	IL	CF	🟨		O	🟦		S	🟪	🟪	O
77			Rollandia	microptera	IL	NV	🟨		O	🟦		S	🟪	🟪	O
78			Tachybaptus	-	IL	CF	🟨		O	🟦		S	🟪	🟪	O
79			Podilymbus	podiceps	IL	CF	🟨		O	🟦		S	🟪	🟪	O
80			Podilymbus	gigas	IL	NV	🟨		O	🟦		S	🟪	🟪	O
81			Poliocephalus	-	IL	CF	🟨		O	🟦		S	🟪	🟪	O
82			Podiceps	-	IL	CF	🟨		O	🟦		S	🟪	🟪	O
83			Podiceps	taczanowskii	IL	NV	🟨		O	🟦		S	🟪	🟪	O
84			Aechmophorus	-	IL	CF	🟨		O	🟦		S	🟪	🟪	O
85	Columbiformes	Columbidae	-	-	WR	GS	▨	▨	▨	▨	▨	▨	▨	▨	▨
86	Mesitornithiformes	Mesitornithidae	-	-	WR	IF	▨	▨	▨	▨	▨	▨	▨	▨	▨
87	Pterocliformes	Pteroclidae	-	-	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
88	Otidiformes	Otididae	-	-	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
89	Musophagiformes	Musophagidae	-	-	WR	IF	▨	▨	▨	▨	▨	▨	▨	▨	▨
90	Cuculiformes	Cuculidae	-	-	WR	GS, IF	▨	▨	▨	▨	▨	▨	▨	▨	▨
91	Caprimulgiformes	Podargidae	-	-	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
92		Caprimulgidae	-	-	IL	GS	▨	▨	▨	▨	▨	▨	▨	▨	▨
93		Nyctibiidae	Nyctibius	-	IL	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
94		Steatornithidae	Steatornis	caripensis	IL	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
95		Aegothelidae	Aegotheles	-	?	?	▨	▨	▨	▨	▨	▨	▨	▨	▨
96		Apodidae	-	-	IL	GS	▨	▨	▨	▨	▨	▨	▨	▨	▨
97		Hemiprocnidae	Hemiprocne	-	IL	GS	▨	▨	▨	▨	▨	▨	▨	▨	▨
98		Trochilidae	-	-	IL	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
99	Opisthocomidiformes	Opisthocomidae	Opisthocomus	hoazin	WR	IF	🟨		F	▨	▨	▨	▨	▨	▨
100	Gruiformes	Sarothruridae	-	-	WR	IF	🟨		?	▨	▨	▨	▨	▨	▨
101		Rallidae	-	-	WR	IF	🟨		O	?	?	S	🟪		F
102			Fulica	-	WR	IF	🟨		O	🟦		S	🟪		O
103		Heliornithidae	-	-	WR	IF	🟨		O	?	?	S	🟪		F
104		Aramiidae	Aramus	guarauna	WR	CF	🟨		F	▨	▨	▨	▨	▨	▨
105		Psophiidae	-	-	WR	IF	▨	▨	▨	▨	▨	▨	▨	▨	▨
106		Gruiidae	-	-	WR	GS	🟨		F	▨	▨	▨	▨	▨	▨
107	Charadriiformes	Chionidae	Chionis	-	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
108		Pluvianellidae	Pluvianellus	socialis	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
109		Burhinidae	-	-	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
110		Pluvianidae	Pluvianus	aegyptius	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
111		Recurvirostridae	Himantopus	-	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
112			Cladorhynchus	-	WR	CF	🟨		F	▨	▨	▨	▨	▨	▨
113			Recurvirostra	-	WR	CF	🟨		O	▨	▨	▨	▨	▨	▨
114		Ibidorhynchidae	Ibidorhyncha	struthersii	WR	CF	🟨	?	O	▨	▨	▨	▨	▨	▨
115		Haematopodidae	-	-	WR	CF	?		?	▨	▨	▨	▨	▨	▨
116		Charadriidae	-	-	WR	CF	🟨		F	▨	▨	▨	▨	▨	▨
117		Pedionomidae	-	-	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
118		Thinocoridae	-	-	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
119		Rostratulidae	-	-	WR	CF	🟨		?	▨	▨	▨	▨	▨	▨
120		Jacanidae	-	-	WR	CF	🟨		F	▨	▨	▨	▨	▨	▨
121		Scolopacidae	Bartramia	longicauda	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
122			Numenius		WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
123			Limosa		WR	CF	🟨		F	▨	▨	▨	▨	▨	▨
124			Arenaria		WR	CF	🟨		F	▨	▨	▨	▨	▨	▨
125			Prosobonia		WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
126			Calidris		WR	CF	🟨		F	▨	▨	▨	▨	▨	▨
127			Limnodromus		WR	CF	🟨		F	▨	▨	▨	▨	▨	▨
128			Lymnocryptes	minimus	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
129			Scolopax		WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
130			Coenocorypha		WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
131			Gallinago		WR	CF	🟨		F	▨	▨	▨	▨	▨	▨
132			Xenus	cinereus	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
133			Phalaropus		WR	CF	🟨		O	▨	▨	▨	▨	▨	▨
134			Actitis		WR	CF	🟨		F	▨	▨	▨	▨	▨	▨
135			Tringa		WR	CF	🟨		F	▨	▨	▨	▨	▨	▨
136		Turnicidae	-	-	WR	IF	▨	▨	▨	▨	▨	▨	▨	▨	▨
137		Dromadidae	-	-	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
138		Glareolidae	-	-	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
139		Stercocariidae	-	-	WR	GS	🟨		O	▨	▨	▨	▨	▨	▨
140		Alcidae	Alle	alle	IL	CF	🟨		O		🟦	S		🟪	O
141			Uria	-	IL	CF	🟨		O		🟦	S		🟪	O
142			Alca	torda	IL	CF	🟨		O		🟦	S		🟪	O
143			Cepphus	-	WR	CF	🟨	🟨	O	🟦	🟦	S	🟪	🟪	O
144			Brachyramphus	-	IL	CF	🟨		O		🟦	S		🟪	O
145			Synthliboramphus	-	IL	CF	🟨		O		🟦	S		🟪	O
146			Ptychoramphus	aleuticus	IL	CF	🟨		O		🟦	S		🟪	O
147			Aethia	-	IL	CF	🟨		O		🟦	S		🟪	O
148			Cerorhinca	-	WR	CF	🟨		O		🟦	S		🟪	O
149			Fratercula	-	WR	CF	🟨		O		🟦	S		🟪	O
150		Laridae	-	-	WR	GS	🟨		O	?		P	🟪	🟪	O
151	Eurypygiformes	Rhynochetidae	Rhynochetos	jubatus	WR	NV	▨	▨	▨	▨	▨	▨	▨	▨	▨
152		Eurypygidae	Eurypyga	helias	WR	GS	▨	▨	▨	▨	▨	▨	▨	▨	▨
153	Phaethontiformes	Phaethontidae	Phaethon	-	IL	GS	?		?	?	?	P		🟪	F
154	Gaviiformes	Gaviidae	Gavia	-	IL	CF	🟨		O	🟦		S	🟪	🟪	O
155	Sphenisciformes	Spheniscidae	-	-	WR	NV		🟨	O		🟦	S		🟪	O

156	Procellariformes	Diomedeidae	-	-	WR	GS	🟨		O	🟩	🟩	S, P		🟪	F
157		Oceanitidae	-	-	WR	GS	🟨		O	🟩	🟩	S		🟪	F
158		Hydrobatidae	-	-	WR	GS	🟨		O	🟩	🟩	S		🟪	F
159		Procellariidae	Macronectes	-	WR	GS	🟨		O	🟩	🟩	S, P		🟪	F
160			Fulmarus	-	IL	GS	🟨		O	🟩	🟩	S, P		🟪	F
161			Thalassoica	antarctica	IL	GS	🟨		O	🟩	🟩	S, P		🟪	O
162			Daption	capense	IL	GS	🟨		O	🟩	🟩	S, P		🟪	O
163			Pagodroma	nivea	IL	GS	🟨		O	🟩	🟩	S, P		🟪	O
164			Aphrodroma	brevirostris	IL	GS	🟨		O	🟩	🟩	S, P		🟪	?
165			Pterodroma	-	IL	GS	🟨		O	🟩	🟩	S, P		🟪	?
166			Halobaena	caerulea	IL	GS	🟨		O	🟩	🟩	S, P		🟪	F
167			Pachyptila	-	IL	GS	🟨		O	🟩	🟩	S, P		🟪	F
168			Bulweria	-	IL	GS	🟨		O	🟩	🟩	?		🟪	?
169			Pseudobulweria	-	IL	GS	🟨		O	🟩	🟩	?		🟪	?
170			Procellaria	-	IL	GS	🟨		O	🟩	🟩	S, P		🟪	O
171			Calonectris	-	IL	GS	🟨		O	🟩	🟩	S, P		🟪	O
172			Ardenna	-	IL	GS	🟨		O	🟩	🟩	S, P		🟪	O
173			Puffinus	-	IL	GS	🟨		O	🟩	🟩	S, P		🟪	O
174			Pelecanoides	-	IL	CF	🟨		O	?	🟩	S, P		🟪	O
175		Ciconiidae	-	-	WR	GS	▨	▨	▨	▨	▨	▨	▨	▨	▨
176	Suliformes	Fregatidae	-	-	IL	GS	▨	▨	▨	▨	▨	▨	▨	▨	▨
177		Sulidae	-	-	IL	GS	🟨		O	🟩	🟩	S, P		🟪	O
178		Anhingidae	-	-	IL	GS	🟨		O	🟩		S	🟪		O
179		Phalacrocoraxidae	-	-	IL	GS	🟨		O	🟩		S	🟪	🟪	O
180			-	harrisi	IL	NV	🟨		O	🟩		S	🟪	🟪	O
181	Pelecaniformes	Pelecanidae	Pelecanus	-	WR	GS	🟨		O	?	?	S, P		🟪	F
182		Balaenicipitidae	Balaeniceps	rex	WR	GS	▨	▨	▨	▨	▨	▨	▨	▨	▨
183		Scopidae	Scopus	umbretta	WR	GS	▨	▨	▨	▨	▨	▨	▨	▨	▨
184		Ardeidae	-	-	WR	GS	🟨		F	▨	▨	▨	▨	▨	▨
185		Threskiornithidae	-	-	WR	GS	▨	▨	▨	▨	▨	▨	▨	▨	▨
186	Cathartiformes	Cathartidae	-	-	WR	GS	▨	▨	▨	▨	▨	▨	▨	▨	▨
187	Accipitriformes	-	-	-	WR	GS	▨	▨	▨	▨	▨	▨	▨	▨	▨
188		Pandionidae	Pandion	-	WR	GS		🟨	F	?	🟩	P	🟪	🟪	O
189	Strigiformes	-	-	-	WR	GS	▨	▨	▨	▨	▨	▨	▨	▨	▨
190	Coliiformes	Coliidae	-	-	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
191	Leptosomiformes	Leptosomidae	Leptosomus	discolor	WR	?	▨	▨	▨	▨	▨	▨	▨	▨	▨
192	Trogoniformes	Trogonidae	-	-	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
193	Bucerotiformes	-	-	-	WR	CF, IF	▨	▨	▨	▨	▨	▨	▨	▨	▨
194	Coraciiformes	Todidae	-	-	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
195		Momotidae	-	-	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
196		Alcedinidae	Alcedo	-	IL	CF	▨	▨	▨		🟩	P	🟪	🟪	O
197			Ceyx	-	IL	CF	▨	▨	▨		?	P	?	?	?
198			Corythornis	-	IL	CF	▨	▨	▨		🟩	P	🟪	🟪	O
199			Corythornis	madagascariensis	IL	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
200			Ispidina	-	IL	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
201			Lacedo	pulchella	IL	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
202			Dacelo	-	IL	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
203			Clytoceyx	rex	IL	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
204			Cittura	cyanotis	IL	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
205			Pelargopsis	-	IL	CF	▨	▨	▨		🟩	P	🟪	🟪	O
206			Halcyon	-	IL	CF	▨	▨	▨		?	P	?	?	?
207			Todiramphus	-	IL	CF	▨	▨	▨		?	P	?	?	?
208			Caridonax	fulgidus	IL	CF	▨	▨	▨		?	P	?	?	?
209			Melidora	macrorrhina	IL	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
210			Actenoides	-	IL	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
211			Syma	-	IL	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
212			Tanysiptera	-	IL	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
213			Megaceryle	-	IL	CF	▨	▨	▨		🟩	P	🟪	🟪	O
214			Ceryle	rudis	IL	CF	▨	▨	▨		🟩	P	🟪	🟪	O
215			Chloroceryle	-	IL	CF	▨	▨	▨		🟩	P	🟪	🟪	O
216		Meropidae	-	-	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
217		Coraciidae	-	-	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
218		Brachypteraciidae	-	-	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
219	Galbuliformes	-	-	-	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
220	Piciformes	-	-	-	WR	CF, FB	▨	▨	▨	▨	▨	▨	▨	▨	▨
221	Cariamiformes	Cariamidae	Cariama	-	WR	IF	▨	▨	▨	▨	▨	▨	▨	▨	▨
222	Falconiformes	Falconidae	-	-	WR	GS	▨	▨	▨	▨	▨	▨	▨	▨	▨
223	Psittaciformes	-	-	-	WR	CF	▨	▨	▨	▨	▨	▨	▨	▨	▨
224		-	Strigops	habroptila	WR	NV	▨	▨	▨	▨	▨	▨	▨	▨	▨
225	Passeriformes	-	-	-	WR	CF, FB, GS	▨	▨	▨	▨	▨	▨	▨	▨	▨
226		Cinclidae	Cinclus	cinclus	WR	CF	🟨		O		🟩	S	🟪		O
227				pallasii	WR	CF	🟨		O		🟩	S	🟪		O
228				mexicanus	WR	CF	🟨		O		🟩	S	🟪		O
229				leucocephalus	WR	CF	🟨		?	▨	▨	▨	▨	▨	▨
230				schulzii	WR	CF	?		?	▨	▨	▨	▨	▨	▨

Table 2: The relative advantages and disadvantages of foot-propelled and wing-propelled diving. References are to papers introducing the preceding hypothesis or to relevant discussions and tests of the preceding hypothesis.

	ADVANTAGES	**DISADVANTAGES**
FOOT-PROPULSION	FP A1: Thrust is produced primarily through drag, which is effective at low swim speeds and for hovering during bottom-feeding (Lovvorn and Liggins, 2002; Ribak et al., 2010).	FP D1: Thrust is produced primarily through drag, which is ineffective at high swim speeds and inefficient across speeds (Fish, 2016; Johansson and Norberg, 2001; Lovvorn and Liggins, 2002; Richman and Lovvorn, 2008) FP D2: Thrust is only produced during extension of the hindlimb, leading to unsteadiness and therefore lowered swimming efficiency (Heath et al., 2006; Lovvorn and Liggins, 2002; Richman and Lovvorn, 2008). FP D3: Foot-propulsion favors increased mass in the pelvic girdle to power the feet underwater, increasing flight costs (Gadow, 1902; Storer, 1960; Watanabe et al., 2011).
WING-PROPULSION	WP A1: Thrust is produced through lift, which is efficient across swim speeds and allows high swim speeds (Johansson and Aldrin, 2002; Johansson and Norberg, 2001; Lovvorn, 2001; Lovvorn and Liggins, 2002). WP A2: Thrust is produced during both half-strokes, reducing unsteadiness and thereby increasing swimming efficiency (Johansson and Aldrin, 2002; Lapsansky and Tobalske, 2019; Lovvorn, 2001; Lovvorn and Liggins, 2002) WP A3: Thrust is produced by the same muscles which power flight, circumventing a conflict of muscle mass allocation (Watanabe et al., 2011).	WP D1: Thrust is produced primarily through lift, which is ineffective at low swim speeds (Richman and Lovvorn, 2008). WP D2: Wing movements are hampered by dense vegetation in benthic environments (Richman and Lovvorn, 2008; Storer, 1960) WP D3: Wing-propulsion favors increased mass in the pectoral girdle, limiting aerial flight capabilities (Kovacs and Meyers, 2000; Storer, 1960) and possibly increasing parasite drag (Wilson et al., 2008). WP D4: Selection for wing-propelled diving favors reduced wing sizes, limiting aerial flight capabilities (Bock and von Wahlert, 1965; Cody, 1973; Elliott et al., 2013; Kuroda, 1954; Pennycuick, 1987; Pennycuick, 2008; Rayner, 1988; Storer, 1960; Thaxter et al., 2010; Thompson et al., 1998)

Table 4: F statistics and P Values of tests for allometric differences in hindlimb muscle mass [g] vs. body mass [g] between obligate foot-propelled diving species and non-diving species. Values shown are mean ± standard deviation (lower 5% quantile – upper 95% quantile) of estimates for 100 trees from the Ericson or Hackett backbone. Column pairs separate tests run on the full set of species (“All species”) and those on a subset of species represented by genetic data in birdtree.org phylogenies (“Species with genetic data”).



	All species		Species with genetic data	
	F Statistic	P Value	F Statistic	P Value
Intercept: Ericson	0.26 ± 0.41 (0.0016 − 0.84)	0.7 ± 0.21 (0.36 − 0.97)	0.26 ± 0.4 (0.0017 − 0.85)	0.7 ± 0.2 (0.36 − 0.97)
Intercept: Hackett	0.16 ± 0.21 (3e−04 − 0.55)	0.76 ± 0.17 (0.46 − 0.99)	0.16 ± 0.21 (0.00049 − 0.55)	0.76 ± 0.17 (0.46 − 0.98)

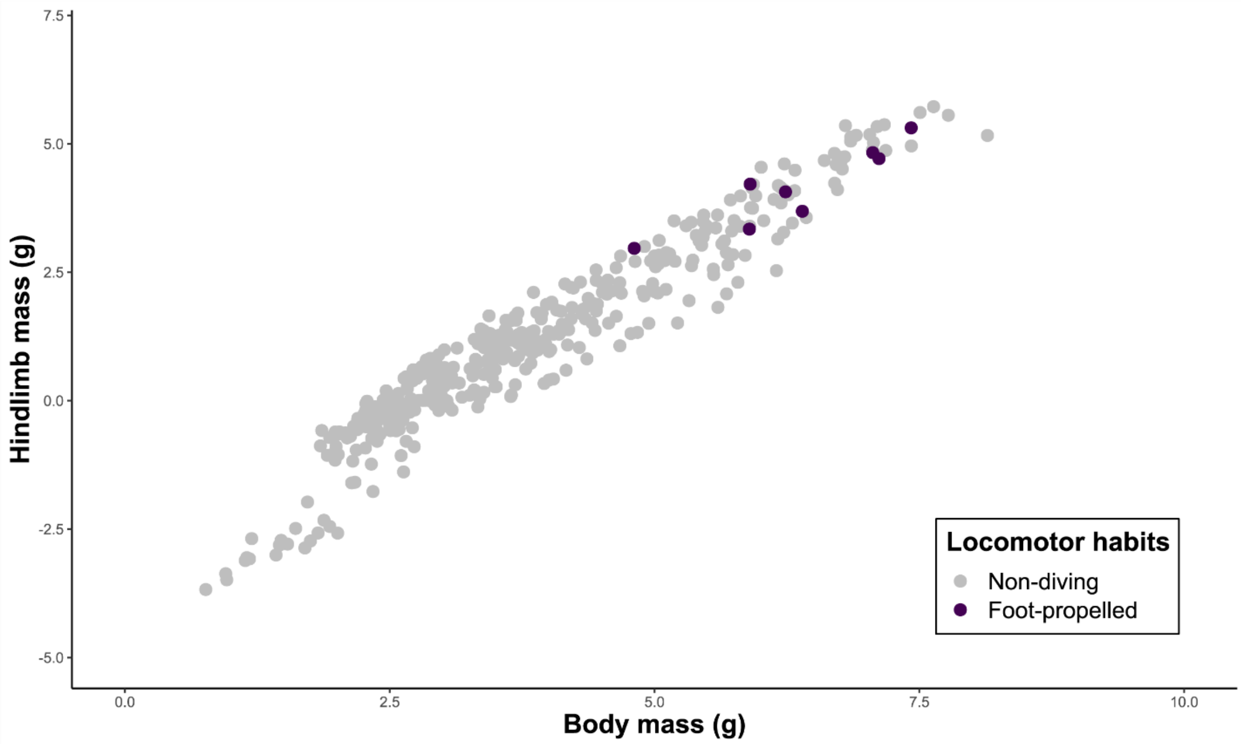
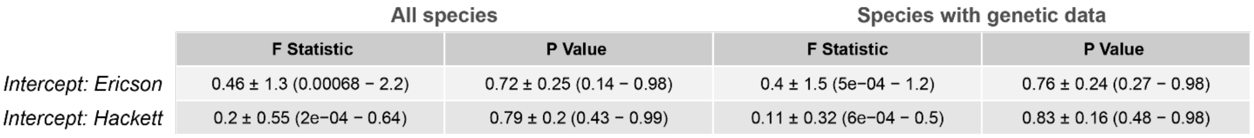


Figure 1: Mass of the muscle in the hindlimb [g] versus body mass [g] for 404 species of birds. Data are presented on a log-log scale**.** Non-diving species are shown in gray and exclusively foot-propelled divers are shown in purple. Data from Hartman (1961).

Table 5: F statistics and P Values of tests for allometric differences in pectoralis muscle mass [g] vs. body mass [g] between diving species which utilize aquatic wing propulsion and non-diving species + exclusively foot-propelled diving species. Values shown are mean ± standard deviation (lower 5% quantile – upper 95% quantile) of estimates for 100 trees from the Ericson or Hackett backbone. Column pairs separate tests run on the full set of species ("All species") and those on a subset of species represented by genetic data in birdtree.org phylogenies ("Species with genetic data").



	All species		Species with genetic data	
	F Statistic	P Value	F Statistic	P Value
Intercept: Ericson	0.46 ± 1.3 (0.00068 − 2.2)	0.72 ± 0.25 (0.14 − 0.98)	0.4 ± 1.5 (5e−04 − 1.2)	0.76 ± 0.24 (0.27 − 0.98)
Intercept: Hackett	0.2 ± 0.55 (2e−04 − 0.64)	0.79 ± 0.2 (0.43 − 0.99)	0.11 ± 0.32 (6e−04 − 0.5)	0.83 ± 0.16 (0.48 − 0.98)

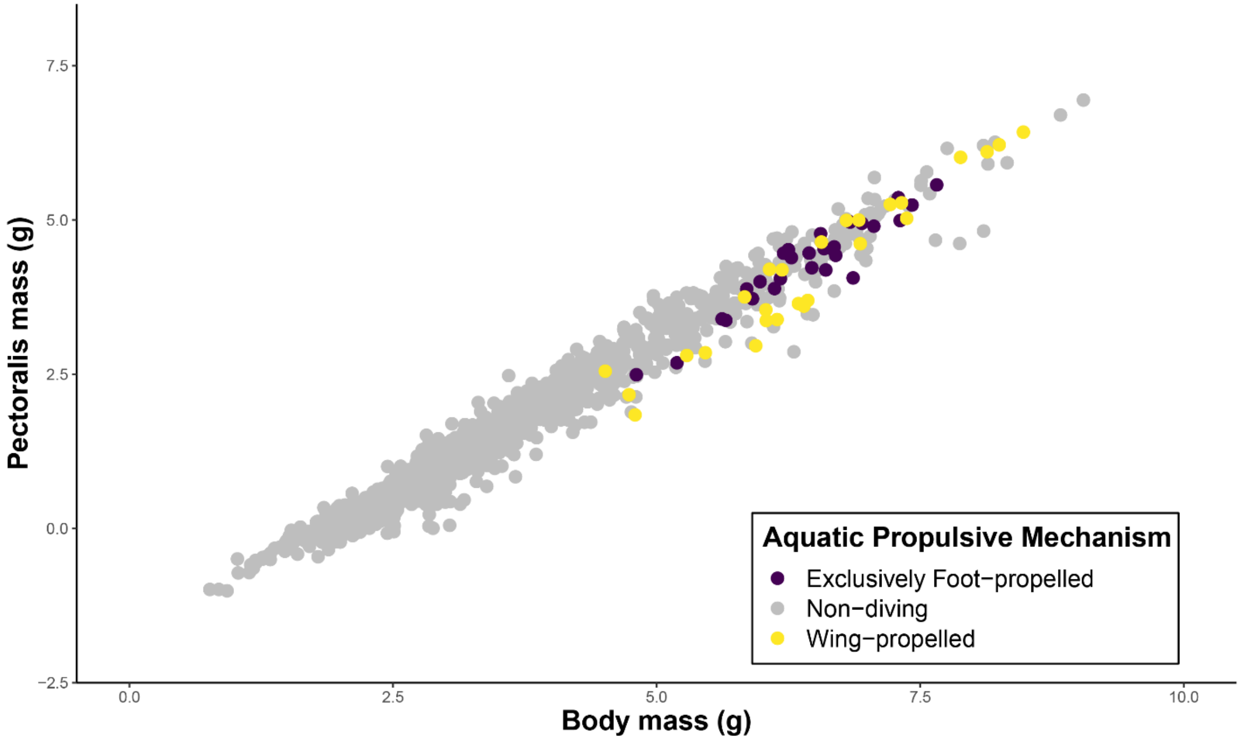
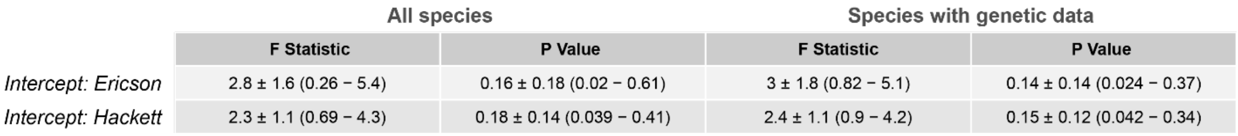


Figure 2: Mass of the pectoralis muscle [g] versus body mass [g] for 1,116 species of birds. Data are presented on a log-log scale. Non-diving species are shown in gray, wing-propelled divers in yellow, and exclusively foot-propelled divers in purple.

Table 6: F statistics and P Values of tests for allometric differences in supracoracoideus muscle mass [g] vs. body mass [g] between diving species which utilize aquatic wing propulsion and non-diving species + exclusively foot-propelled divers. Values shown are mean ± standard deviation (lower 5% quantile – upper 95% quantile) of estimates for 100 trees from the Ericson or Hackett backbone. Column pairs separate tests run on the full set of species (“All species”) and those on a subset of species represented by genetic data in birdtree.org phylogenies (“Species with genetic data”).



	All species		Species with genetic data	
	F Statistic	**P Value**	**F Statistic**	**P Value**
Intercept: Ericson	2.8 ± 1.6 (0.26 − 5.4)	0.16 ± 0.18 (0.02 − 0.61)	3 ± 1.8 (0.82 − 5.1)	0.14 ± 0.14 (0.024 − 0.37)
Intercept: Hackett	2.3 ± 1.1 (0.69 − 4.3)	0.18 ± 0.14 (0.039 − 0.41)	2.4 ± 1.1 (0.9 − 4.2)	0.15 ± 0.12 (0.042 − 0.34)

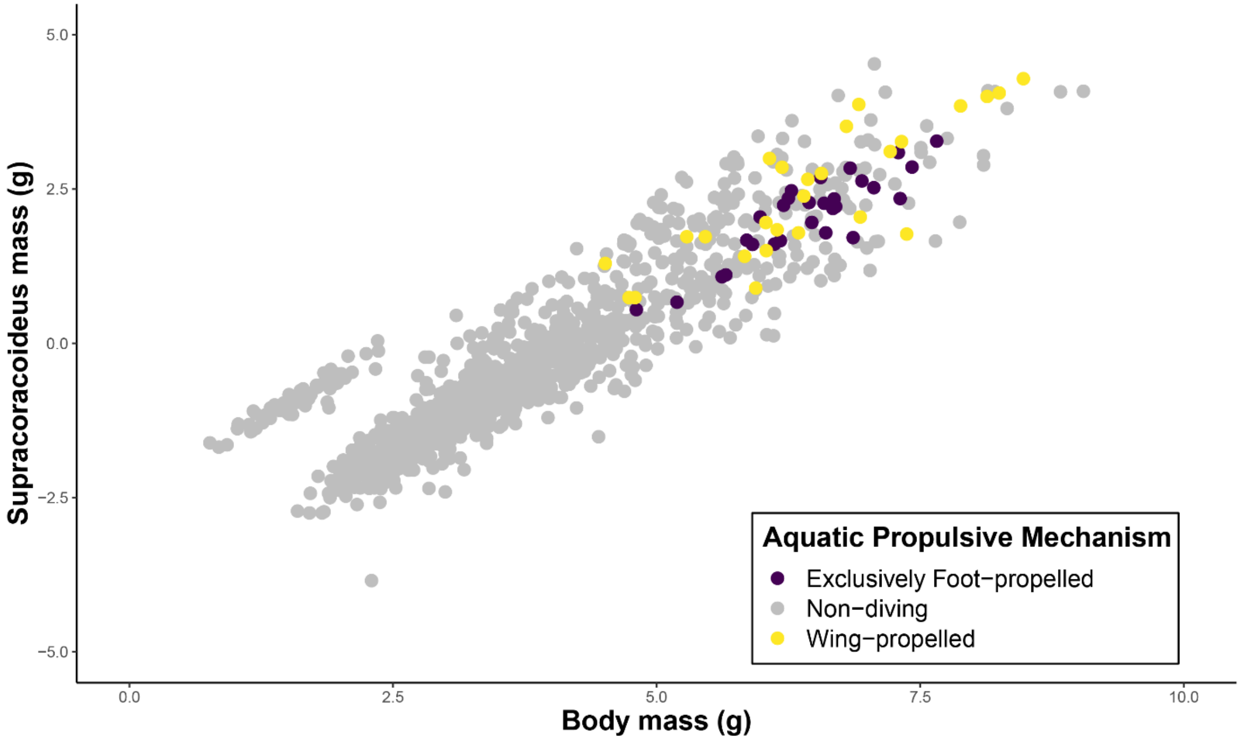
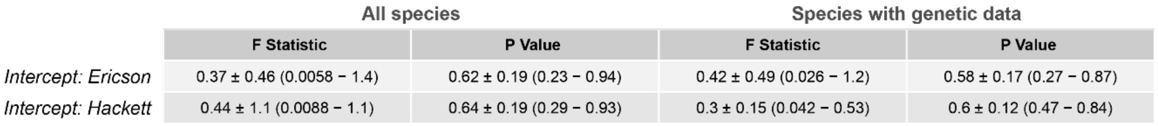


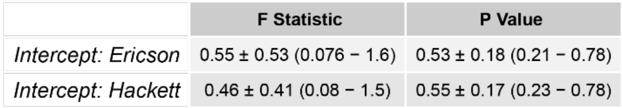
Figure 3: Mass of the supracoracoideus muscle [g] versus body mass [g] for 1,116 species of birds. Data are presented on a log-log scale. Non-diving species are shown in gray, wing-propelled divers in yellow, and exclusively foot-propelled divers in purple.

Table 7: F statistics and P Values of tests for allometric differences in combined pectoral muscle mass (pectoralis + supracoracoideus) [g] vs. body mass [g] between exclusively foot-propelled divers and all other species. Values shown are mean ± standard deviation (lower 5% quantile – upper 95% quantile) of estimates for 100 trees from the Ericson or Hackett backbone. Column pairs separate tests run on the full set of species ("All species") and those on a subset of species represented by genetic data in birdtree.org phylogenies ("Species with genetic data").



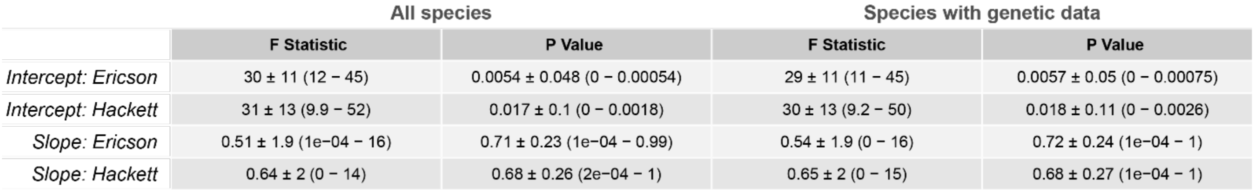
	All species		Species with genetic data	
	F Statistic	**P Value**	**F Statistic**	**P Value**
Intercept: Ericson	0.37 ± 0.46 (0.0058 − 1.4)	0.62 ± 0.19 (0.23 − 0.94)	0.42 ± 0.49 (0.026 − 1.2)	0.58 ± 0.17 (0.27 − 0.87)
Intercept: Hackett	0.44 ± 1.1 (0.0088 − 1.1)	0.64 ± 0.19 (0.29 − 0.93)	0.3 ± 0.15 (0.042 − 0.53)	0.6 ± 0.12 (0.47 − 0.84)

Table 8: F statistics and P Values of tests for allometric differences in combined pectoral muscle mass (pectoralis + supracoracoideus) [g] vs. body mass [g] between diving species which utilize aquatic wing propulsion and exclusively foot-propelled divers. Values shown are mean ± standard deviation (lower 5% quantile – upper 95% quantile) of estimates for 100 trees from the Ericson or Hackett backbone. All diving species in this dataset were represented by genetic data in birdtree.org phylogenies.



	F Statistic	P Value
Intercept: Ericson	0.55 ± 0.53 (0.076 − 1.6)	0.53 ± 0.18 (0.21 − 0.78)
Intercept: Hackett	0.46 ± 0.41 (0.08 − 1.5)	0.55 ± 0.17 (0.23 − 0.78)

Table 9: F statistics and P Values of tests for allometric differences in wing area [cm^2] vs. body mass [g] between volant species and flightless species. There was consistent support for unique intercepts (rows 1 and 2), but not unique slopes (rows 3 and 4). Values shown are mean ± standard deviation (lower 5% quantile – upper 95% quantile) of estimates for 100 trees from the Ericson or Hackett backbone. Column pairs separate tests run on the full set of species ("All species") and those on a subset of species represented by genetic data in birdtree.org phylogenies ("Species with genetic data").



	All species		Species with genetic data	
	F Statistic	**P Value**	**F Statistic**	**P Value**
Intercept: Ericson	30 ± 11 (12 − 45)	0.0054 ± 0.048 (0 − 0.00054)	29 ± 11 (11 − 45)	0.0057 ± 0.05 (0 − 0.00075)
Intercept: Hackett	31 ± 13 (9.9 − 52)	0.017 ± 0.1 (0 − 0.0018)	30 ± 13 (9.2 − 50)	0.018 ± 0.11 (0 − 0.0026)
Slope: Ericson	0.51 ± 1.9 (1e−04 − 16)	0.71 ± 0.23 (1e−04 − 0.99)	0.54 ± 1.9 (0 − 16)	0.72 ± 0.24 (1e−04 − 1)
Slope: Hackett	0.64 ± 2 (0 − 14)	0.68 ± 0.26 (2e−04 − 1)	0.65 ± 2 (0 − 15)	0.68 ± 0.27 (1e−04 − 1)

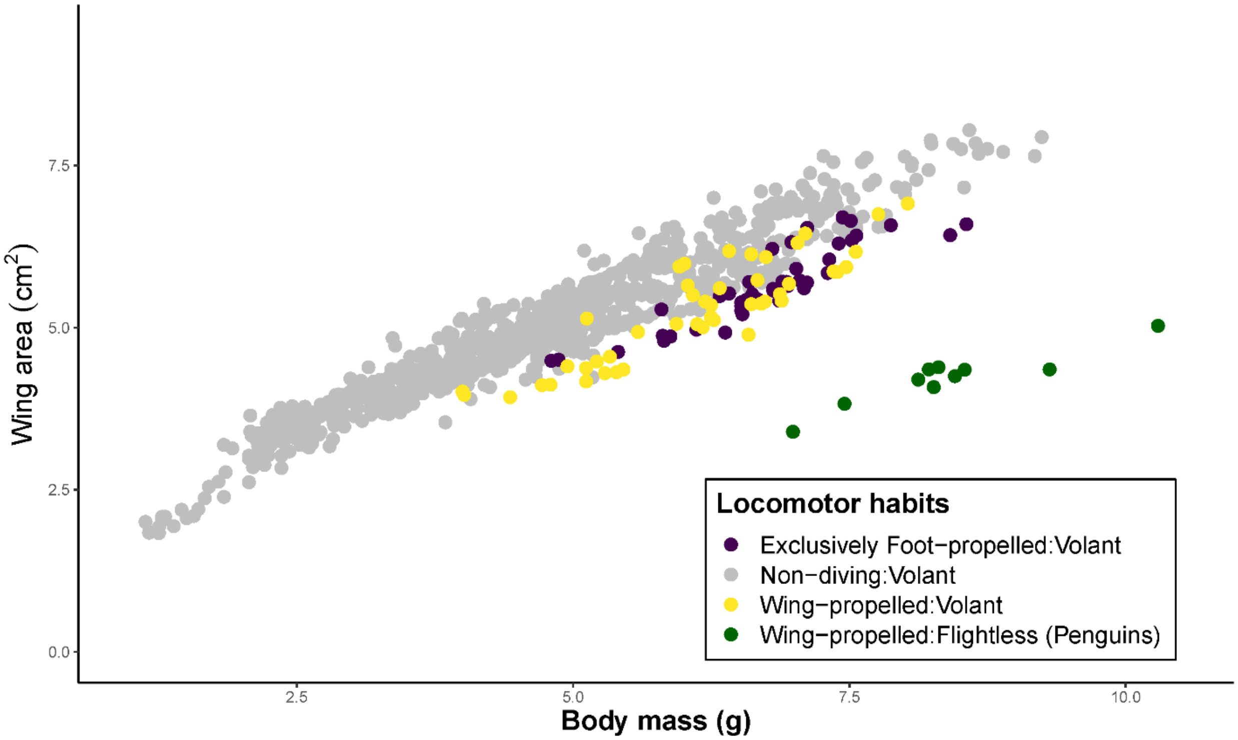
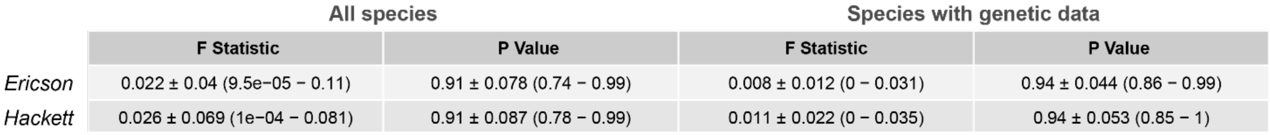


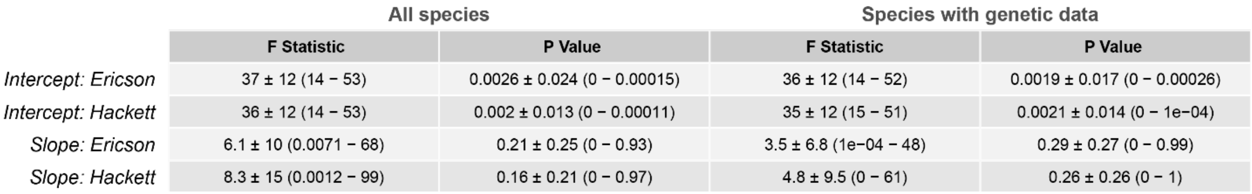
Figure 4: Wing area [cm^2] versus body mass [g] for 951 species of birds. Data are presented on a log-log scale. Non-diving species are shown in gray, wing-propelled divers in yellow, exclusively foot-propelled in purple, and flightless species (penguins) in green.

Table 10: F statistics and P Values of tests for allometric differences in wing area vs. body mass between wing-propelled and exclusively foot-propelled divers. Values shown are mean ± standard deviation (lower 5% quantile – upper 95% quantile) of estimates for 100 trees from the Ericson or Hackett backbone. Column pairs separate tests run on the full set of species ("All species") and those on a subset of species represented by genetic data in birdtree.org phylogenies ("Species with genetic data").



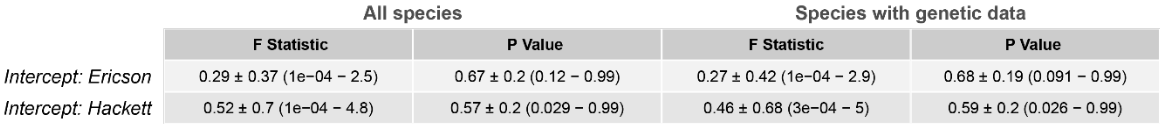
	All species		Species with genetic data	
	F Statistic	**P Value**	**F Statistic**	**P Value**
Ericson	0.022 ± 0.04 (9.5e−05 − 0.11)	0.91 ± 0.078 (0.74 − 0.99)	0.008 ± 0.012 (0 − 0.031)	0.94 ± 0.044 (0.86 − 0.99)
Hackett	0.026 ± 0.069 (1e−04 − 0.081)	0.91 ± 0.087 (0.78 − 0.99)	0.011 ± 0.022 (0 − 0.035)	0.94 ± 0.053 (0.85 − 1)

Table 11: F statistics and P Values of tests for allometric differences in wing area vs. body mass between divers and non-divers. There was consistent support for unique intercepts (rows 1 and 2), but not unique slopes (rows 3 and 4). Values shown are mean ± standard deviation (lower 5% quantile – upper 95% quantile) of estimates for 100 trees from the Ericson or Hackett backbone. Column pairs separate tests run on the full set of species ("All species") and those on a subset of species represented by genetic data in birdtree.org phylogenies ("Species with genetic data").



	All species		Species with genetic data	
	F Statistic	**P Value**	**F Statistic**	**P Value**
Intercept: Ericson	37 ± 12 (14 − 53)	0.0026 ± 0.024 (0 − 0.00015)	36 ± 12 (14 − 52)	0.0019 ± 0.017 (0 − 0.00026)
Intercept: Hackett	36 ± 12 (14 − 53)	0.002 ± 0.013 (0 − 0.00011)	35 ± 12 (15 − 51)	0.0021 ± 0.014 (0 − 1e−04)
Slope: Ericson	6.1 ± 10 (0.0071 − 68)	0.21 ± 0.25 (0 − 0.93)	3.5 ± 6.8 (1e−04 − 48)	0.29 ± 0.27 (0 − 0.99)
Slope: Hackett	8.3 ± 15 (0.0012 − 99)	0.16 ± 0.21 (0 − 0.97)	4.8 ± 9.5 (0 − 61)	0.26 ± 0.26 (0 − 1)

Table 12: F statistics and P Values of tests for allometric differences in wing second moment of area vs. wing area between diving and non-divers. Values shown are mean ± standard deviation (lower 5% quantile – upper 95% quantile) of estimates for 100 trees from the Ericson or Hackett backbone. Column pairs separate tests run on the full set of species ("All species") and those on a subset of species represented by genetic data in birdtree.org phylogenies ("Species with genetic data").



	All species		Species with genetic data	
	F Statistic	P Value	F Statistic	P Value
Intercept: Ericson	0.29 ± 0.37 (1e−04 − 2.5)	0.67 ± 0.2 (0.12 − 0.99)	0.27 ± 0.42 (1e−04 − 2.9)	0.68 ± 0.19 (0.091 − 0.99)
Intercept: Hackett	0.52 ± 0.7 (1e−04 − 4.8)	0.57 ± 0.2 (0.029 − 0.99)	0.46 ± 0.68 (3e−04 − 5)	0.59 ± 0.2 (0.026 − 0.99)

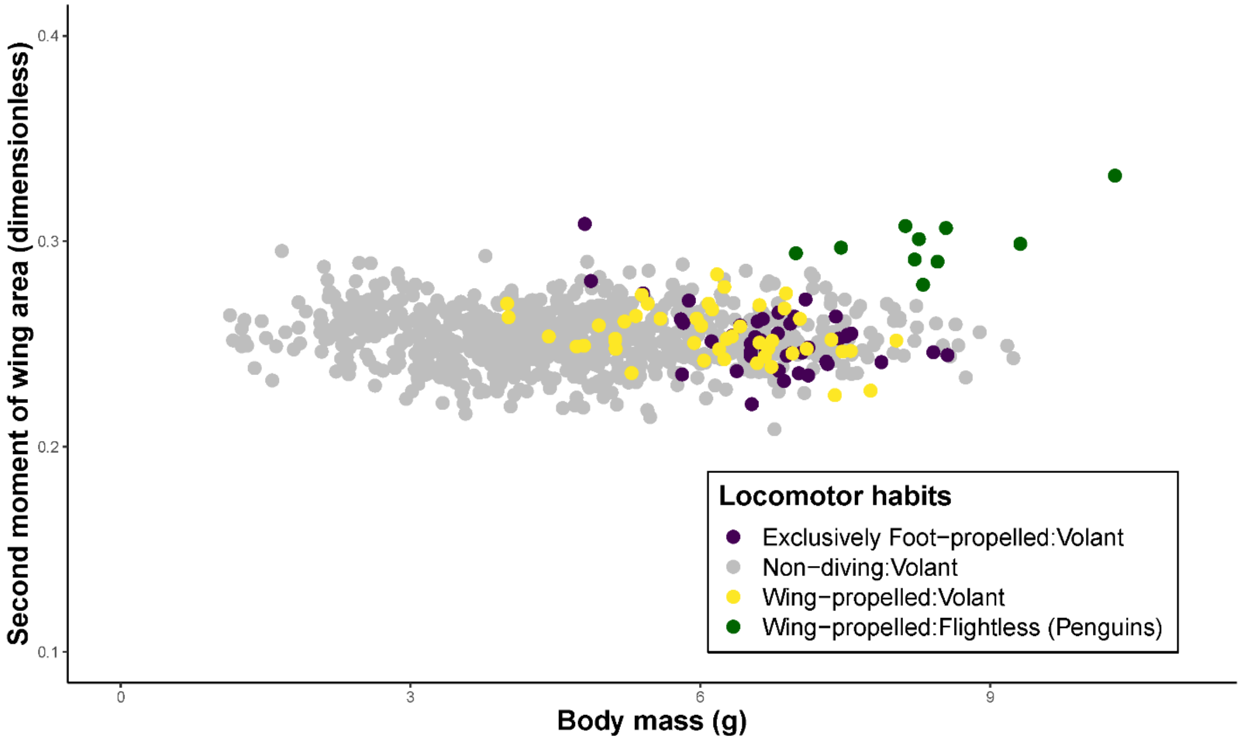


Figure 5: Second moment of wing area [dimensionless] versus body mass [g] for 941 volant species of birds. Body mass is log-transformed, but not second moment of area, as this parameter is dimensionless. Exclusively foot-propelled divers are shown in purple, non-diving species in gray, volant wing-propelled divers in yellow, and flightless wing-propelled divers in green.

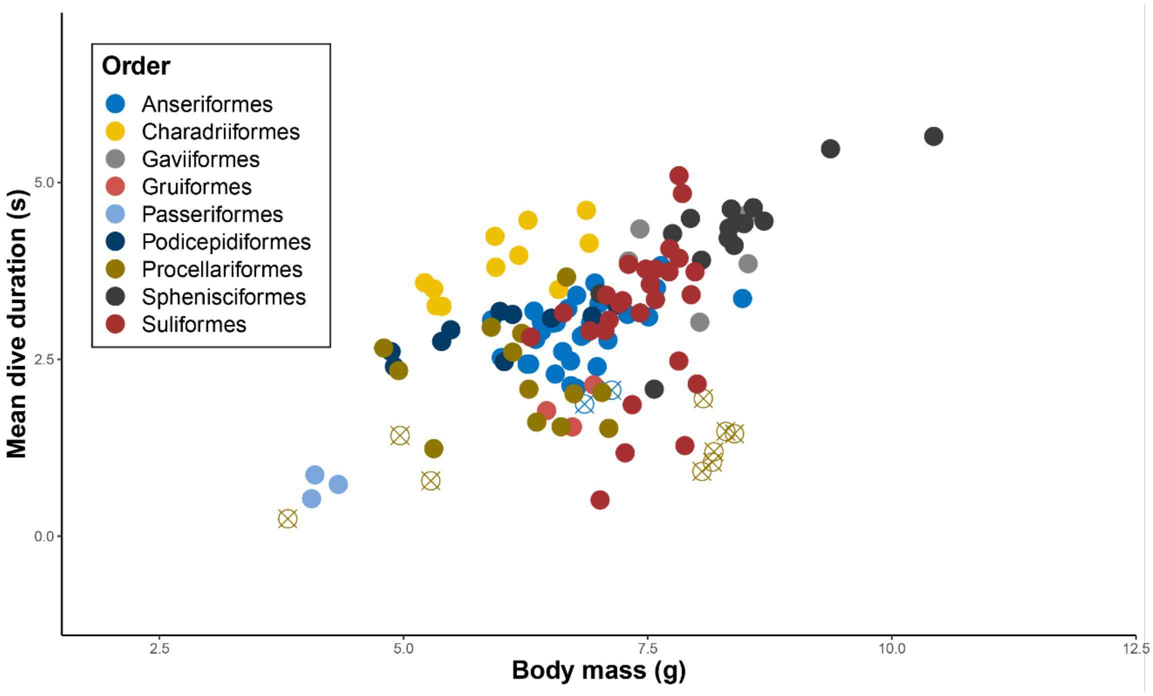


Figure 6: Average dive duration [s] versus body mass [g] for 127 species of diving birds. Data are presented on a log-log scale. Facultative divers are denoted with unfilled circles.

Appendix 1: Video and scientific references for avian aquatic behavior (see Table 1)

#	GROUP	DIVING VIDEO REFERENCE	SCIENTIFIC REFERENCES
1	Struthioniformes	-	-
2	Rheiformes	-	-
3	Tinamiformes	-	-
4	Casuariiformes	-	-
5	Apterygiformes	-	-
6	Anhimidae	-	-
7	Anseranas semipalmata	-	(Frith and Davies, 1961)

8	Dendrocynga	https://www.youtube.com/watch?v=yC6MhSSS2Ao;
		https://www.youtube.com/watch?v=2pTkHZ50i8g;
		https://www.youtube.com/watch?v=GsKM_bbkaD8;
		https://www.youtube.com/watch?v=edowUtOZHPQ
			(Clark, 1978; Johnsgard, 1967; Siegfried, 1973a)

9	Thalassornis	https://macaulaylibrary.org/asset/722862	(Johnsgard, 1967)
10	Anser	-	-
11	Branta	-	-
12	Cereopsis novaehollandiae	-	-
13	Strictonetta naevosa	-	-
14	Cyanochen cyanoptera	-	-
15	Cygnus	-	-
16	Coscoroba coscoroba	-	-
17	Sarkidiornis	-	-
18	Pteronetta hartlaubii	-	-
19	Oressochen	-	-
20	Chleophaga	-	-
21	Radjah radjah	-	-
22	Alopochen aegyptiaca	-	-
23	Tadorna	-	(Düttmann, 1992)
24	Plectropterus gambensis	-	-
25	Tachyeres patchonicus	https://macaulaylibrary.org/asset/201638591; https://macaulaylibrary.org/asset/201350781; https://macaulaylibrary.org/asset/201694131	(Humphrey and Livezey, 1982; Livezey and Humphrey, 1983; Livezey and Humphrey, 1986; Ryan et al., 1988)
26	Tachyeres pteneres	https://macaulaylibrary.org/asset/200864671	
27	Tachyeres brachypterus	https://macaulaylibrary.org/asset/201795571; https://macaulaylibrary.org/asset/201691341; https://macaulaylibrary.org/asset/201691351; https://macaulaylibrary.org/asset/201686251; https://macaulaylibrary.org/asset/201686241	
28	Tachyeres leucocephalus	-	
29	Lophonetta specularioides	https://macaulaylibrary.org/asset/201713901	-
30	Speculanas specularis	-	-
31	Cairina moschata	-	-
32	Nettapus pulchellus	-	(Nye and Dickman, 2005)
33	Nettapus coromandelianus	-	(Porte and Gupta, 2019)
34	Nettapus auratus	-	(Johnsgard, 1978)
35	Callonetta leucophrys	-	-

36	Aix	https://www.youtube.com/watch?v=zNm6V7l5QqU;
		https://www.youtube.com/watch?v=TJDWn_SalpE;
		https://www.youtube.com/watch?v=PiTOi_lcSvw
			(Briggs, 1978; Kear and Johnsgard, 1968)

37	Chenonetta	https://www.youtube.com/watch?v=u44QVK-OFKQ	-
38	Amazonetta brasilensis	-	-
39	Hymenolaimus malacorhynchos	https://macaulaylibrary.org/video/200914251; https://macaulaylibrary.org/video/200911091; https://macaulaylibrary.org/asset/201432891	(Collier and Wakelin, 1996; Veltman et al., 1995)
40	Merganetta armata	https://macaulaylibrary.org/asset/248895471; https://macaulaylibrary.org/asset/201015661; https://macaulaylibrary.org/asset/201541621	(Cerón and Trejo, 2009)
41	Salvadorina waigiuensis	https://macaulaylibrary.org/asset/201013481; https://macaulaylibrary.org/asset/457911; https://macaulaylibrary.org/asset/457910; https://macaulaylibrary.org/asset/457909	(Johnsgard, 1966)
42	Sibirionetta Formosa	-	-
43	Spatula	https://www.youtube.com/watch?v=irPv6I0i7q0; https://www.youtube.com/watch?v=ZWyErx_kHLo	(Kear and Johnsgard, 1968)
44	Mareca	https://www.youtube.com/watch?v=YE5nR6kUDno	(Kear and Johnsgard, 1968; Wishart, 1983)

45	Anas sp.	https://www.youtube.com/watch?v=i_xzhHoZ3_k; https://www.youtube.com/watch?v=-oTaLr1LZCY	(Brodsky, 1985; C K Myline, 1954; Kear and Johnsgard, 1968; McCanch, 2012; Miller, 1983; Paulus, 1988)
46	Anas capensis	-	(Kear and Johnsgard, 1968; Winterbottom, 1974)
47	Anas aucklandica	-	(Weller, 1975)
48	Anas nesiotis	-	-
49	Anas chlorotis	https://macaulaylibrary.org/asset/201072941	(Weller, 1974)
50	Malacorhynchus membranaceus	-	-
51	Marmaronetta angustirostris	-	(Green, 1998)
52	Rhodonessa caryophyllacea	-	(Kear, 2005)
53	Asarcornis scutulata	-	(Green, 1993)
54	Netta	https://macaulaylibrary.org/video/201121841; https://macaulaylibrary.org/asset/201915681; https://macaulaylibrary.org/video/201922851	(Amat, 1984; Kear, 2005)
55	Aythya	https://macaulaylibrary.org/asset/227012291; https://macaulaylibrary.org/asset/305119421; https://macaulaylibrary.org/asset/201012201	(Butler and Woakes, 1979; Cronan, 1957; Draidi et al., 2019; Lalas, 1983; Siegfried, 1976; Stephenson et al., 1986)
56	Polysticta stelleri	https://macaulaylibrary.org/asset/201367751; https://macaulaylibrary.org/asset/201229011	(Laubhan and Metzner, 1999)
57	Somateria	https://macaulaylibrary.org/asset/201817441; https://macaulaylibrary.org/asset/201374451; https://macaulaylibrary.org/asset/201369051	(Bustnes and Lønne, 1997; Gough et al., 2015; Guillemette et al., 2004; Heath et al., 2006; MacCharles, 1997)
58	Histrionicus histionicus	https://macaulaylibrary.org/asset/234548481; https://macaulaylibrary.org/asset/234546781; https://macaulaylibrary.org/asset/201845311; https://macaulaylibrary.org/asset/201827721	(Goudie, 2009; Mittelhauser et al., 2008; Townsend, 1909)
59	Melanitta perspicillata	https://macaulaylibrary.org/asset/286905701; https://macaulaylibrary.org/asset/216453321; https://www.youtube.com/watch?v=sufoZq2yHpc	(Beauchamp, 1992; Humphrey, 1957; Humphrey, 1957; Kaiser et al., 2006; Lewis, 2005; Lovvorn et al., 2013; Mullarney, 1983; Townsend, 1909)
60	Melanitta fusca	https://macaulaylibrary.org/asset/201494461; https://macaulaylibrary.org/asset/201427121; https://macaulaylibrary.org/asset/200835311;	
61	Melanitta deglandi	https://macaulaylibrary.org/asset/276504641; https://macaulaylibrary.org/asset/201465151; https://www.youtube.com/watch?v=vvOvB_etaJ4	
62	Melanitta stejnegeri	https://macaulaylibrary.org/asset/201380811	
63	Melanitta nigra	https://macaulaylibrary.org/asset/271088361	
64	Melanitta americana	https://macaulaylibrary.org/asset/282321981; https://macaulaylibrary.org/asset/275333321; https://macaulaylibrary.org/asset/201363501	

65	Clangula hyemalis	https://www.youtube.com/watch?v=oQxtr3AMbw;
		https://www.youtube.com/watch?v=QbftwiB7m1g;
		https://macaulaylibrary.org/video/201365381
			(Reynolds, 1987; Snell, 1984)

66	Bucephala	https://macaulaylibrary.org/asset/283243771; https://macaulaylibrary.org/asset/292734141; https://macaulaylibrary.org/asset/312220431	(Beauchamp, 1992; Bent, 1919; Heintzelman, 1963; Nilsson, 1972)
67	Mergellus albellus	https://macaulaylibrary.org/video/201946481; https://macaulaylibrary.org/video/201376451; https://macaulaylibrary.org/asset/417976	(Nilsson, 1970; Nilsson, 1974; Savitskii and Matishov, 2011)
68	Lophodytes cucullatus	https://macaulaylibrary.org/asset/484408; https://macaulaylibrary.org/asset/475202; https://macaulaylibrary.org/asset/306521581	(Brooks, 1945)
69	Mergus	https://macaulaylibrary.org/asset/201082881; https://macaulaylibrary.org/asset/483951; https://macaulaylibrary.org/asset/479854; https://macaulaylibrary.org/video/201481451	(Nilsson, 1970; White, 1957)
70	Heteronetta atricapilla	-	(Weller, 1968)
71	Nomonyx dominicus	https://macaulaylibrary.org/asset/410587; https://macaulaylibrary.org/asset/410588	(Goodman et al., 2017; Jenni, 1969; Jenni and Gambs, 1974)
72	Oxyura	https://macaulaylibrary.org/asset/475156; https://macaulaylibrary.org/asset/400196; https://macaulaylibrary.org/asset/201413661	(Lalas, 1983; Siegfried, 1973b; Siegfried, 1976; Tome and Wrubleski, 1988)
73	Biziura lobata	https://macaulaylibrary.org/video/201638021; https://macaulaylibrary.org/asset/244893131	(Osterrieder et al., 2014)
74	Galliformes	-	-
75	Phoenicopteriformes	-	-

76	Rollandia rolland	https://macaulaylibrary.org/asset/201287931; https://macaulaylibrary.org/asset/201287921; https://macaulaylibrary.org/asset/201287891	(Livezey, 1989a; Roots, 2006)
77	Rollandia microptera	https://macaulaylibrary.org/video/201251181; https://macaulaylibrary.org/asset/201260961	(Livezey, 1989a; Roots, 2006)
78	Tachybaptus	https://macaulaylibrary.org/asset/221972771; https://macaulaylibrary.org/asset/268994431; https://macaulaylibrary.org/asset/201939411	(Jenni, 1969; Ladhams, 1968; Ropert-Coudert and Kato, 2009)
79	Podilymbus podiceps	https://macaulaylibrary.org/asset/292561231; https://macaulaylibrary.org/asset/287918701	(Bleich, 1975; Jenni and Gambs, 1974)
80	Podilymbus gigas	-	(Livezey, 1989a; Roots, 2006)
81	Poliocephalus	https://macaulaylibrary.org/asset/257573401; https://macaulaylibrary.org/asset/201881751; https://macaulaylibrary.org/asset/201444461	(Ropert-Coudert and Kato, 2009)
82	Podiceps sp.	https://macaulaylibrary.org/video/201701141; https://macaulaylibrary.org/asset/292561221	(Dow, 1964; Jehl, 1988; Kloskowski, 2004; Lalas, 1983)
83	Podiceps taczanowskii	https://macaulaylibrary.org/asset/200954771; https://macaulaylibrary.org/asset/201104471; https://macaulaylibrary.org/asset/201948661	
84	Aechmophorus	https://macaulaylibrary.org/asset/215105421; https://macaulaylibrary.org/asset/201754141; https://macaulaylibrary.org/asset/201450211	(Forbes and Sealy, 1988; Lawrence, 1950)
85	Columbidae	-	-
86	Mesitornithidae	-	-
87	Pteroclidae	-	-
88	Otididae	-	-
89	Musophagidae	-	-
90	Cuculidae	-	-
91	Podargidae	-	-
92	Caprimulgidae	-	-
93	Nyctibius	-	-
94	Steatornis caripensis	-	-
95	Aegotheles	-	-
96	Apodidae	-	-
97	Hemiprocne	-	-
98	Trochilidae	-	-
99	Opisthocomus hoazin	https://www.youtube.com/watch?v=wy7coZyvyW4; http://www.oiseaux-birds.com/card-hoatzin.html	(Abourachid et al., 2019)
100	Sarothruridae	-	(Taylor, 1994)
101	Rallidae sp.	https://macaulaylibrary.org/asset/201796091; https://macaulaylibrary.org/asset/435299	(Fournier and Krementz, 2018; Wintle and Taylor, 1993)
102	Fulica	https://macaulaylibrary.org/asset/222511281; https://macaulaylibrary.org/asset/220625601; https://macaulaylibrary.org/asset/201566061; https://macaulaylibrary.org/asset/261794001; https://macaulaylibrary.org/video/201537351	(Conigliaro et al., 2011; Dow, 1964; Fortunati and Battisti, 2011; García et al., 2008; Ryan and Dinsmore, 1980)
103	Heliornithidae	-	(Alvarez del Toro, 1971)
104	Aramus guaruana	-	(Walkinshaw, 1982)
105	Psophiidae	-	-
106	Gruiidae	https://www.youtube.com/watch?v=EMEEclvmMuA; https://www.youtube.com/watch?v=p4MD_63_O3s	-
107	Chionis	-	(Murphy, 1936)
108	Pluvianellus socialis	-	-
109	Burhinidae	-	-
110	Pluvianus aegyptius	-	-
111	Himantopus	-	(Hamilton, 1975)
112	Cladorhynchus	https://macaulaylibrary.org/asset/201726521	-
113	Recurvirostra	https://www.youtube.com/watch?v=RZUeeE_xmV8; https://macaulaylibrary.org/asset/201737631	(Gyug and Weir, 2017; Hamilton, 1975)
114	Ibidorhyncha struthersii	-	(Ye et al., 2013)
115	Haematopodidae	https://community.rspb.org.uk/chat/f/the-tea-rooms/106219/oystercatcher-swimming?pifragment-4313=1	-
116	Charadriidae	https://vimeo.com/351934031	(Handbook of Australian, New Zealand & Antarctic birds, 1990, 929)
117	Pedionomidae	-	-
118	Thinocoridae	-	-
119	Rostratulidae	https://www.10000birds.com/australian-painted-snipe-breeding-near-broome.htm;	(Hassell and Rogers, 2002; Rogers et al., 2003; Thomas, 2011)

		https://macaulaylibrary.org/asset/71787301; https://macaulaylibrary.org/asset/47796051	
120	Jacanidae	https://macaulaylibrary.org/asset/479197; https://macaulaylibrary.org/asset/264524381	(Miller, 1931; Tarboton and Fry, 1986)
121	Bartramia longicauda	-	-
122	Numenius	-	-
123	Limosa	-	(Gratto-Trevor, 2020; McCaffery and Gill, 2020; Tufts, 1986)
124	Arenaria	-	(John, 1980; Thompson, 1973)
125	Prosobonia	-	
126	Calidris	-	(Wheeler, 1962)
127	Limnodromus	https://www.youtube.com/watch?v=BXOs647QA4M; https://macaulaylibrary.org/asset/333067251	-
128	Limnocryptes minimus	https://samalij.wixsite.com/samsphotopoetry/single-post/2018/12/24/jack-snipe-swimming-on-the-sea	-
129	Scolopax	-	-
130	Coenocorypha	-	-
131	Gallingo	-	(Bowles, 1918)
132	Xenus cinereus	-	(Blokhin, 2004)
133	Phalaropus	https://macaulaylibrary.org/asset/320923421; https://macaulaylibrary.org/asset/297998451; https://macaulaylibrary.org/asset/320937541; https://macaulaylibrary.org/asset/201470231	(Colwell and Oring, 1988; King, 1971; Mercier and Gaskin, 1985; Obst et al., 1996)
134	Actitis	-	(Murie, 1934; Reed et al., 2020; Sutton, 1925)
135	Tringa	https://faculty.ucr.edu/~chappell/INW/birds2/willet.shtml; https://macaulaylibrary.org/asset/192850971	(Cadwalader, 1938; Ingram and Salmon, 1942; Northwood, 1951)
136	Turnicidae	-	-
137	Dromadidae	-	-
138	Glareolidae	-	-
139	Stercocariidae	-	-
140	Alle alle	https://macaulaylibrary.org/asset/201226671	(Harding et al., 2009)
141	Uria	https://elifesciences.org/articles/55774; https://macaulaylibrary.org/asset/201479271; https://macaulaylibrary.org/asset/270060251; https://www.youtube.com/watch?v=nbnJsc-GPaA	(Evans et al., 2013; Hedd et al., 2009; Mehlum et al., 2001; Takahashi et al., 2008; Tremblay et al., 2003; Wanless et al., 1988)
142	Alca torda	https://macaulaylibrary.org/asset/213447051; https://macaulaylibrary.org/asset/201229751	(Paredes et al., 2008; Shoji et al., 2015a)
143	Cepphus	https://macaulaylibrary.org/asset/201298791; https://macaulaylibrary.org/asset/201483831	(Clowater and Burger, 1994; Duffy et al., 1987; Masden et al., 2013; Shoji et al., 2015b)
144	Brachyramphus	https://macaulaylibrary.org/asset/201438491; https://macaulaylibrary.org/asset/200871991; https://macaulaylibrary.org/asset/201469721; https://macaulaylibrary.org/asset/201469711	(Henkel et al., 2004; Thoresen, 1989)
145	Synthliboramphus	https://macaulaylibrary.org/asset/298753421; https://macaulaylibrary.org/asset/201497541	(Elliott et al., 2010)
146	Ptychoramphus aleuticus	-	(Elliott et al., 2010)
147	Aethia	https://macaulaylibrary.org/asset/201387021; https://macaulaylibrary.org/asset/425993	
148	Cerorhinca	https://macaulaylibrary.org/asset/201469941; https://macaulaylibrary.org/asset/449444	(Kuroki et al., 2003)
149	Fratercula	https://macaulaylibrary.org/asset/270051441; https://macaulaylibrary.org/asset/483751	(Shoji et al., 2015a; Spencer, 2012)

150	Laridae	https://www.youtube.com/watch?v=n1woCgYPS8c;
		https://www.youtube.com/watch?v=pbi-DNrbfPI;
		https://www.youtube.com/watch?v=f0RSfoEFKvU
			(Baptist and Leopold, 2010; Taylor, 1983; Verbeek, 1977)

151	Rhynochetos jubatus	-	-
152	Eurypyga helias	-	-
153	Phaethon	-	(Corre, 1997; Sommerfeld and Hennicke, 2010)
154	Gavia	https://movie.biologists.com/video/10.1242/jeb.168831/video-1; https://macaulaylibrary.org/asset/167382711; https://macaulaylibrary.org/asset/168531151	(Clifton and Biewener, 2018; Polak, 2007; Townsend, 1924)
155	Spheniscidae	https://macaulaylibrary.org/asset/201339311; https://macaulaylibrary.org/asset/281567361	(Culik and Wilson, 1994; Hull, 2000, 200; Kato et al., 2008; Mattern et al., 2007; Mills, 2000; Rey et al., 2013; Ropert-Coudert et

			al., 2018; Ryan et al., 2007; Sato, 2004; Tremblay and Cherel, 2003)
156	Diomedidae	https://www.youtube.com/watch?v=tMTfr2NCvdY	(Bentley et al., 2021; Harper, 1987; Harper et al., 1985; Harrison et al., 1991; Hedd et al., 1997; Huin and Prince, 1997; Kazama et al., 2019; Oatley, 1979; Prince et al., 1994; Sakamoto et al., 2009; Voisin, 1981)
157	Oceanitidae	-	(Handbook of Australian, New Zealand & Antarctic birds, 1990, 674)
158	Hydrobatidae	-	(Albores-Barajas et al., 2011; Bried, 2005; Flood et al., 2009)
159	Macronectes	-	(van den Hoff and Newbery, 2006)
160	Fulmarus	https://macaulaylibrary.org/asset/201220771	(Garthe and Furness, 2001; Hobson and Welch, 1992)
161	Thalassoica antarctica	-	(Ainley et al., 1984; Spear and Ainley, 1998)
162	Daption capense	https://macaulaylibrary.org/asset/201437191; https://vimeo.com/151211264	(Harper, 1987; Harper et al., 1985; Prince and Morgan, 1987; Warham, 1996)
163	Pagodroma nivea	-	(Harper et al., 1985; Prince and Morgan, 1987; Spear and Ainley, 1998)
164	Aphrodroma brevirostris	-	(Harper et al., 1985; Spear and Ainley, 1998)
165	Pterodroma	-	(Bester et al., 2011; Harper et al., 1985; Rayner et al., 2008; Spear and Ainley, 1998; Taylor, 2008)
166	Halobaena caerulea	-	(Chastel and Bried, 1996; Croxall and Prince, 1980; Griffiths, 1982; Navarro et al., 2013)
167	Pachyptila	https://macaulaylibrary.org/asset/200905651;	(Chastel and Bried, 1996; Cherel et al., 2002; Harper, 1987; Navarro et al., 2013; Robinson, 1961)
168	Bulweria	-	(Mougin and Mougin, 2000)
169	Pseudobulweria	-	(Ravache et al., 2020; Spear and Ainley, 1998)
170	Procellaria	https://macaulaylibrary.org/video/201430911	(Brown et al., 1978; Huin, 1994; Poupart et al., 2020; Rollinson et al., 2016)
171	Calonectris	https://www.youtube.com/watch?v=1-bEtyhXKCA	(Brown et al., 1978; Burger, 2001; Cianchetti-Benedetti et al., 2017; Grémillet et al., 2014; Matsumoto et al., 2012; Oka, 1994)
172	Ardenna	https://macaulaylibrary.org/video/201317731; https://macaulaylibrary.org/asset/201467411; https://macaulaylibrary.org/asset/201451071; https://macaulaylibrary.org/asset/201431051	(Adams et al., 2019; Dunphy et al., 2015; Oka, 1994; Ronconi et al., 2010; Shoji et al., 2016; Skira, 1979; Taylor, 2008; Weimerskirch and Sagar, 1996)
173	Puffinus	https://macaulaylibrary.org/asset/201915491; https://macaulaylibrary.org/asset/201532811; https://macaulaylibrary.org/asset/201049721; https://macaulaylibrary.org/asset/201431021; https://macaulaylibrary.org/asset/200905951; https://www.youtube.com/watch?v=76WC1JNmFv0	(Aguilar et al., 2003; Bennet et al., 2020; Brown et al., 1978; Péron et al., 2013; Ronconi et al., 2010; Shaffer et al., 2009; Shoji et al., 2016; Taylor, 2008)
174	Pelecanoides	https://macaulaylibrary.org/asset/201811631; https://macaulaylibrary.org/asset/200905541	(Bocher et al., 2000; Brown et al., 1978; Dunphy et al., 2015; Navarro et al., 2014; Ryan and Nel, 1999; Taylor, 2008)
175	Ciconiidae	-	-
176	Fregatidae	-	-

177	Sulidae	https://macaulaylibrary.org/asset/305748281;
		https://www.youtube.com/watch?v=IWbu6r-6VK8&t=20s;https://www.youtube.com/watch?v=mXXuK9eQVUw&t=1s;
		https://www.youtube.com/watch?v=D8vaFl6J87s;
		https://www.youtube.com/watch?v=w_h_KuIk_Vs
			(Garthe et al., 2000; Garthe et al., 2007; Grémillet et al., 2016; Ropert-Coudert et al., 2009; Weimerskirch et al., 2005; Zavalaga et al., 2007)

178	Anhingidae	https://macaulaylibrary.org/asset/201336971; https://macaulaylibrary.org/asset/227853371	(Lalas, 1983)
179	Phalacrocoraxidae sp.	https://www.youtube.com/watch?v=rF5gAUJUZXA; https://macaulaylibrary.org/asset/402027	(Cooper, 1986; Frere et al., 2002; Lalas, 1983; Ribak, 2005; Stonehouse, 1967; Trayler et al., 1989)
180	Phalacrocoraxidae harrisi	https://macaulaylibrary.org/asset/193115251; https://macaulaylibrary.org/asset/193125281	-
181	Pelecanus	-	(Arnqvist, 1992; Carl, 1987; Duffy, 1983; Hall, 1925; Schreiber and Clapp, 1987; Skinner, 1925; Zavalaga et al., 2007)
182	Balaeniceps rex	-	-
183	Scopus umbretta	-	-

184	Ardeidae	https://www.youtube.com/watch?v=ekGYwcYi4b4;
		https://www.youtube.com/watch?v=msgyPyzGedA;
		https://www.youtube.com/watch?v=1g6ODG2sqzQ
			-

185	Threskiornithidae	-	-
186	Cathartidae	-	-
187	Accipitriformes	-	-
188	Pandionidae	https://www.youtube.com/watch?v=nMw-PspfdkQ&t; https://www.youtube.com/watch?v=428L7cR4AMU&t	(Winkler et al., 2020c)
189	Strigiformes	-	-
190	Collidae	-	-
191	Leptosomus discolor	-	-
192	Trogonidae	-	-
193	Bucerotiformes	-	-
194	Todidae	-	-
195	Momotidae	-	-
196	Alcedo	https://macaulaylibrary.org/asset/201516191; https://macaulaylibrary.org/asset/201494131; https://macaulaylibrary.org/asset/201279521; https://www.youtube.com/watch?v=lNcpMauEzMU; https://www.youtube.com/watch?v=sLSQ-XDf_wQ	(Forshaw, 1983; Vilches et al., 2012; Vilches et al., 2013; Woodall, 1991)
197	Ceyx	https://macaulaylibrary.org/asset/201649161; https://macaulaylibrary.org/asset/201651961; https://macaulaylibrary.org/asset/201651941	(Barker and Vestjens, 1989; Burnett, 1996; Forshaw, 1983; Woodall, 1991)
198	Corythornis	https://macaulaylibrary.org/asset/201254641; https://macaulaylibrary.org/asset/201594541	(Libois and Laudelout, 2004; Reyer et al., 1988)
199	Corythornis madagascariensis		(Woodall, 1991; Woodall, 2020)
200	Ispindina		
201	Lacedo pulchella		
202	Dacelo		
203	Clytoceyx rex		
204	Cittura cyanotis		
205	Pelargopsis	https://www.youtube.com/watch?v=5OajTIgbluM; https://www.youtube.com/watch?v=5d40TDAyjRs	(Biswas et al., 2014; Biswas et al., 2015)

206	Halycon	https://macaulaylibrary.org/asset/201676381;
		https://www.youtube.com/watch?v=doYxrSjfHHg;
		https://www.youtube.com/watch?v=-CgrNok5k4M;
		https://www.youtube.com/watch?v=C9DHCsyL4Zc
			(Naher and Sarker, 2014; Woodall, 1991)

207	Todiramphus	https://www.youtube.com/watch?v=vbfLMXVnw_E; https://www.youtube.com/watch?v=-gN_WXNGqvs	(Fitzsimons and Thomas, 2011)
208	Caridonax fulgidus	-	(Woodall and Kirwan, 2020)
209	Melidora macrorrhina	-	-
210	Actenoides	-	-
211	Syma	-	-
212	Tanysiptera	-	-
213	Megaceryle	https://macaulaylibrary.org/asset/201472031; https://macaulaylibrary.org/asset/201344031; https://www.youtube.com/watch?v=wF0Xxy61cBI	(Arkell, 1979; Brush, 2020; Kasahara and Katoh, 2008; Kelly et al., 2020)
214	Ceryle rudis	https://www.youtube.com/watch?v=1Kh5CGvEj9o; https://www.youtube.com/watch?v=HgJJ4l4ScNM	(Katzir and Camhi, 1993; Labinger et al., 1991)
215	Chloroceryle	https://macaulaylibrary.org/asset/309727341	(Remsen, 1991; Willard, 1985)
216	Meropidae	-	-
217	Coraciidae	-	-
218	Brachypteraciidae	-	-
219	Galbuliformes	-	-
220	Piciformes	-	-
221	Cariama sp.	-	-

222	Falconidae	-	-
223	Psittaciformes	-	-
224	Strigops habroptila	-	-
225	Passeriformes sp.	-	-
226	Cinclus cinclus	https://macaulaylibrary.org/asset/294873831; https://macaulaylibrary.org/video/201119371; https://www.youtube.com/watch?v=uKHR8PJMj-Q	(Brownlow, 1949; Crisp, 1865; Dewar, 1938; Holmes, 1939; Ingram, 1938; Ingram et al., 1938; Jones and King, 1952; Tyler and Ormerod, 1994)
227	Cinclus pallasii	https://macaulaylibrary.org/asset/201361231; https://macaulaylibrary.org/asset/201345451; https://www.youtube.com/watch?v=wEUM8G0bAeY	(Eguchi, 1990; Tyler and Ormerod, 1994)
228	Cinclus mexicanus	https://macaulaylibrary.org/asset/201668521; https://macaulaylibrary.org/asset/201668551; https://www.youtube.com/watch?v=cV6IDY1TSC0	(Goodge, 1957; Goodge, 1959; Murrish, 1970; Tyler and Ormerod, 1994)
229	Cinclus leucocephalus	https://macaulaylibrary.org/asset/107415681	(Tyler and Ormerod, 1994)
230	Cinclus schulzii	-	(Tyler and Ormerod, 1994)

Chapter 2

Multifunctionality constrains diversification in the avian wing

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Abstract:

The morphological systems of organisms often serve multiple functions. How multifunctionality influences the evolution of morphology is an open question in biology. Here, I test whether multifunctionality in the wings of volant diving birds has constrained or facilitated the diversification of wing shape and size. To do so, I characterized the wings of 2,326 wings from 955 species using geometric morphometrics – the largest dataset of avian wing shapes or sizes assembled to date. I find that wing shape has evolved more slowly in birds which use their wings for locomotion in both air and water relative to birds which use their wings in a single fluid, including other diving birds. Thus, multifunctionality has constrained the diversification of the avian wing. Interestingly, the wings of wing-propelled divers are not different from those of foot-propelled divers, indicating that selection for wing-propelled aquatic locomotion has not driven modification toward any specific wing shape. Finally, I find that the phylogenetic signal in wing shape is substantially lower than in previous studies, suggesting that there may be a functional link between wing shape and flight behavior after all.

Introduction:

We typically think of selection as acting on morphological systems for a single behavior, but nature is rarely so simple. More often, morphological systems are multifunctional – they contribute to performance in multiple behaviors and across environmental contexts. How the number of functions affects the evolution of morphological systems is an open question in biology (Bergmann and McElroy, 2014; Corn et al., 2021; Muñoz, 2019; Polly, 2020; Stayton et al., 2018). On one hand, traits which serve multiple functions may experience functional trade-offs (Rose and Lauder, 1996; Stearns, 1992). This would likely constrain morphological diversification, as evolutionary modifications which improve performance in one context would decrease performance in another (Arnold, 1983; Arnold, 2003; Ghalambor, 2003; Schluter et al., 1991; Walker, 2007). Thus, the range of phenotypic states available to multifunctional systems should be narrow relative to traits which serve fewer functions. For this reason, it has been argued, that decoupling of functional traits promotes diversification (Alfaro et al., 2004; Gatesy and Dial, 1996; Wainwright and Price, 2016). On the other hand, multifunctionality might actually promote morphological diversification by transforming the adaptive landscape from one with a single peak to one with multiple local maxima (Polly, 2020; Stayton et al., 2018).

Empirical studies which test whether multifunctionality constrains or promotes morphological diversification are rare. Stayton et al. (2018) suggest that this is “likely because of the difficulty of identifying study systems where multiple different functions are known to contribute to fitness, but where not every species performs the same number of functions.”

There have been few studies conducted with the explicit goal of testing this question in natural systems. Stayton et al. (2018) tested whether the shells of terrestrial turtles are more diverse and/or have diversified more rapidly than those of aquatic turtles.

Turtle shells serve multiple functions (armor, heat exchange, etc.), but only the shells of aquatic turtles experience enough drag to constrain shell shape. Data from 274 species indicated that the shells of terrestrial turtles are more diverse (disparate) than those of aquatic turtles, but that this is not due to differences in the rate of morphological evolution (Stayton et al., 2018). Corn et al. (2021) tested whether the cranial morphology and kinematics of fishes evolved more quickly in groups which feed only through suction versus those which bite and suck. Surprisingly, the data from 44 species indicate that percomorph fishes which bite and suck have experienced faster rates of evolution on their static morphology, but slower rates of evolution on feeding kinematics (Corn et al., 2021).

While these studies represent significant advancements toward understanding how multifunctionality affects morphological diversification, their results are somewhat limited by their study systems. The evolution of terrestriality represents a reduction in the number of shell functions in turtles, but the relative significances of armor, heat dissipation, and righting performance versus drag to organism fitness is unclear, and likely shift between air and water. The evolution of biting in percomorph fishes represents an increase in the number of functions in the cranial system, but the strength of selection to retain suction feeding in biting fishes is unknown. As well, in both systems, a change in the number of trait functions is conflated with changes in life-history, which may also influence trait and lineage diversification.

Diving birds represent a powerful model system to test whether multifunctionality constrains or promotes morphological diversification. Diving – obtaining food from a medium in which an animal cannot continually survive or reproduce – has evolved independently at least 10 times across the avian phylogeny, with over 200 extant species relying on diving for much, if not all, of their food (obligate divers). Of these, only the penguins and a few others have lost aerial flight (Chapter 1). Of the remaining diving birds, 83 species rely on their wings for steady-state aquatic locomotion (e.g., eiders, puffins, shearwaters, gannets). Thus, the wings of these birds are under selection for their ability to efficiently produce force in two fluids (two locomotor functions), whereas the wings of volant non-diving birds, and those of flightless diving birds (i.e., penguins), are only under selection for their ability to efficiently produce force in one (one locomotor function). Thus, like turtles, the shift from air to water signals a change in the number of contexts in which a morphological system must perform. More important, however, is that not all diving birds use the same morphological system for aquatic locomotion; 115 volant species rely exclusively on their feet for steady-state aquatic locomotion (e.g., grebes, loons, cormorants, some ducks, and coots). Therefore, while wing-propelled and foot-propelled divers face selection for diving, share similar habitats, and rely on similar resources, they differ in their number of wing functions (Chapter 1). Thus, by comparing the diversity of wing shapes of diving birds which use different mechanisms for aquatic locomotion relative to volant non-divers and flightless divers, we can test whether the number of functions constrains or promotes morphological diversification while controlling for ecology.

To that end, I characterized the shape and size of 2,326 wings from 955 species – including 49 wing-propelled divers [WPD species] from five separate lineages, 46 species of exclusively foot-propelled divers [FPD species] from five separate lineages, and 860 species of volant-non-diving and flightless-diving [NDFD] birds – using geometric morphometrics. I then use phylogenetic comparative methods to estimate the rate of evolution in wing shape experienced by birds in each group and tested whether the disparity of wing shapes exhibited by WPD species differs from FPD species in intra- and interspecific contexts. I hypothesized that WPD species would exhibit slower rates of morphological evolution and lower morphological disparity, both among and within species, due to the demands of wing-propelled locomotion in multiple fluids.

Methods:

The wings used in this study were from two museums: the Burke Museum of Natural History and Culture and the Slater Museum of Natural History. Both have extensive collections of spread wings, with the Burke Museum holding the largest collection of spread wings in the world. At the Burke Museum, spread wings were photographed using a Canon EOS Rebel T2i digital camera attached to a Beseler CS-20 copy stand and leveled via a bubble-type level. To facilitate digitization, wings were placed on their ventral side on a green “chromakey” background and illuminated via two Britek photo lights. Photos of wings from the Slater Museum were downloaded from the Slater Museum of Natural History’s digital collections. Only wings of females were used in this study, both to reduce intraspecific variation and because sexual dimorphism may co-vary with diving behavior. As well, only wings which were prepared with an approximately straight leading edge, as exhibited during mid-downstroke in aerial flight, were photographed. Species were classified according to their diving behavior following Chapter 1. Only obligate divers were classified as WPD species or FPD species for this study, as it is unclear to what extent species are selected for facultative diving (Chapter 1).

Digitization, statistical tests, and plotting were performed in R (R Core Team, 2020). I characterized the shape of each wing using the package “StereoMorph” (Olsen and Haber, 2019). By using geometric morphometrics rather than traditional univariate measures (e.g., aspect ratio, wing area), I avoided making any *a priori* assumptions about what aspects of wing shape might vary between and within birds. Given that wings have few consistent landmarks across species, I followed a previous study on wing shape (Wang and Clarke, 2015) by digitizing both the outer edge of the wing (not including the root, i.e., the edge near the body) and the distal edge of the covert feathers for each wing as curves. I then used the package “lambda” and the function *lasec* to determine how many semi-landmarks were necessary to capture the variation in wing shape, settling on 60 semi-landmarks around the outer edge of the wing and 30 semi-landmarks on the edge of the covert feathers (Watanabe, 2018).

All wing data were subjected to a Generalized Procrustes Analysis (GPA) using the *gpagen* function in the package “geomorph” (Adams and Otárola-Castillo, 2013; Adams et al., 2021). Potential outliers were identified using the function *plotOutliers* and removed following visual comparison to the wings of the same or similar species, leaving 2,326 wings from 955 species. The mean shape and centroid size (CS) of each species was computed and realigned using the *gpagen* function so that species which were more heavily sampled [often diving species] did not have undue influence on the alignment. The mean shape and centroid size of each species were used for all subsequent analyses. The degree of digitization error was determined based on the Procrustes variance of 19 wings inadvertently photographed and digitized on separate days.

Values for each species cannot be treated as independent data given their shared evolutionary history. Thus, all analyses were conducted using the phylogenetic comparative methods implemented in “geomorph” (Adams and Otárola-Castillo, 2013; Adams et al., 2021). To account for phylogenetic uncertainty, I conducted all tests 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). Thus, I followed Rubin’s rule (Nakagawa and De Villemereuil, 2019) by running all analyses with the complete set of species in the dataset as well as with the subset of species represented by genetic data in birdtree.org phylogenies (Upham et al., 2019).

The statistical tests implemented in “geomorph” assume a Brownian motion model of trait evolution (Adams and Collyer, 2018; Adams and Otárola-Castillo, 2013; Clavel and Morlon, 2020). With a few exceptions, this is due to current limitations in multivariate statistics (Adams and Collyer, 2019). Thus, I used the function *physignal* in “geomorph” and *mvgls* in the package “mvMORPH” to calculate the multivariate version of Blomberg’s K (Adams, 2014; Blomberg et al., 2003) and Pagel’s λ (Pagel, 1999), respectively (Adams et al., 2021; Clavel et al., 2020). Previous studies suggested that much of the variation in wing shape is explained by phylogenetic history (i.e., K and λ are close to 1), but these studies were based on fewer species (Baliga et al., 2019; Wang and Clarke, 2015). Technically, one could also use “mvMORPH” to fit models assuming non-Brownian motion models of evolution, but my testing indicated that these methods were not appropriate in this case given the number of species and landmarks in my dataset (e.g., it would require a 320 GB data matrix). Further, this method may suffer from a high rate of model misspecification (Adams and Collyer, 2018).

As explained by Stayton et al. (2018), the evolution of shape and size are often correlated with one another – so called, evolutionary allometry. This could affect the estimated rate of wing shape evolution and the shape disparity between species. For example, if divers occupy a narrower range of body sizes than other birds for reasons unrelated to diving, this alone could drive differences in wing shape disparity. In the face of allometry, it is possible to analyze the evolution of shape alone by generating allometry-free shapes from the residuals of the shape versus size relationship (Stayton et al., 2018). This only makes statistical sense if there is also no significant interaction between allometry among groups (i.e., only if groups share a common allometry) (see below). To fully explore the evolution of wing shape, I generated allometry-free shapes following Stayton et al. (2018). All disparity and rate analyses were conducted for both raw shapes and allometry-free shapes, across 200 trees, and for both an "all species" and a "species with genetic data" subset.

To test whether WPD and FPD species occupy unique regions of the wing morpho-space and share a common allometry, I used the function *procD.pgls* in "geomorph" (Adams et al., 2021).

To explore whether the disparity (i.e., variance) in wing shape differs between groups, I used two methods. First, I tested whether groups differed in their intraspecific disparity (variance in wing shape within a species). To perform this test, I used the function *morphol.disparity* from "geomorph" to calculate the Procrustes variance for each species represented by three or more individuals (Adams et al., 2021). I then fit a phylogenetic ANOVA (Garland et al., 1993) using the function *aov.phylo* from “geiger” to test for differences in intraspecific disparity between WPD species, FPD species, and NDFD groups (Harmon et al., 2020). Second, I tested whether WPD species and FPD species differed in their interspecific shape disparity, following Stayton et al. (2018), using a custom R script. Specifically, this script calculated the ratio of Procrustes variances of FPD species versus WPD species using the *procD.lm* and *morphol.disparity* functions in “geomorph”. To assess whether this ratio was significantly different from 1.0, the script then simulated shape evolution 999 times across each tree assuming a Brownian motion model of evolution (using *sim.char* from “geiger”) and calculated the same ratio for each iteration. Comparing the observed disparity ratio to the distribution of simulated ratios allowed me to compute a p-value for each tree and dataset. In general, this method constitutes a test of whether the observed difference in disparity is the result of the age/evolutionary history of each group or the result of differences in the number of wing functions.

To compare the rate of evolution between groups, I used the function *compare.evol.rates* in “geomorph” (Adams et al., 2021). Because the phylogenetic signal in wing shape departed significantly from the assumption of Brownian motion (see below), which could have substantial impacts on estimates of evolutionary rate, I followed previous analyses (Eliason et al., 2020; Price et al., 2010) by performing a sensitivity analysis with trees transformed by Pagel’s λ (Pagel, 1999). Branch length transformations were conducted using the *rescale* function in the “geiger” package (Harmon et al., 2020). Both methods of assessing statistical significance for the *compare.evol.rates* function provided by "geomorph" assume Brownian motion (Adams and Collyer, 2018; Adams and Collyer, 2019; Adams and Otárola-Castillo, 2013; Clavel and Morlon, 2020). Thus, significance tests for differences in the mean rate estimate between WPD species and FPD species were conducted using a randomization test (*IndependenceTest* function) implemented in the "coin" package (Hothorn et al., 2021).

Results:

Phylogenetic signal

Previous studies of avian wing shape found that much of the variation is explained by phylogeny (Baliga et al., 2019; Wang and Clarke, 2015), but this was not the case for our dataset. While both K and λ were close to 1.0 for wing size [log (CS)], the phylogenetic signal for wing shape was considerably lower across test conditions (Figure 1).

Wing shape

Multivariate phylogenetic least-squared regressions found no consistent differences in wing shape between WPD species, FPD species, and NDFD groups (Table 2). The high degree of overlap between WPD species and FPD species is visible in a plot of the first two principal components of wing shape (Figure 2). There was a consistent and significant relationship between wing shape and size. Finally, while there was some evidence for unique allometries among groups (the interaction between size and group on wing shape), the R-squared value and F-statistics for these group-by-allometry interactions were always low (Table 1). In other words, it is safe to assume that the relationship between wing shape and size is the same across groups. Thus, to fully explore the effect of multifunctionality on the evolution of wing shape, all subsequent analyses were conducted on both the raw shapes and a set of shapes with the effect of wing size removed (allometry-free shapes).

Disparity

Multifunctionality could constrain the evolution of WPD species without appreciable impacts on the rate of wing shape evolution. This would occur if the wings of WPD species occupy only a narrow range of possible shapes exhibited by FPD species, but the shape of the wing within this narrow range shifts relatively quickly through evolutionary time. Though this does not appear to be the case based on Figure 2, only the first two principal component axes are shown, and variation may exist at lower levels. I used simulation-based methods to test whether WPD species have explored a narrower range of wing shapes than FPD species given their branch lengths and the frequency of evolving each strategy. The interspecific disparity of FPD species was greater than that of WPD species across all test conditions and was significant when calculated using allometry-free wing shapes ($p_{\text{Ericson\_allSpecies}} = 0.003 \pm 0.003$, $p_{\text{Hackett\_allSpecies}} = 0.006 \pm 0.004$, $p_{\text{Ericson\_genSpecies}} = 0.006 \pm 0.007$, $p_{\text{Ericson\_genSpecies}} = 0.01 \pm 0.06$). For no trees was the difference in disparity significant given raw wing shapes.

There was no significant difference in intraspecific disparity between any of the three groups (Table 3), as shown by Figure 3.

Evolutionary rate

For untransformed trees, the rate of wing shape evolution was lower in WPD species than in FPD species. This was true both when considering all species (Figure 4A & 4B, $\lambda = 1$) and when considering only those species represented by genetic data in birdtree.org trees (Figure 5A & 5B, $\lambda = 1$). Though the distributions of rate estimates overlap considerably when taken as a whole ((Figure 4 & 5, λ = 1), if comparing the rates for WPD species and FPD species directly and for a given tree, the estimate for WPD species was lower than that for FPD species for > 95 % of all trees. As well, randomization tests indicated that rate ratios for WPD species were significantly lower or nearly significantly lower than those for FPD species across all conditions (λ = 1, All species: Raw – p=0.056, Allo-free – p=3.4e-08; Genetic data species: Raw – p=1.1e-14, Allo-free – p < 2.2e-16).

The available method of calculating the rate of multivariate shape evolution assumes a Brownian motion (BM) model of evolution. Because the phylogenetic signal in wing shape was considerably lower than that expected under BM (Figure 1), I assessed the sensitivity of the above result to this assumption by transforming the branch lengths of all trees by Pagel's λ (0-0.9 in increments of 0.1) and recalculating the rate of wing shape evolution for each group. Again, the rate of wing shape evolution was lower in WPD species than in FPD species. This result was robust across all levels of Pagel's λ except for 0 – which represents a star phylogeny – including trees transformed by the precise value of Pagel's λ for that tree-by-shapes combination (scatter points in Figures 4 & 5). Interestingly, a slight opposite trend was found for wing size [log (CS)]. However, this trend was not significant according to a randomization test (p = 0.67).

Discussion:

Multifunctionality has constrained the evolution of avian wing shape. The rate of evolution in wing shape is lower for birds which use their wings for locomotion in both air and water. This is not simply due to selection for diving, as the rate of evolution in wing shape is consistently lower for WPD species than for species which also dive but which exclusively use their feet for aquatic locomotion (FPD species). This result is robust across all test conditions except those which treat species as evolving independently (Pagel's $\lambda = 0$), which is almost certainly unrealistic (Figures 4 & 5). In addition, when considering wing shape alone (allometry-free shapes), the wings of WPD species have explored a narrower range of potential wing shapes than FPD species. Thus, we can conclude that an increase in the number of locomotor functions, rather than a shift in ecology, has constrained the evolution of the wing in WPD species.

When treated in aggregate, the wing shapes of WPD species are not significantly different from those of FPD species (Table 2). Thus, that the evolution of wing shape in WPD species is constrained may seem paradoxical. But, while no specific wing shape can be used as a diagnostic characteristic of all WPD or FPD species, this does not preclude species from experiencing directional selection on wing shape. The optimal wing shapes for species within a clade are determined by each species' specific diving and flight strategies, and these strategies differ between clades (Chapter 1). Thus, WPD species can experience constraints on wing shape evolution while still exhibiting a diversity of wing shapes when considered as a single group.

Recent studies have indicated that much of the variation in wing shape – historically thought to be determined by flight style (Rayner, 1988; Savile, 1957) – can be explained by evolutionary history (Baliga et al., 2019; Wang and Clarke, 2015). Importantly, Baliga et al. (2019) demonstrated that the range of motion in the wing is strongly associated with flight behavior. Wing shape, on the other hand, was more strongly determined by ancestry, such that the level of phylogenetic signal in wing shape, as measured by Blomberg's K (Adams, 2014; Blomberg et al., 2003), was close to 1.0

(Baliga et al., 2019). In contrast, I found that phylogenetic signal in wing shape was relatively low (Figure 1) – often less than K = 0.3. The difference between our two studies could either be due to the difference in the number of species (61 species vs. 955 species), the distribution of species (broad taxonomic sampling vs. broad and deep sampling), the landmarks used to characterize wing shape (outer edge vs. outer edge + coverts), the extent of those landmarks (closed outline vs. outer edge, excluding the root), or variation in either wing preparation or digitization in my study (i.e., error).

To explore the likelihood of each scenario, I recalculated phylogenetic signal for 1) the wings of 955 species excluding the covert landmarks, 2) a subsample of species which mirrored those in Baliga et al. (2019) [61 species in said study or their close relatives], and for 3) the mirrored subsampled also excluding the covert landmarks. Removing the covert feathers from consideration had little effect on the estimated phylogenetic signal in raw wing shape for 955 species ($K_{\text{Ericson}} = 0.24 \pm 0.06$, $K_{\text{Hackett}} = 0.24 \pm 0.06$). However, the phylogenetic signal in raw wing shape for the subsample of 61 species was considerably higher ($K_{\text{Ericson}} = 0.68 \pm 0.04$, $K_{\text{Hackett}} = 0.70 \pm 0.04$), with little impact of removing the coverts from consideration ($K_{\text{Ericson}} = 0.61 \pm 0.03$, $K_{\text{Hackett}} = 0.62 \pm 0.03$). Importantly, I found that phylogenetic signal in wing shape of WPD species and FPD species (91 species) was no greater – and often lower – than that for the full set of species (Figure 1). Thus, the fact that phylogenetic signal in wing shape was considerably lower in this study than in others is likely due to the taxonomic depth of my sampling, rather than the number of species. The remaining difference in phylogenetic signal calculated here [~0.7] versus in Baliga et al. (2019) [~0.95] may be because I did not digitize the root of the wing or due to variation in either wing preparation or digitization. Variation in digitization seems unlikely given the low value of digitization error (Figure 3, blue lines). This does not detract from the major result of Baliga et al. (2019) – that the range of motion in the avian wing is both labile and strongly correlated with flight behavior. However, the relatively low levels of phylogenetic signal I found indicate that avian wing shape may be linked to flight behavior afterall.

Stayton et al. (2018) tested whether the shells of terrestrial turtles are more diverse and/or have diversified more rapidly than those of aquatic turtles, finding that the shells of terrestrial turtles are more diverse than those of aquatic turtles, but that this is not due to differences in the rate of morphological evolution. Corn et al. (2021) tested whether the cranial morphology and kinematics of fishes evolved more quickly in groups which feed only through suction versus those which bite and suck, finding that those which bite and suck have experienced faster rates of evolution on their static morphology, but slower rates of evolution on feeding kinematics. Thus, in combination with the results shown here, the consensus is that multifunctionality constrains the evolution of morphological systems, at least in terms of their static morphology.

However, results from these systems may not be directly comparable, as they differ in whether multifunctionality was gained or lost. Terrestrial turtles have lost a shell function relative to aquatic turtles, whereas biting and sucking percomorph fishes have gained a cranial function relative to pure suction feeders. Likewise, given that the common ancestor of birds was likely volant and non-diving, species which use their wings in air and water have gained a wing function. How this gain vs. loss influences the effect of multifunctionality on morphological evolution is unclear. There might also be a fundamental difference between systems with two-vs.-one function and those with many-vs.-many-minus-one functions.

Finally, the results of Corn et al. (2021) illustrate convincingly that the effects of multifunctionality on evolution might be different for static morphological traits than for dynamic traits [such as feeding kinematics or wing range of motion]. Thus, exploring the effects of multifunctionality on the evolution of wing range of motion (Baliga et al., 2019) in WPD species, FPD species, and NDFD would be especially informative.

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Figure 1: Phylogenetic signal in wing shape and size. Phylogenetic signal in raw shapes, allometry-free shapes, and centroid size was calculated for 100 phylogenetic trees for each of two backbones. Signals from trees based on the Ericson backbone are in blue; Hackett are in gray. Signals are presented for four datasets [All species, species with genetic data in birdtree.org phylogenies, all diving species, and divers with genetic data in birdtree.org phylogenies].

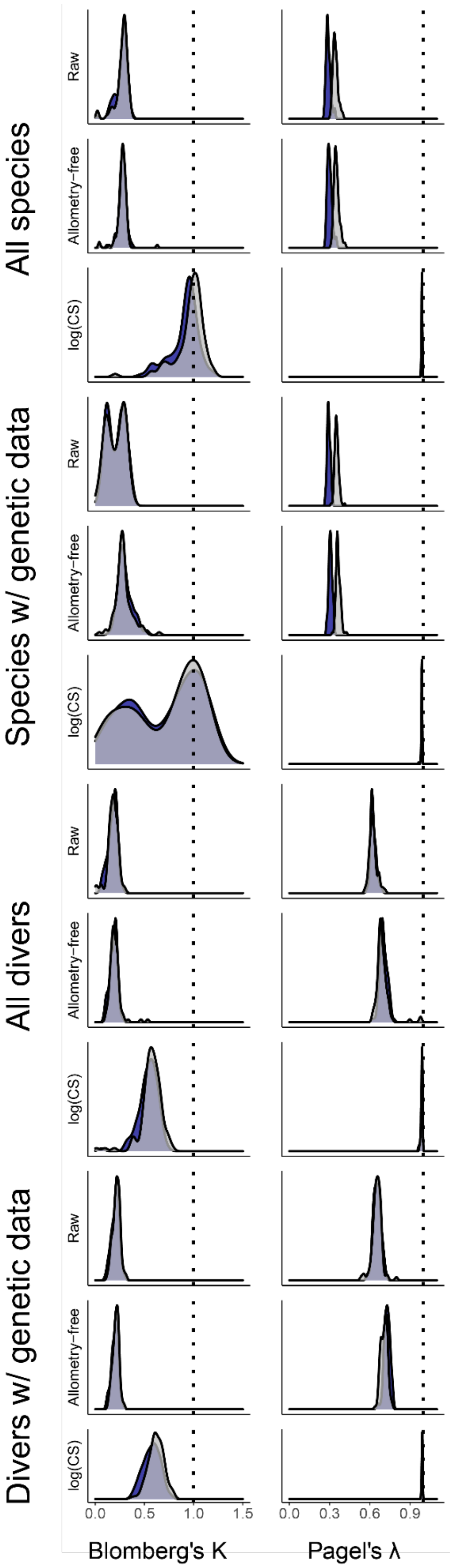


Table 1: Differences in wing shape between WPD species, FPD species, NDFD groups. Values shown are mean, range, and standard deviation for the R-squared, F-statistic, and p-value generated by each test across 100 trees from each of two phylogenetic backbones. All values have been rounded to two significant digits.

Dataset	Factor	R squared	F Statistic	p Value
Ericson: All species	log(CS)	0.037 ± 0.053 (0.0068 − 0.33)	41 ± 69 (6.5 − 470)	0.0011 ± 0.00061 (0.001 − 0.006)
	Shape	0.0025 ± 0.00044 (0.00034 − 0.0034)	1.2 ± 0.25 (0.17 − 2)	0.24 ± 0.098 (0.067 − 0.57)
	log(CS) X Shape	0.0089 ± 0.012 (0.0022 − 0.085)	4.6 ± 6.5 (1 − 45)	0.058 ± 0.073 (0.001 − 0.32)
Ericson: Genetic only	log(CS)	0.17 ± 0.18 (0.01 − 0.63)	260 ± 360 (9.2 − 1600)	0.001 ± 0.00024 (0.001 − 0.003)
	Shape	0.0023 ± 0.00055 (0.0011 − 0.0036)	1.3 ± 0.28 (0.76 − 2.2)	0.25 ± 0.099 (0.042 − 0.52)
	log(CS) X Shape	0.0056 ± 0.0026 (0.0017 − 0.014)	3.4 ± 2.2 (0.77 − 8.9)	0.11 ± 0.14 (0.001 − 0.55)
Hackett: All species	log(CS)	0.034 ± 0.074 (0.0066 − 0.71)	98 ± 690 (6.4 − 7000)	0.0011 ± 0.00053 (0.001 − 0.006)
	Shape	0.0025 ± 0.00056 (0.00038 − 0.0036)	1.3 ± 0.6 (0.19 − 6.6)	0.23 ± 0.094 (0.004 − 0.47)
	log(CS) X Shape	0.018 ± 0.059 (0.002 − 0.43)	21 ± 110 (0.96 − 970)	0.07 ± 0.083 (0.001 − 0.36)
Hackett: Genetic only	log(CS)	0.17 ± 0.19 (0.01 − 0.73)	280 ± 430 (9.3 − 2500)	0.0011 ± 0.00054 (0.001 − 0.006)
	Shape	0.0024 ± 0.00076 (0.00033 − 0.004)	1.3 ± 0.44 (0.16 − 3.6)	0.23 ± 0.11 (0.01 − 0.75)
	log(CS) X Shape	0.0057 ± 0.0033 (0.0011 − 0.019)	3.6 ± 2.9 (0.54 − 15)	0.097 ± 0.12 (0.001 − 0.55)

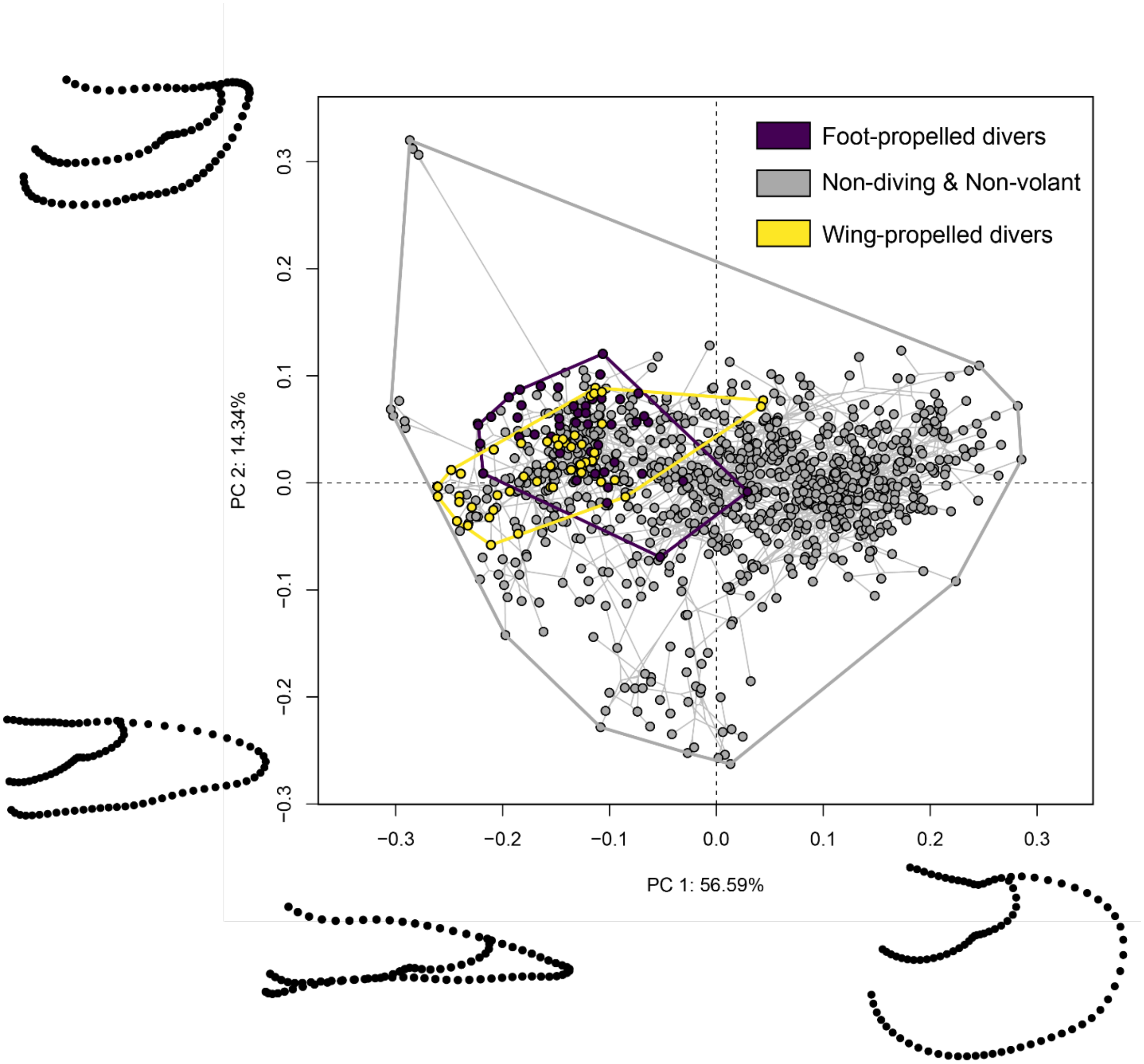
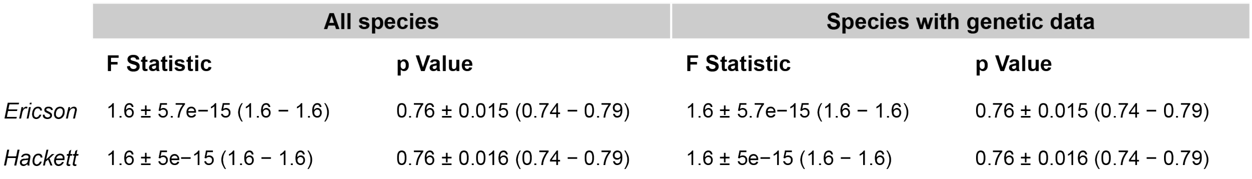


Figure 2: Phylo-morphospace of wing shape. The wing shapes of all species based on the first two principal components of wing shape variation. Wireframe diagrams indicate shapes associated with the extremes of each PC axis.

Table 2: Differences in intraspecific disparity between WPD species, FPD species, NDFD groups. Values shown are mean, range, and standard deviation for the F-statistic and p-value generated by each test across 100 trees from each of two phylogenetic backbones. All values have been rounded to two significant digits.



	All species		Species with genetic data	
	F Statistic	**p Value**	**F Statistic**	**p Value**
Ericson	1.6 ± 5.7e−15 (1.6 − 1.6)	0.76 ± 0.015 (0.74 − 0.79)	1.6 ± 5.7e−15 (1.6 − 1.6)	0.76 ± 0.015 (0.74 − 0.79)
Hackett	1.6 ± 5e−15 (1.6 − 1.6)	0.76 ± 0.016 (0.74 − 0.79)	1.6 ± 5e−15 (1.6 − 1.6)	0.76 ± 0.016 (0.74 − 0.79)

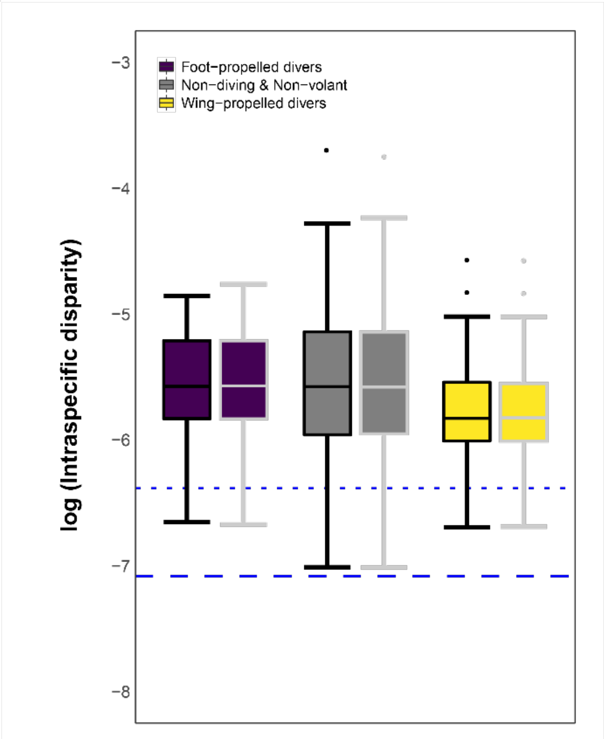


Figure 3: Intraspecific disparity in wing shape versus group. Intraspecific disparity was calculated as the Procrustes variance for species represented by 3 or more individuals. Boxes on the left of each group pair (outlined in black) are data for all species; the right of each group pair (outlined in gray) are for the subset of species with genetic data. The average and average + standard deviation of digitization error are indicated by the blue dashed and dotted lines, respectively.

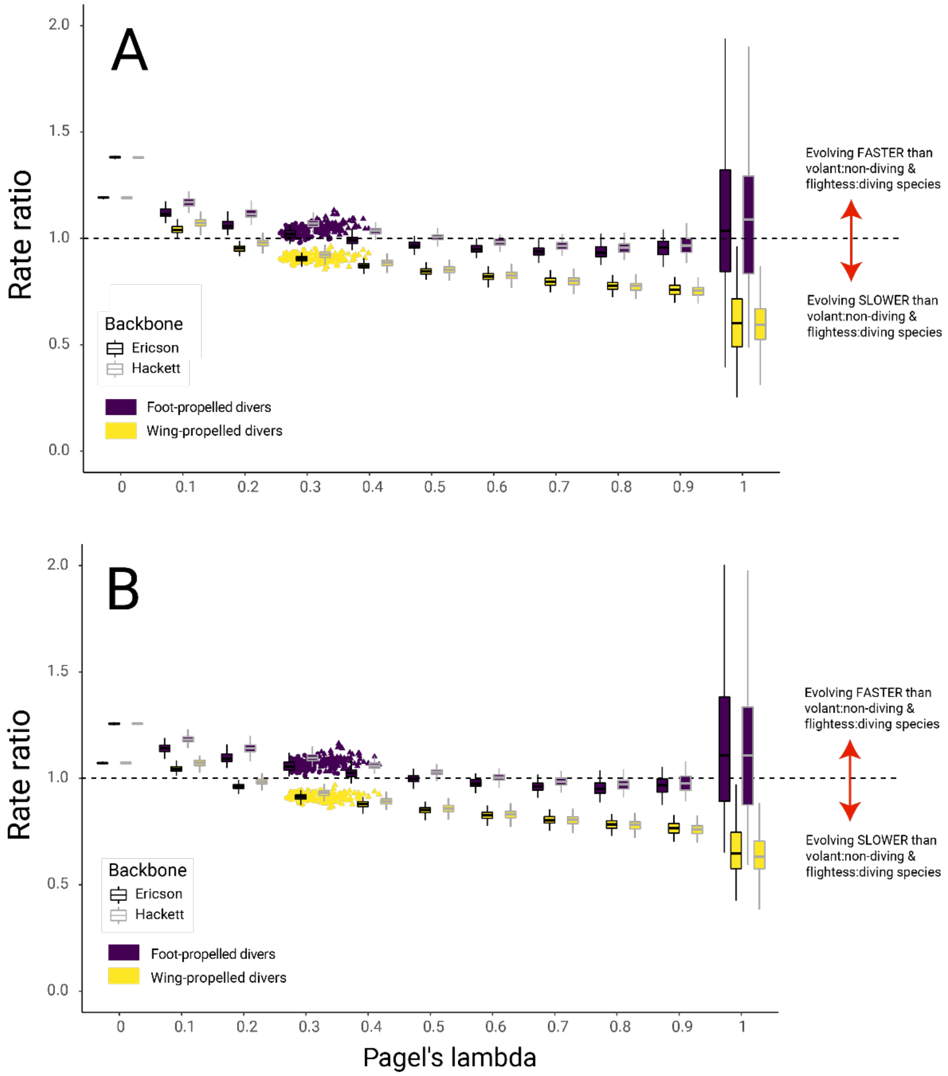


Figure 4: Evolutionary rates in wing shape for all WP and FP species. Evolutionary rates for each group are expressed relative to the rate found for NDFD species. Because the phylogenetic signal in wing shape was lower than expected under Brownian motion, the x-axis indicates the value of Pagel's λ used for the tree transformation, with 1 indicating no transformation and 0 indicating a star phylogeny. The scatter points are for λ-transformations based on precise value of λ calculated for each specific tree-by-shapes combination ("precise λ-transformation"). (A) Raw wing shapes. (B) Allometry-free wing shapes.

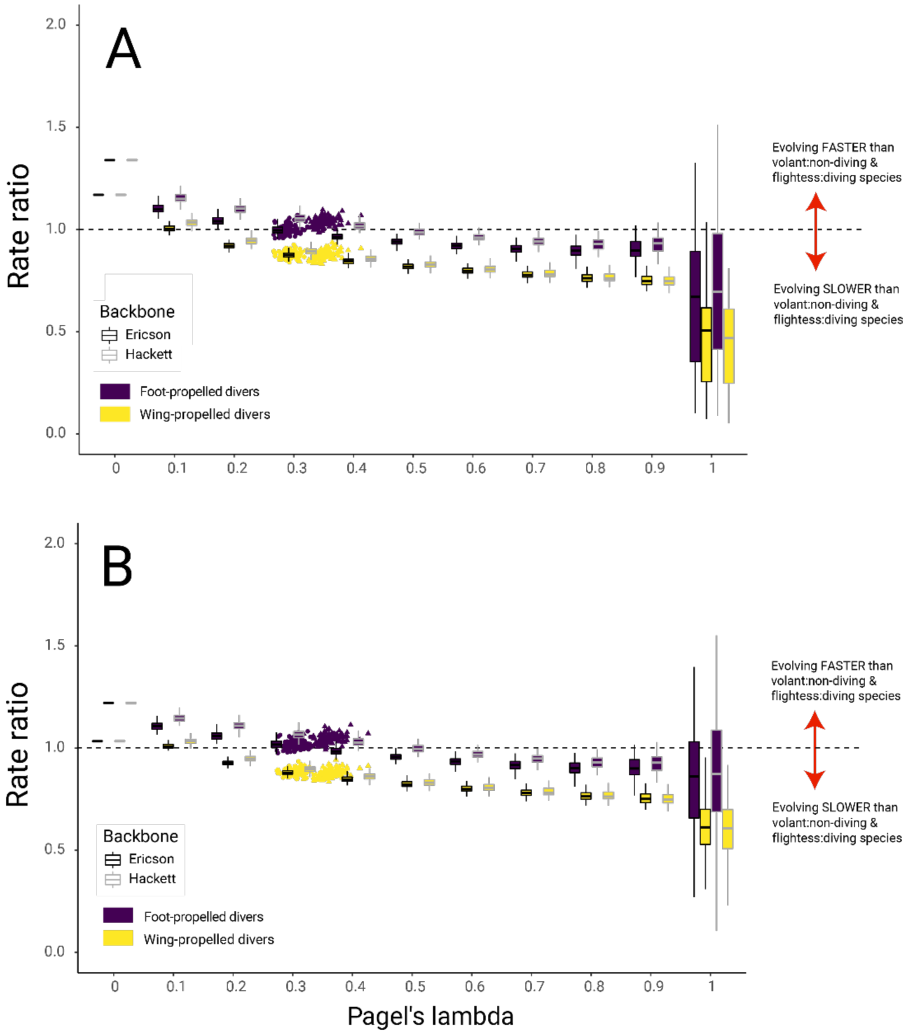


Figure 5: Evolutionary rates in wing shape for species with genetic data. Evolutionary rates for FPD species and WPD species are expressed relative to the rate found for NDFD species. Because the phylogenetic signal in wing shape was lower than expected under Brownian motion, the x-axis indicates the value of Pagel's λ used for the tree transformation, with 1 indicating no transformation and 0 indicating a star phylogeny. The scatter points are for λ-transformations based on precise value of λ calculated for each specific tree-by-shapes combination ("precise λ-transformation"). (A) Raw wing shapes. (B) Allometry-free wing shapes.

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RESEARCH ARTICLE

Upstroke-based acceleration and head stabilization are the norm for the wing-propelled swimming of alcid seabirds

Anthony B. Lapsansky* and Bret W. Tobalske

ABSTRACT

Alcids, a family of seabirds including murres, guillemots and puffins, exhibit the greatest mass-specific dive depths and durations of any birds or mammals. These impressive diving capabilities have motivated numerous studies on the biomechanics of alcid swimming and diving, with one objective being to compare stroke–acceleration patterns of swimming alcids with those of penguins, where upstroke and downstroke are used for horizontal acceleration. Studies of free-ranging, descending alcids have found that alcids accelerate in the direction of travel during both their upstroke and downstroke, but only at depths <20 m, whereas studies of alcids swimming horizontally report upstroke-based acceleration to be rare (≤16% of upstrokes). We hypothesized that swimming trajectory, via its interaction with buoyancy, determines the magnitude of acceleration produced during the upstroke. Thus, we studied the stroke–acceleration relationships of five species of alcid swimming freely at the Alaska SeaLife Center using videography and kinematic analysis. Contrary to our prediction, we found that upstroke-based acceleration is very common (87% of upstrokes) during both descending and horizontal swimming. We reveal that head-damping – wherein an animal extends and retracts its head to offset periodic accelerations – is common in swimming alcids, underscoring the importance of head stabilization during avian locomotion.

KEY WORDS: Stroke acceleration patterns, Charadriiformes, Auk, Underwater locomotion, Diving

INTRODUCTION

When animals transition between air and water, they must cope with dramatic changes to their sensory perception, their respiration and the force regime to which they are subjected (Dial et al., 2015; Fish, 2016). Despite these challenges, the phylogeny of birds provides abundant examples of secondary adaption to life in water (Vermeij and Dudley, 2000). These species (e.g. ducks, cormorants, loons, puffins, penguins, etc.) can reach depths that rival those of much larger diving mammals (Ponganis, 2015).

Within birds, penguins (order Sphenisciformes, family Spheniscidae) appear to have been the most successful at re-invading the aquatic realm. The current records for dive depth and duration in birds are held by the ∼25 kg emperor penguin (*Aptenodytes forsteri*) at 564 m and 27.6 min, respectively, with other penguin species not far behind (Ponganis, 2015). This aquatic accomplishment by penguins is often attributed to their loss of flight (Elliott et al., 2013; Storer, 1960). The rationale behind this argument is that because air and water are drastically different (Denny, 1993), selection cannot optimize a species for movement in both fluids concurrently. In other words, abandoning flight has allowed penguins to better exploit the aquatic environment (Simpson, 1946).

However, the diving performance of alcids (order Charadriiformes), a family of seabirds closely related to gulls and terns, seems to contradict this notion. The alcid family contains 24 extant species including puffins, murres, guillemots and their relatives notable for their ability to ‘fly’ underwater as well as in the air. The current records for the depth and duration of a single dive by an alcid are 210 m and 224 s, respectively, held by the ∼1 kg thick-billed murre (*Uria lomvia*), making this species, on a mass-specific basis, the deepest and longest-duration diver on Earth (Croll et al., 1992). When corrected for body size, alcids exhibit dive durations and depths far greater than penguins, despite remaining volant (Halsey et al., 2006; Watanuki and Burger, 1999).

The impressive diving capabilities of alcids have motivated multiple, independent studies on the biomechanics of alcid swimming and diving (Hamilton, 2006; Johansson and Aldrin, 2002; Kikuchi et al., 2015; Lovvorn et al., 2004; Watanuki and Sato, 2008; Watanuki et al., 2003, 2006), with one key focus being to compare stroke–acceleration patterns of swimming alcids with those of penguins.

The stroke–acceleration patterns of flying birds are well defined, both by empirical study and aerodynamic theory. To maintain speed, a flying bird must produce enough thrust to counteract drag. Flying alcids and similar species (e.g. ducks) are thought to produce this thrust primarily or entirely via the downstroke of their wing (Izraelevitz et al., 2018; Pennycuick, 1987; Rayner, 1988, 1995). The upstroke contributes to weight support, along with the downstroke, but is thought to produce only negligible thrust outside of slow flight (Crandell and Tobalske, 2015). Thus, owing to its stroke–acceleration pattern, an alcid maintaining speed during level, cruising flight should experience a horizontal deceleration during the upstroke followed by a horizontal acceleration of equal magnitude on the downstroke.

Though their style of swimming resembles the aerial flight of birds, swimming penguins deviate from this general stroke–acceleration pattern in ways hypothesized to increase to their efficiency (energy required to move at a given speed) (Clark and Bemis, 1979; Hui, 1988; Lovvorn, 2001; Watanuki et al., 2006). Swimming penguins accelerate forward during both downstroke and upstroke (Clark and Bemis, 1979; Hui, 1988; Watanuki et al., 2006). Perhaps owing to modifications of their flight apparatus only feasible through the loss of flight (Raikow et al., 1988), penguins produce significant amounts of thrust via their upstroke, as well as their downstroke, which is great enough to overcome the drag (and sometimes buoyancy) of their body. By accelerating during both halves of the stroke cycle, penguins minimize the magnitude of

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accelerations needed to maintain speed (Watanuki et al., 2006). The alternative – large deceleration during the upstroke followed by compensatory acceleration during the downstroke – causes an animal to experience large deviations from its average velocity. This is especially true in water, where the drag is greatly increased relative to air (Denny, 1993). Because drag increases quadratically with velocity, and because it is energetically expensive to accelerate a body and its entrained fluid, an animal that moves at a more constant velocity spends less energy to move at the same average velocity (Daniel, 1984; Lovvorn, 2001; Vogel, 1994). Thus, by accelerating forward during the upstroke in addition to during the downstroke, penguins appear to have developed a highly efficient swimming strategy.

All alcids studied to date have shown at least some capacity to accelerate forward (hereafter, accelerate) during the upstroke when swimming, in addition to during the downstroke, but the conditions that determine the presence and frequency of upstroke-based acceleration remain unclear. Using the pattern of bubbles released by the plumage of a captive pigeon guillemot (*Cepphus columba*) as evidence, Rayner (1995) suggested that alcids had a hydrodynamically inactive aquatic upstroke that functioned exclusively to reset the wing for the next downstroke. Subsequent data collected via 3D videography of horizontally swimming alcids at relatively shallow depths found that the upstroke was capable of producing thrust, contrary to Rayner's assertion, but that this thrust rarely caused acceleration. Specifically, Johansson and Aldrin (2002) reported acceleration during 2 of 24 (8%) upstrokes by Atlantic puffins (*Fratercula arctica*) and Hamilton (2006) reported acceleration during 5 of 32 (16%) upstrokes by common murres (*Uria aalge*), suggesting that the force created by the upstroke of a swimming alcid is only rarely sufficient to overcome drag. In contrast, data collected via accelerometers on free-ranging alcids indicate that these animals regularly accelerate during the upstroke when descending, but that the magnitude of this acceleration decreases to below zero past depths of approximately 20 m (Lovvorn et al., 2004; Watanuki et al., 2003, 2006).

Previous authors have evoked the decrease in buoyancy with depth (as air in the lungs and plumage compress as described by Boyle's law) to explain the negative relationship between the magnitude of acceleration during the upstroke and depth (Lovvorn et al., 2004; Watanuki et al., 2003, 2006). However, if alcids accelerate during the upstroke when buoyancy is high, it is unclear why Johansson and Aldrin (2002) and Hamilton (2006) did not detect consistent upstroke-based acceleration in alcids swimming in shallow water.

We hypothesized that trajectory might determine the use of upstroke-based acceleration in swimming alcids via the relationship between trajectory and buoyancy. When descending in shallow water, work against buoyancy is a major contributor to the total work required to swim. In contrast, when swimming at depth and horizontally, little work must be done against buoyancy to maintain speed (Lovvorn, 2001), perhaps alleviating the need for upstroke-based acceleration. Thus, the interaction between trajectory and buoyancy may explain the decrease in upstroke-based acceleration with depth over the course of the same dive in descending alcids (Lovvorn et al., 2004; Watanuki and Sato, 2008; Watanuki et al., 2003, 2006) and the rarity of upstroke-based acceleration in horizontally swimming alcids (Hamilton, 2006; Johansson and Aldrin, 2002). To test this hypothesis, we studied the stroke–acceleration relationships of five species of alcids from three genera using videography and kinematic analysis. Our study subjects were captive birds swimming freely in an aquarium at the Alaska SeaLife Center in Seward, Alaska.

MATERIALS AND METHODS

Study area and animals

Study animals included common murres [*Uria aalge* (Pontoppidan 1763)], pigeon guillemots (*Cepphus columba* Pallas 1811), rhinoceros auklets [*Cerorhinca monocerata* (Pallas 1811)], horned puffins [*Fratercula corniculata* (Naumann 1821)] and tufted puffins [*Fratercula cirrhata* (Pallas 1769)]. This work was performed with permission from the Alaska SeaLife Center in Seward, Alaska, USA, from 23 to 31 June 2018 under the auspices of the University of Montana's Institutional Animal Care and Use Committee (AUP 004-19BTDBS-020419). The Alaska SeaLife Center is to home to an outdoor aviary exhibit with a large area for aerial flight (approximately 20 m wide, 20 m long and 8–10 m tall) over a 397,500 liter saltwater tank. The surface of the water measures approximately 10.5×11 m and is approximately 6.5 m deep at its deepest point. The southern edge of the tank is inset with a large glass viewing window approximately 3.5 m wide that extends from ∼2 m above the waterline to the floor of the tank. The glass of the viewing window varies from ∼6.5 to ∼25.0 cm thick from the waterline to the floor of the tank.

At the time of this study, the exhibit contained 12 horned puffins, 10 tufted puffins, four pigeon guillemots, six common murres and two rhinoceros auklets. Individuals of each species of alcid regularly swam past the viewing window, performing both horizontal and descending swimming bouts, either for transport around the exhibit or to retrieve food tossed in the water by aquarium staff. The birds swam on their own volition and selected their own swimming speeds and descent angles.

Videography

Videos were taken using a GoPro Hero6 Black (GoPro, Inc., San Mateo, CA, USA) at 119.88 frames s^{-1} and a shutter speed of 1/480 s in the 'Linear View' mode, which removes the 'fisheye' distortion common to action cameras (Tyson Hedrick, personal communication). The camera was positioned on a tripod and leveled using a bubble-type level embedded in the tripod. Because birds chose when and where to dive, swimming bouts were sampled opportunistically. The camera was triggered via a GoPro Smart Remote when A.B.L. noticed a bird about to initiate a dive or swim past the viewing window. The camera was positioned approximately 1 m below the waterline, thus all analyzed dives were between 0 and 3 m deep.

Kinematic and data analyses

Swimming bouts were selected for kinematic analysis based on whether birds appeared to swim at an approximately constant speed, parallel to the viewing window (perpendicular to the camera) as determined by A.B.L. We were stringent in this assessment, selecting less than 5% of all footage for analysis. Preference was given to videos taken on days with brighter natural light to facilitate the digitization process. We analyzed 41 swimming bouts totaling 166 downstrokes and 153 upstrokes (for condition- and species-specific values, see Table 1).

Although each bird in the tank had unique colored leg bands, we were unable to confidently identify individuals in video sequences. Thus, we considered each wingbeat as having been sampled from a greater population of wingbeats representing each species. Previous research on diving kinematics has indicated that this method provides a reasonably accurate kinematic description for a given species (Lovvorn et al., 1991). Given the number of individuals of each species in the tank and the number of swimming bouts we analyzed, it is unlikely that our data for any one species is based on fewer than two individuals (≤6.25%).

Table 1. Sample sizes for each alcid species and swimming trajectory

Species	Horizontal bouts	Descending bouts	Downstrokes during horizontal bouts	Upstrokes during horizontal bouts	Downstrokes during descending bouts	Upstrokes during descending bouts
Common murre	7	2	25	25	10	11
Horned puffin	6	3	25	23	10	8
Pigeon guillemot	5	3	27	25	8	8
Rhinoceros auklet	6	–	24	18	–	–
Tufted puffin	6	3	25	24	12	11

We performed kinematic analyses using MATLAB (2018a & b, MathWorks, Inc., Natick, MA, USA) using the DLTdv6 digitization tool described in Hedrick (2008) with additional analyses performed using MATLAB and IGOR Pro (v. 6.01, Wavemetrics, Inc., Beaverton, OR, USA). We assigned each swimming bout as being either horizontal (trajectory <5 deg from horizontal) or descending (>20 deg). We did not obtain video of rhinoceros auklets engaged in descending swimming.

We digitized the eye, the wrist and the tip of the tail in every frame of each video. To reduce digitizing error for the eye, we digitized the eye using three consecutively blind, replicate passes for horizontal bouts and averaged the three points at each frame. We only digitized the eye one time for descending bouts after realizing that birds were head-damping, wherein an animal extends and retracts the head to offset periodic accelerations and stabilize head position (Necker, 2007; Pete et al., 2015). An additional two points were digitized (at a single frame) corresponding to the waterline at opposite sides of the viewing window so that we could calculate the angle of descent. More than 43,000 points were hand-digitized for this study.

The *x*–*y* points determined via digitization were exported to MATLAB for analysis via a custom script. The script first computed the angle between the vector describing the true horizontal (i.e. the waterline) and the *x*-direction of the video. The script then rotated all digitized points about this angle, which was usually less than 1 deg, to account for small errors in the manual leveling of the camera setup. For descending bouts, the script then computed the angle between the vectors describing the bird's mean path and the vector corresponding to the waterline. The script then converted, via a 2D Euler-angle rotation matrix, the points from a global coordinate system to a local, bird-centered coordinate system in which the *x*- and *y*-axes were parallel and perpendicular to the bird's swimming direction, respectively. For horizontal bouts, we assumed that the *x*- and *y*-axes were reasonably aligned with the birds' cranial-caudal and dorsal-ventral axes and, therefore, did not transform the digitized points. Following transformation of the descending bouts, the MATLAB scripts were identical.

We used the body length of the bird in each frame, as determined by the distance between the eye and the tail in each frame, to convert the *x*–*y* points to a consistent coordinate system. This method of calibration accounts for variability in the distance between the camera and the bird as well as any distortion of the image that may have occurred as the light reflecting off the bird passed from water to glass to air before reaching the camera. Specifically, we computed the length of the body (in pixels) for each frame as the distance between the eye and the tail using the Pythagorean theorem. Visual inspection of these data revealed pronounced head movement (relative to the body) in sync with the wingbeat cycle (i.e. body length varied with position in the stroke cycle). Because of this observation, we smoothed the raw body-length data using the 'smoothingspline' method of fitting in MATLAB and a smoothing parameter of 1E-4 to account for the head movement of the bird (Curve Fitting ToolBox User's Guide, 2019; https://www.mathworks.com/help/pdf_doc/curvefit/curvefit.pdf). The *x*–*y* points for each frame were then divided by the body length at that frame to convert the points' pixel units to units of body length. It should be noted that even if this calibration process was imperfect – for example, if the smoothing failed to remove the effects of head-damping completely – it would not alter our major conclusions about the hydrodynamic function of the upstroke. Upstroke with periods of acceleration would still have periods of acceleration, as body length was used simply to scale the data to units of species-specific body length. Only the magnitude of that acceleration could change.

We opted not to convert from body length units to SI units, as data on body length while swimming are available only for the common murre (within Hamilton, 2006). Because alcids flex their neck when diving, measurements taken from birds in the hand or from museum species are not accurate proxies for the body length a species adopts when swimming. Thus, we felt that using an estimate of body length for the other four species would add error to our results without improving our ability to test our hypothesis. However, we include rough estimates of body lengths during swimming for comparison: common murre, 0.36 m; horned puffin, 0.31 m; pigeon guillemot, 0.27 m; rhinocerous auklet, 0.30 m; tufted puffin, 0.35 m. We caution against using these values as true data points or in strict analyses. The conversion factor for the common murre comes from Hamilton (2006) and is based on two birds. Those for the tufted puffin, horned puffin and rhinoceros auklet (which are all, technically, puffins; Wilson and Manuwal, 1986) stem from the measured body length of a single Atlantic puffin (0.290±0.006 m), found by using ImageJ to compute the distance between 20 pairs of beak and tail points displayed in fig. 3B of Johansson and Aldrin (2002). Assuming geometric similarity between these four closely related species, we computed body length estimates in meters using mean masses from Dunning (2008). For the pigeon guillemot, we report a value measured on wild birds in the hand (we think) from Cody (1973). This value is almost certainly an overestimate and should be treated with caution. We encourage future studies to publish body lengths of animals during locomotion to facilitate research on animal locomotion under conditions in which calibration to metric units is infeasible (e.g. birds flying in the natural environment).

To account for digitization error, we smoothed the kinematic data using the same 'smoothingspline' method of fitting in MATLAB as above but using a smoothing parameter of 0.01 (Curve Fitting ToolBox User's Guide, 2019; https://www.mathworks.com/help/pdf_doc/curvefit/curvefit.pdf), based on Clifton and Biewener (2018) (Fig. 1). We computed instantaneous velocity (body lengths s^{-1}; hereafter BL s^{-1}) in the *x*-direction as the change in *x*-position between frames divided by the duration of the frame (1/119.88 s or 0.0083 s) for both eye and tail points (separately). We subsequently computed instantaneous acceleration (BL s^{-2}) as the change in velocity between frames divided by the duration of the frame. Because we digitized distal portions of the body rather than the center of mass, pitching motions of the body could impact our

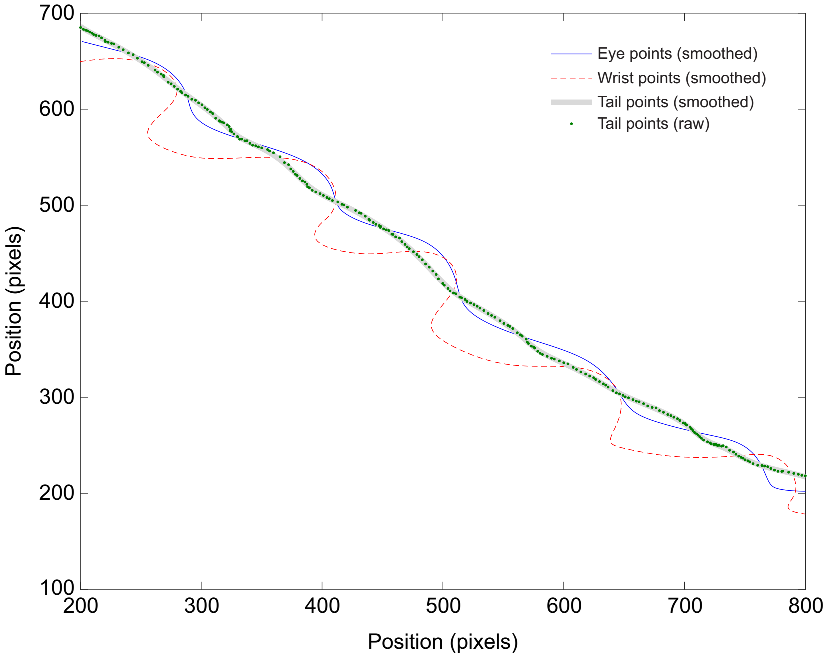

Fig. 1. Wing and body kinematics of a descending tufted puffin. Included are the raw, digitized tail points (green dots) and smoothed points corresponding to the tail, eye and wrist. Data from this bout are illustrated in Figs 2 and 3.

estimates of overall body acceleration. To resolve this potential issue, we first computed the pitch angle (rad) in each frame relative to the horizontal. This allowed us to remove the component of our velocity calculation that was due to pitching from the overall velocity calculation described above. Specifically, we assumed that the body pitched around a point midway between the eye and the tail, or about the approximate center of mass. Thus, the velocity due to body pitch was calculated as the change in *x*-oriented body length, where the *x*-oriented body length was computed as 0.5 times the body length times the cosine of the pitch angle. We removed this pitching velocity (BL s^{-1}) from the overall velocity of both the eye and the tail before computing acceleration. Because the change in pitch angle between adjacent frames was generally quite small relative to the change in body position, and because the pitch angles themselves were small relative to each bird's trajectory, pitching generally accounted for <5% of total acceleration. To this end, we repeated our analyses while ignoring the effects of pitching and found no significant changes to our major results.

To differentiate between the upstroke and downstroke, we computed the elevation of the wrist (relative to the midline of the body defined as a line between the eye and tail). These data, along with the velocity and acceleration data, were then exported to IGOR Pro. We then manually picked the start and stop of each wing stroke, defined by the maximum and minimum elevation of the wrist, and used a custom macro to obtain the instantaneous velocity and acceleration data based on the tail and eye points between the two points in time.

Visual inspection of the body-length data revealed obvious head movement relative to the body in all five species (Fig. 2). For this reason, we present acceleration data based on the tail points, but for the sake of comparison with previous work (Hamilton, 2006; Johansson and Aldrin, 2002), we also used the eye points to compute the proportion of upstrokes with positive instantaneous acceleration.

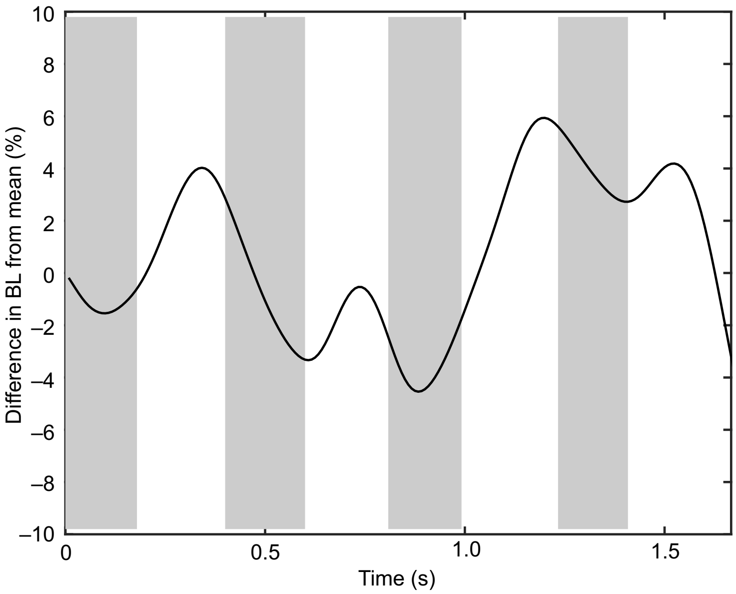

Fig. 2. Percent difference in body length (BL) relative to mean body length for a descending tufted puffin as a function of time (s). Gray background, downstroke; white background, upstroke, based on the position of the wrist. Body length is measured as the distance between the eye and the tail at each frame, after smoothing. These data were obtained from the sequence of wingbeats shown in Fig. 1.

We feel that the tail is a valid indicator of overall body motion in this study. Although the tail may be used for maneuvering in some species, we did not digitize bouts in which alcids changed direction or turned. In addition, the tail is folded when diving, and thus represents a fairly stiff offshoot of the body. Though it may have been worthwhile to digitize multiple points around the border of the body to estimate the location of the center of mass of each bird for each frame, the time required for such a process makes it unfeasible for a study with this large of a sample size. Further, automated tracking methods were unable to distinguish the bird from other objects in the tank, given the complex background.

To determine whether a given stroke resulted in acceleration, we used the 'findpeaks' function in MATLAB to locate the position and magnitude of the largest local maximum acceleration (hereafter, 'peak acceleration'), which typically occurred at around mid-stroke (Fig. 3). We chose this method over simply selecting the largest accelerations to avoid sampling momentary positive accelerations occurring at the stroke reversals and to better replicate the methods of past studies, which specifically refer to acceleration peaks (Hamilton, 2006; Watanuki et al., 2006).

The upstroke and downstroke of alcids contain highly negative and positive instantaneous accelerations that are variable in their timing between wingbeats. We found that because of this variability in timing, averaging the instantaneous acceleration across wing strokes leads to the deconstruction of the overall pattern (negative features overlap with positive features owing to slight variation in timing). Presumably for this reason, past studies have presented 'representative' acceleration profiles rather than average plots (Lovvorn et al., 2004; Watanuki et al., 2003, 2006). In addition to a representative plot, for both downstroke and upstroke we plot the average peak acceleration (i.e. the largest local maximum occurring during each half-stroke, as described above), average minimum acceleration, and average acceleration at the downstroke-to-upstroke transition, along with the standard error in mean and timing of said values, to illustrate the overall shape of the acceleration profiles for each species.

Statistics

Plots were made using MATLAB's basic plotting functions. To determine whether alcids in our study head-bobbed or head-damped, we compared the coefficient of variation in velocity (calculated as the standard deviation in velocity divided by the mean velocity; hereafter, $CV_{velocity}$) for each complete wingbeat cycle based on either tail points or eye points. To test for a significant difference between these measures, we used a linear mixed-effects model (with random effects on the intercept for both species and bout) in MATLAB. Head-bobbing is exhibited by many bird species in walking and swimming and occurs when a bird alternates between a globally fixed head position and a thrusting head movement in sync with the stroke cycle (Clifton and Biewener, 2018; Necker, 2007). Head-damping occurs when a bird uses relative head movement to smooth or damp the acceleration patterns of the body, thereby creating a more stable visual field. If birds head-bobbed, then we would expect higher $CV_{velocity}$ values owing to the alternation between hold and thrust phases of the head, whereas head-damping would result in lower $CV_{velocity}$ values. For values of maximum upstroke and downstroke, standard deviations were computed as the square root of the summed squared-errors for maximum upstroke and downstroke. We report means±s.e.m.

RESULTS

Stroke–acceleration pattern

On average, alcids accelerated during the downstroke and decelerated during the upstroke in both level and descending bouts (Table 2). However, 100 of 115 (87%) upstrokes during horizontal bouts and 33 of 38 (87%) upstrokes during descending bouts produced peak accelerations greater than zero (Table 2). In other words, alcids experienced moments of acceleration during the majority of upstrokes. The general stroke-acceleration pattern as a function of time was M-shaped across all five species, with minima near the stroke reversals and peaks at about mid-stroke (Figs 4 and 5). The relative height of mean peak upstroke-acceleration to mean peak downstroke-acceleration ranged from 0.23±0.28 BL s^{-2} in the pigeon guillemot to 0.61±0.22 BL s^{-2} in the tufted puffin for horizontal swimming, and from 0.06±0.50 in the horned puffin to 0.89±0.35 BL s^{-2} in the pigeon guillemot for descending swimming (Figs 4 and 5, Table 2). The timing of peak acceleration during the downstroke was much more consistent than that during the upstroke, as illustrated by the width of the error bars in Figs 4 and 5. The peak

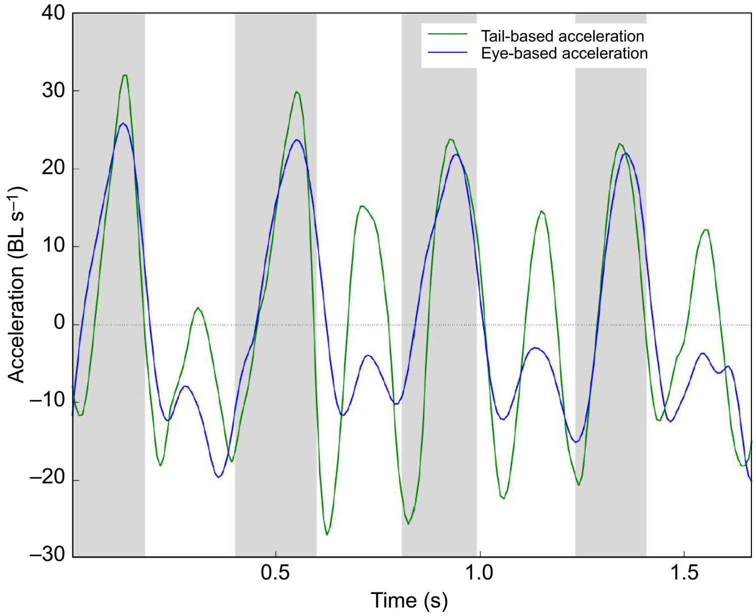

Fig. 3. Acceleration pattern (BL s^{-2}) of a descending tufted puffin, based on both head and tail points, versus time (s). Gray background, downstroke; white background, upstroke, based on the position of the wrist. These data are taken from the sequence of wingbeats shown in Fig. 1.

Table 2. Stroke–acceleration patterns for five species of alcid engaged in descending and horizontal swimming

	Common murre	Horned puffin	Pigeon guillemot	Rhinoceros auklet	Tufted puffin
Horizontal					
Mean downstroke acceleration (BL s^{-2})	6.32±1.20	8.64±0.67	3.98±0.89	7.88±1.89	4.03±0.75
Mean upstroke acceleration (BL s^{-2})	−2.44±0.50	−4.13±0.79	−3.56±0.65	−4.24±1.48	−0.923±0.56
Peak downstroke acceleration (BL s^{-2})	15.46±1.57	24.99±0.94	15.23±1.21	23.41±2.25	16.89±2.16
Peak upstroke acceleration (BL s^{-2})	6.07±0.73	9.04±1.82	3.57±0.97	8.68±1.95	10.23±1.88
Min. downstroke acceleration (BL s^{-2})	−5.29±0.98	−11.46±1.83	−8.73±1.00	−11.54±2.26	−8.58±2.18
Min. upstroke acceleration (BL s^{-2})	−11.51±1.17	−19.19±1.92	−13.05±1.14	−19.61±3.03	−10.93±1.65
Upstroke peak/downstroke peak	0.39±0.16	0.36±0.20	0.23±0.28	0.37±0.24	0.61±0.22
Prop. downstrokes with peak acceleration>0	24/25	25/25	27/27	23/24	25/25
Prop. upstrokes with peak acceleration>0	22/25	19/23	19/25	17/18	23/24
Prop. upstrokes with peak acceleration>0, based on head points	11/25	9/23	8/25	6/18	18/24
Descent					
Mean downstroke acceleration (BL s^{-2})	1.84±0.88	9.65±1.41	2.34±2.83		6.32±0.89
Mean upstroke acceleration (BL s^{-2})	−1.60±0.67	−5.18±0.55	−0.834±3.52		−3.92±0.74
Peak downstroke acceleration (BL s^{-2})	13.38±1.04	27.45±2.25	17.11±2.55		26.78±1.17
Peak upstroke acceleration (BL s^{-2})	6.35±1.11	1.53±0.76	15.22±4.77		7.77±1.08
Min. downstroke acceleration (BL s^{-2})	−11.38±1.86	−10.62±1.90	−19.88±2.21		−14.30±1.60
Min. upstroke acceleration (BL s^{-2})	−11.79±1.37	−16.52±1.23	−17.03±2.37		−16.84±1.46
Upstroke peak/downstroke peak	0.47±0.19	0.06±0.50	0.89±0.35		0.29±0.15
Prop. downstrokes with peak acceleration>0	10/10	10/10	8/8		12/12
Prop. upstrokes with peak acceleration>0	9/11	6/8	7/8		11/11
Prop. upstrokes with peak acceleration>0, based on head points	10/11	2/8	5/8		3/11

All data are based on tail points unless otherwise specified.
Data are presented as averages of the mean, peak and minimum accelerations, in terms of body lengths s^{-2} (BL s^{-2}) from all half-strokes±s.e.m.

downstroke-acceleration tended to be larger, and the peak upstroke-acceleration tended to be smaller, for descending swimming relative to horizontal swimming, though the general stroke–acceleration pattern is consistent under both conditions (Figs 4 and 5).

Head-damping and impacts on perceived stroke-acceleration patterns

Alcids of all five species exhibited head movement relative to the movement of their bodies in sync with their stroke cycle (Fig. 2). We were interested in whether this head movement reflected ‘head-bobbing’ or ‘head-damping’ (Necker, 2007; Pete et al., 2015). To test between these two options, we compared $CV_{velocity}$ when computed based on the eye versus that computed based on the tail for all complete wingbeats. The mean $CV_{velocity}$ based on the eye was significantly lower than that based on the tail (*P*=0.015), thus indicating head-damping.

In comparing stroke–acceleration patterns based on the tail- versus eye-position, head-damping had a clear effect on whether we detected

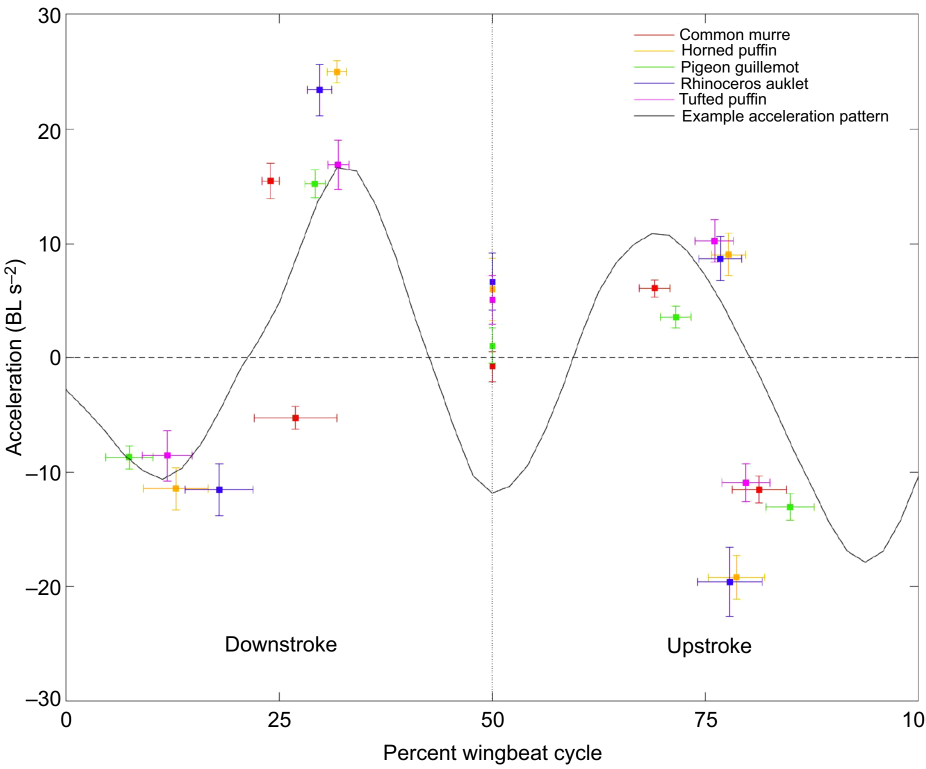

Fig. 4. Acceleration (BL s^{-2}) patterns of five species of alcid in horizontal swimming, based on tail points. Points correspond to the average of all peak and minimum accelerations from each of the sampled half-strokes, along with the average acceleration at the downstroke–upstroke transition. Vertical error bars are the standard error in the magnitude of each point and horizontal error bars are the standard error in the timing of when the peak or minimum acceleration occurred in a given half-stroke. See Table 1 for sample sizes.

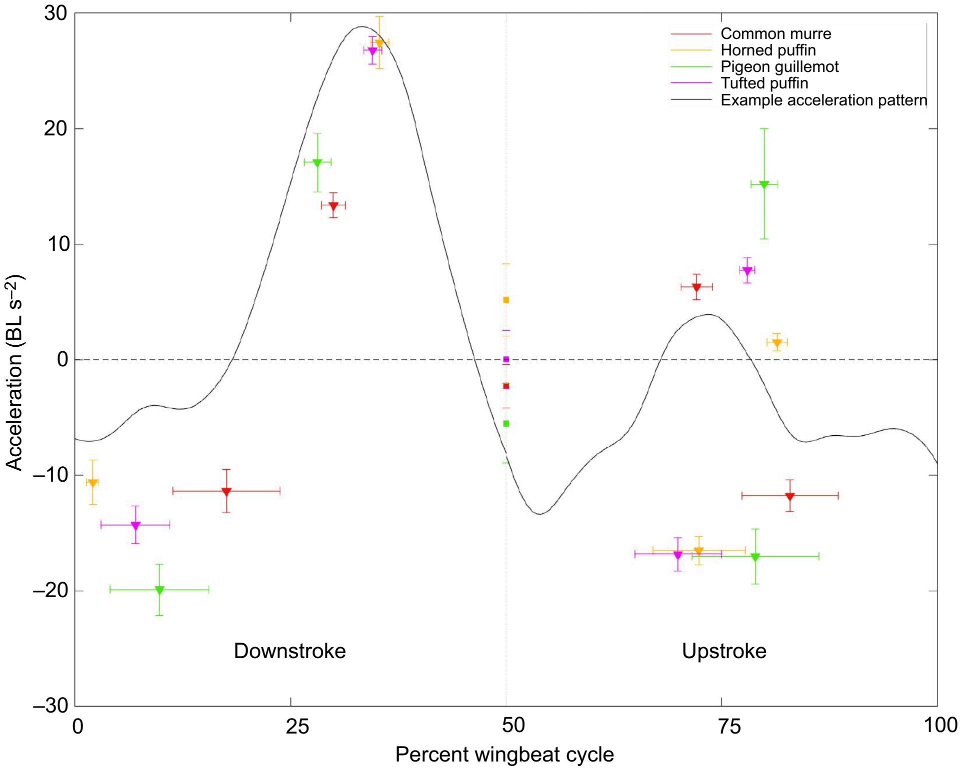

Fig. 5. Acceleration (BL s^{-2}) patterns of four species of alcid in descending swimming, based on tail points. Points correspond to the average of all peak and minimum accelerations from each of the sampled half-strokes, along with the average acceleration at the downstroke–upstroke transition. Vertical error bars are the standard error in the magnitude of each point and horizontal error bars are the standard error in the timing of when the peak or minimum acceleration occurred in a given half-stroke. See Table 1 for sample sizes.

acceleration on the upstroke. When acceleration was calculated based on the position of the tail, 100 of 115 (87%) horizontal upstrokes and 31 of 38 (87%) descending upstrokes had peak accelerations >0 BL s^{-2} (Table 2). In contrast, when acceleration was calculated based on the position of the eye, 52 of 115 (45%) horizontal upstrokes and 20 of 38 (53%) of descending upstrokes had peak accelerations >0 BL s^{-2} (Table 2). For example, in a single sequence of wingbeats from a descending tufted puffin, 4 of 4 upstrokes showed peak accelerations >0 BL s^{-2} when computed based on tail points, whereas 0 of 4 showed peak accelerations >0 BL s^{-2} when computed based on head points (Fig. 3).

DISCUSSION

Our results revise understanding of the stroke–acceleration patterns of swimming alcids and offer new insights into the ubiquity of visual stabilization in avian locomotion.

Contrary to our hypothesis that the presence of upstroke-based acceleration was determined by swimming trajectory, we found that the upstroke consistently resulted in acceleration of the body (133 of 153 upstrokes, 87%) in both horizontal and descending swimming, with peak accelerations ranging from 23 to 61% and 6 to 89% of that produced during the downstroke in horizontal and descending swimming, respectively (Table 2, Figs 4 and 5). This result is contrary to those of two previous studies of horizontal swimming in alcids, which found peak accelerations significantly greater than zero in only 2 of 24 (8%) upstrokes of Atlantic puffins (Johansson and Aldrin, 2002) and 5 of 32 (16%) upstrokes of common murres (Hamilton, 2006). Our unique result is likely due to previous kinematic studies including either the position of the head, or regions of the body that are distorted by head movement, in their computations of body acceleration. Our study indicates that the position of the head is not a reliable indicator of overall body position for swimming alcids (Fig. 2). Had we used the head to compute body accelerations, we would have obtained results more consistent with those of past studies (see data within Table 2, 72 of 153 upstrokes producing acceleration, 47%).

Our study also differs from those of Johansson and Aldrin (2002) and Hamilton (2006) in other, contrasting ways. Thanks to recent advancements in high-speed camera technology, we were able to record birds swimming in a much larger volume of water (397,000 liters) than in past kinematic studies. Johansson and Aldrin (2002) and Hamilton (2006) were limited to the use of small tanks to meet the lighting requirements of early-2000s high-speed cameras. Johansson and Aldrin (2002) studied Atlantic puffins in a tank measuring 5×1×1 m and Hamilton (2006) studied common murres in a water tunnel with a working section measuring 4.4×0.8×0.6 m. These dimensions may have restricted the range of motion of the animals. In addition, Johansson and Aldrin (2002) studied wild-caught birds, whereas we and Hamilton (2006) studied captive-raised birds. The lack of opportunities to engage in sustained flight in captive birds may affect the flight muscles in ways that affect swimming performance. Further, Johansson and Aldrin (2002) filmed birds as they fled from an approaching researcher, and Hamilton (2006) measured accelerations at series of fixed swimming velocities, whereas birds in our study were free to choose when, where and how fast to swim.

Nonetheless, birds in our study were confined to swim at rather shallow depths (<6.5 m), and our sampled bouts of swimming were at depths ≤3 m. This has implications for interpreting our results in relation to diving in the wild because of the likely effects of buoyancy. Penguins prepare extensively for dives by increasing their breathing rate (Wilson, 2003) and appear to modulate their lung volume based on the depth of the upcoming dive (Sato et al., 2002, 2011). We know of no study in alcids on the relationship between lung volume and dive depth, but, similar to Wilson (2003), we did observe pre-dive panting in rhinoceros auklets, tufted puffins and horned puffins. In addition, common murres opened their beak to a wide angle just before diving. If alcids control the volume of air in their lungs based on the depth of the upcoming dive like penguins, then alcids in our study were likely less buoyant than free-ranging birds. Thus, the magnitude of acceleration during the upstroke we measured may be larger than these species experience when diving to greater depths.

The pitching motions alcids exhibit when swimming may have also disguised the stroke–acceleration patterns of animals in previous kinematic studies; however, our data suggest that this is unlikely. We accounted for the impacts of pitching in our acceleration calculations, but had we not, our results for the relative frequency of upstroke-based acceleration would have been similar. When the effects of pitching were ignored, and acceleration was computed based on the position of the tail, alcids appeared to accelerate on 104 of 115 (90%) upstrokes during horizontal bouts and 33 of 38 (87%) upstrokes during descending bouts. When the effects of pitching were ignored, and acceleration was computed based on the position of the eye, alcids appeared to accelerate on 57 of 115 (50%) upstrokes during horizontal bouts and 21 of 38 (55%) upstrokes during descending bouts. These results largely mirror our pitch-controlled results, suggesting that head-damping is the primary reason that previous kinematic studies failed to detect consistent upstroke-based acceleration in swimming alcids (Hamilton, 2006; Johansson and Aldrin, 2002). The body angle of swimming alcids is generally quite close to their angle of descent (generally <10 deg difference), limiting the impact of pitching on acceleration calculations.

Studies that have used accelerometers to track the stroke–acceleration patterns of free-ranging alcids have found that alcids accelerate during the upstroke only in shallow water (0–20 m) (Lovvorn et al., 2004; Watanuki et al., 2003, 2006). These authors have hypothesized that the decrease in buoyancy with depth, which occurs as air volumes in the bird's respiratory system and plumage compress, is responsible for the decrease in peak upstroke-based acceleration. Our results indicate that this phenomenon is not driven by the trajectory of the animal (Lovvorn et al., 2004; Watanuki and Sato, 2008; Watanuki et al., 2006).

Interestingly, alcids decrease upstroke-based acceleration with depth while maintaining relatively consistent downstroke kinematics (Watanuki and Sato, 2008; Watanuki et al., 2006). As an explanation for this behavior, Watanuki and Sato (2008) and others suggest that alcids vary upstroke kinematics to control their speed in response to changing buoyancy. In other words, as buoyancy decreases with depth, alcids reduce the thrust produced by their upstroke rather than increase their speed, perhaps to minimize drag costs (Watanuki et al., 2003). This explanation fits with evidence from Lovvorn et al. (1999), who found that many diving birds have characteristic speeds with minimum coefficients of drag. However, given that a less-pulsatile acceleration profile should decease the cost of swimming at a given speed (Lovvorn, 2001; Vogel, 1994), it is unclear why birds would decrease the thrust produced by the upstroke alone, rather than vary the kinematics of both the downstroke and upstroke in conjunction to control their speed.

We offer a potential explanation for why alcids rely on the upstroke to regulate swimming speed based on the volume of the muscle powering the stroke and the characteristic efficiency of muscle fibers. This explanation assumes the contractile dynamics of the major wing muscles (pectoralis and supracoracoideus) may be inferred from wing motion. Watanuki and Sato (2008) found that upstroke duration, but not downstroke duration, varies significantly with depth. Assuming that stroke amplitude does not vary concurrently with depth, the results of Watanuki and Sato (2008) indicate that alcids alter upstroke velocity, and, by relation, strain rate of the supracoracoideus muscle, to alter the thrust produced by their upstroke. Muscle fibers of a given fiber type are most efficient over a narrow range of strain rates (Goldspink, 1977; He et al., 2000; Reggiani et al., 1997). Thus, varying strain rate with depth, while likely minimizing drag costs (Lovvorn et al., 1999), probably reduces the average contractile efficiency of supracoracoideus contraction. However, the cost of contracting fibers in the supracoracoideus at an inefficient strain rate may be relatively small, as the supracoracoideus is small relative to the pectoralis (Kovacs and Meyers, 2000). The total energetic cost of a contraction at an inefficient strain rate is equal to the cost per muscle fiber times the number of fibers involved. Thus, it may require less energy to contract the supracoracoideus at highly inefficient rates of strain, given its small volume, rather than vary strain rate to a lesser extent in both the supracoracoideus and the larger pectoralis. In other words, alcids may minimize the energetic costs of swimming by maintaining downstroke kinematics across depths at values that maximize the contractile efficiency of the pectoralis – varying upstroke kinematics instead – despite the acceleration-related costs.

Alcids in the present study appeared to utilized head-damping to smooth instantaneous accelerations while swimming, rather than exhibiting the more traditional pattern of head-bobbing observed in foot-propelled swimming loons (Clifton and Biewener, 2018) and grebes (Gunji et al., 2013). Head-bobbing is characterized by alternating between the hold and thrust phases of the head, each of which may have a different function. According to Necker (2007), the hold phase likely aids in object detection, whereas the thrust phase may improve a bird's ability to determine depth based on the rate of optic flow, defined as the rate that the image of the world moves across the retina (Martin, 2017). Head-damping has been more commonly documented in flying birds and is a critical aspect of flight, wherein it functions to stabilize optic flow (Dakin et al., 2016; Goller and Altshuler, 2014; Pete et al., 2015; Ros and Biewener, 2016, 2017; Walsh et al., 2013). Head-damping in swimming alcids may perform a function similar to its role in aerial flight. Alternatively, owing to the kinematic similarities between aerial flight and wing-propelled swimming in these species, alcids may perform head-damping involuntarily because of to rigid connections between motor neurons and vestibular/ocular pathways in the brain. Moreover, excluding pigeon guillemots, alcids have much shorter necks than either loons or grebes, and head-bobbing may be ineffective for species lacking long necks. Exploring the head motion of diving alcids may reveal novel insights into the general functioning of optic flow in avian locomotion, and thus merits further study.

Based on the pattern of bubbles released from a swimming pigeon guillemot, Rayner (1995) predicted that the upstroke of all swimming alcids was inactive. Although studies of other alcid species have since disproved this position, it has remained possible that Rayner (1995) was correct with regards to pigeon guillemots, which are morphologically and ecologically distinct from other alcids (Ashmole, 1971). Relative to other alcids, pigeon guillemots are highly maneuverable in slow flight (A.B.L., personal observation) and forage in shallow water (Clowater and Burger, 1994). Our results indicate that the wing-propelled swimming of pigeon guillemots is not distinct from that of other alcids. Instead, as pointed out by Johansson and Aldrin (2002), Rayner (1995) may not have observed vorticity produced by the upstroke, which would indicate force production, because the force of the water pressing on the upper surface of the wing during the upstroke prevented the release of bubbles from the feathers.

Penguins have been shown to experience accelerations of near-equal magnitude during both downstroke and upstroke (Clark and

Bemis, 1979; Hui, 1988; Watanuki et al., 2006). This information has been used as evidence that penguins are supremely adapted to swimming and, thus, more efficient underwater than alcids (Lovvorn et al., 2004; Rayner, 1995), which produce more unequal forces owing, potentially, to the trade-offs between aerial and aquatic performance. However, the fact that alcids have longer mass-specific dive durations than penguins (Halsey et al., 2006; Watanuki and Burger, 1999), and therefore seem to consume their oxygen supply more efficiently than penguins, calls into question this assumption. In line with this logic, we found that alcids experience upstroke-based accelerations ranging from 6 to 89% and 23 to 61% of that produced by downstroke in descending and horizontal swimming, respectively. In comparison, Watanuki et al. (2006) reports a downstroke-to-upstroke acceleration ratio for descending little penguins (*Eudyptula minor*) of approximately 74% at 2 m, while Hui (1988) reports a downstroke-to-upstroke acceleration ratio of 58% for Humboldt penguins (*Spheniscus humboldti*) swimming horizontally in shallow water. Thus, alcids produce thrust on both halves of their stroke cycle – enough thrust to cause acceleration during both half-strokes – and the available information indicates that the distribution of force production between upstroke and downstroke in alcids is only slight less even than that in penguins, at least in shallow water.

An additional factor in determining the efficiency of swimming is the hydrodynamic method of thrust production. Penguins produce force via lift-based hydrodynamic mechanisms on both the upstroke and downstroke thanks to the symmetric foil shape of their wings (Bannasch, 1995; Hui, 1988). At high speeds, lift-based propulsion is more efficient, in terms of the energy required to produce a given net thrust, than drag-based propulsion from both theoretical (Daniel and Webb, 1987; Jackson et al., 1992) and empirical perspectives (Baudinette and Gill, 1985; Fish, 1996; Richman and Lovvorn, 2008; Schmid et al., 1995; Vogel, 1994; Williams, 1999). If we assume that drag-based propulsion is synonymous with ‘rowing’ and lift-based propulsion with ‘flapping’ (Walker and Westneat, 2002), which is a coarse but reasonable approximation for the wing-propelled locomotion of diving birds (but see Johansson and Lindhe Norberg, 2000; Johansson and Lindhe Norberg, 2001; Johansson and Norberg, 2003), then lift-based propulsion is more efficient at all speeds (Walker and Westneat, 2000). By this logic, penguins have been considered especially efficient swimmers. However, our data present some evidence that the aquatic upstroke-thrust of alcids is also lift-based.

During the upstroke of alcids in our study, the wing appears to move forward (in addition to upward) relative to the body of the animal. Because the animal itself is moving forward, the wing moves forward relative to the water, as well (Fig. 1). If the upstroke were to produce force via drag, then it would have to move backward relative to the fluid to produce thrust. Thus, the upstroke of a swimming alcid appears to produce a lift force directed forward and downward – much like the upstroke of a penguin. Johansson (2003) reached a similar conclusion based on data from Atlantic puffins. Similarly, the alcid downstroke moves downward and slightly forward relative to the water (Fig. 1), suggesting that alcids produce lift forces for propulsion during both half-strokes (Johansson and Aldrin, 2002). However, because rowing kinematics are capable of producing larger forces at slow speeds (Walker and Westneat, 2000), alcids may utilize a more drag-based downstroke at slow speeds (to accelerate or counter large buoyant forces) and shift toward a more lift-based downstroke at high speeds. Further research is necessary to elucidate the exact hydrodynamic mechanisms by which alcids produce force in water, especially if we wish to build bioinspired robots based on these animals (Lock et al., 2010, 2012, 2013).

Conclusions

Our study of five species from three genera confirms that alcids routinely accelerate during both the downstroke and upstroke in both horizontal and descending swimming at shallow depths. We found that the head is not a reliable indicator of body acceleration in swimming alcids because of head-damping, offering a potential explanation for the rarity upstroke-based acceleration detected in past studies of horizontally swimming alcids. Future studies should track the tail or, ideally, the center of mass of diving birds to eliminate the effects of relative head movement on force calculations. The use of head-damping reveals the ubiquity of the need for head stabilization during avian wing-propelled locomotion.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: A.B.L., B.W.T.; Methodology: A.B.L., B.W.T.; Software: A.B.L.; Validation: A.B.L.; Formal analysis: A.B.L.; Investigation: A.B.L.; Resources: B.W.T.; Writing - original draft: A.B.L.; Writing - review & editing: A.B.L.; Visualization: A.B.L.; Supervision: B.W.T.; Project administration: B.W.T.; Funding acquisition: A.B.L., B.W.T.

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RESEARCH ARTICLE

Alcids 'fly' at efficient Strouhal numbers in both air and water but vary stroke velocity and angle

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Abstract Birds that use their wings for 'flight' in both air and water are expected to fly poorly in each fluid relative to single-fluid specialists; that is, these jacks-of-all-trades should be the masters of none. Alcids exhibit exceptional dive performance while retaining aerial flight. We hypothesized that alcids maintain efficient Strouhal numbers and stroke velocities across air and water, allowing them to mitigate the costs of their 'fluid generalism'. We show that alcids cruise at Strouhal numbers between 0.10 and 0.40 – on par with single-fluid specialists – in both air and water but flap their wings ~ 50% slower in water. Thus, these species either contract their muscles at inefficient velocities or maintain a two-geared muscle system, highlighting a clear cost to using the same morphology for locomotion in two fluids. Additionally, alcids varied stroke-plane angle between air and water and chord angle during aquatic flight, expanding their performance envelope.

Introduction

The 'jack of all trades' concept – the idea that the ability to function in multiple environments can only be achieved by sacrificing maximal performance (**MacArthur, 1972**) – is commonly invoked in discussing the locomotor performance of wing-propelled diving birds (**Elliott et al., 2013**; **Simpson, 1946**; **Stettenheim, 1959**; **Storer, 1960**; **Thaxter et al., 2010**). These species, which include some or all members of the alcids (*Alcidae*), ducks (*Anatidae*), petrels and shearwaters (*Procellariidae*), dippers (*Cinclus*), and the penguins (*Spheniscidae*), use their wings to propel themselves underwater. Wing-propelled diving birds which have retained their ability to fly in the air – hereafter, 'dual-medium' species (sensu **Kovacs and Meyers, 2000**) – are fluid generalists. These animals use the same locomotor apparatus to 'fly' in both air and water, and are, therefore, expected to fly poorly relative to strictly aerial and strictly aquatic fliers in each environment.

Interestingly, birds in the family Alcidae (puffins, murres, and their relatives) seem to contradict the notion of a trade-off between aerial and aquatic flight performance. As with many dual-medium birds, alcids have high wing-loading (the ratio of body mass to wing area), and therefore display poor maneuverability in aerial flight relative to non-diving birds (**Ortega-Jimenez et al., 2011**; **Shepard et al., 2019**). However, the wing-loadings of alcids and other dual-medium birds are nearly indistinguishable from those of volant birds which use their feet for aquatic locomotion (based on data from **Alerstam et al., 2007**; **Bruderer et al., 2010**; **Spear and Ainley, 1997**), indicating that high wing-loading is likely the result of selection by the aquatic environment for large body sizes or low buoyancy (**Ponganis, 2015**), rather than a trade-off specific to dual-medium flight. The current records for the depth and duration of a single dive by an alcid are 210 m and 224 s, respectively, held by the ~1 kg thick-billed murre (*Uria lomvia,* Linnaeus 1758), making this alcid, on a mass-specific basis, the deepest and longest-duration diver on earth (**Croll et al., 1992**). When corrected for

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body size, alcids exhibit dive durations and depths far greater than even penguins (**Halsey et al., 2006**).

One possible explanation for the aquatic performance of alcids is that they have mitigated the costs of dual-medium flight. Specifically, by maintaining efficient Strouhal numbers (*St*) and stroke velocities across air and water, birds in the family Alcidae may lessen the perceivable differences between aerial and aquatic flight, thereby reducing the costs of fluid generalism.

To swim or fly, an animal must impart momentum to the surrounding fluid. Strouhal number ($St = fAU^{-1}$, where f is wingbeat frequency, A is wing excursion, and U is forward speed) describes the pattern of vortices shed into the fluid wake by a flapping foil as it imparts that momentum (**Triantafyllou et al., 1993**). Extensive research has determined that peak efficiency (in terms of the power required to flap a foil relative to the thrust output to the fluid) for a simple heaving and pitching foil occurs at around $0.2 < St < 0.4$ (**Anderson et al., 1998**; **Triantafyllou et al., 1991**; **Triantafyllou et al., 1993**). Most flapping and swimming animals studied to date fall within or near that range, with the previously studied, strictly aerial birds exhibiting $0.12 < St < 0.47$ during cruising flight (**Taylor et al., 2003**). That most species fall near the efficient range of *St* suggests that natural selection has tuned the kinematics of animals to fly and swim efficiently (**Nudds et al., 2004**; **Taylor et al., 2003**). Thus, alcids could achieve efficient fluid wake production in both air and water by maintaining $0.2 < St < 0.4$, and efficiency on par with previously studied single-media species by maintaining $0.12 < St < 0.47$, but the 'jack of all trades' concept suggests that they may unable to do so given the substantial differences in density and viscosity between the two fluids.

Stroke velocity describes the speed at which the wing is swept through its arc during either the downstroke or the upstroke of the wing. This parameter is likely important in determining the cost of locomotion given that it should be proportional to the contractile velocity of the major flight muscles, the pectoralis and the supracoracoideus (**Hamilton, 2006**; **Tobalske and Dial, 1994**; **Tobalske et al., 1999**). Muscles fibers of a given fiber type and myosin isoform are most efficient at converting metabolic power into mechanical power over a narrow range of contractile velocities (**Goldspink, 1977**; **He et al., 2000**; **Reggiani et al., 1997**; **Rome et al., 1988**). Thus, it would behoove alcids to operate the fibers in their flight muscles at the contractile velocity which maximizes muscle efficiency, and for that velocity to be shared across aerial and aquatic flight. Otherwise, alcids could maintain two populations of fibers – an aerial set and an aquatic set – but this would add mass to the animal, increasing the cost of aerial flight (**Ellington, 1984a**). Previous research has demonstrated that diving alcids maintain stroke velocities within a narrow range across dive depths, despite large variations in buoyancy, suggesting that they are responsive to the challenge of maintaining contractile velocity (**Watanuki and Sato, 2008**; **Watanuki et al., 2006**). Although researchers have not yet examined myosin isoforms in alcids, the two species of alcids for which histochemical data are available possess only 'fast' muscle fibers (**Kovacs and Meyers, 2000**; **Meyers et al., 1992**).

Recently, **Kikuchi et al., 2015** measured the kinematics of flying and diving rhinoceros auklets (*Cerorhinca monocerata*) using a combination of videography and accelerometry. The authors used bootstrapping to coalesce measurements from various individuals to determine the range of *St* exhibited by this species. The results of this study strongly suggest that this small alcid maintains optimal *St* in air and water. We wanted to extend this work to determine if individuals tune their kinematics to match optimal *St* on a per-flight basis. Alternatively, it is possible that the average kinematics of this species are simply centered between $0.2 < St < 0.4$. These authors also suggest, based on wingbeat frequency, that stroke velocities of rhinoceros auklets are lower in water, but were unable to statistically compare stroke velocities during aerial versus aquatic flight. While wingbeat frequencies are different between aquatic and aerial flight (~2–4 Hz versus 7–11 Hz, respectively), wingbeat amplitude may vary between the two environments, allowing for similar stroke velocities.

To improve understanding of potential evolutionary trade-offs between aerial and aquatic flight, we tested whether alcids exhibit efficient *St* and maintain consistent stroke velocities when flying in water and air. We used videography to measure the wing kinematics of four species of alcids from three genera. These species differ substantially in body mass (450 g to 1 kg) and represent opposite branches of the alcid phylogeny. In addition to *St* and stroke velocity, we report a variety of kinematic parameters, including stroke-plane and chord angles relative to the body to contrast how the flight apparatus is used in air versus water and during horizontal versus descending aquatic flight.

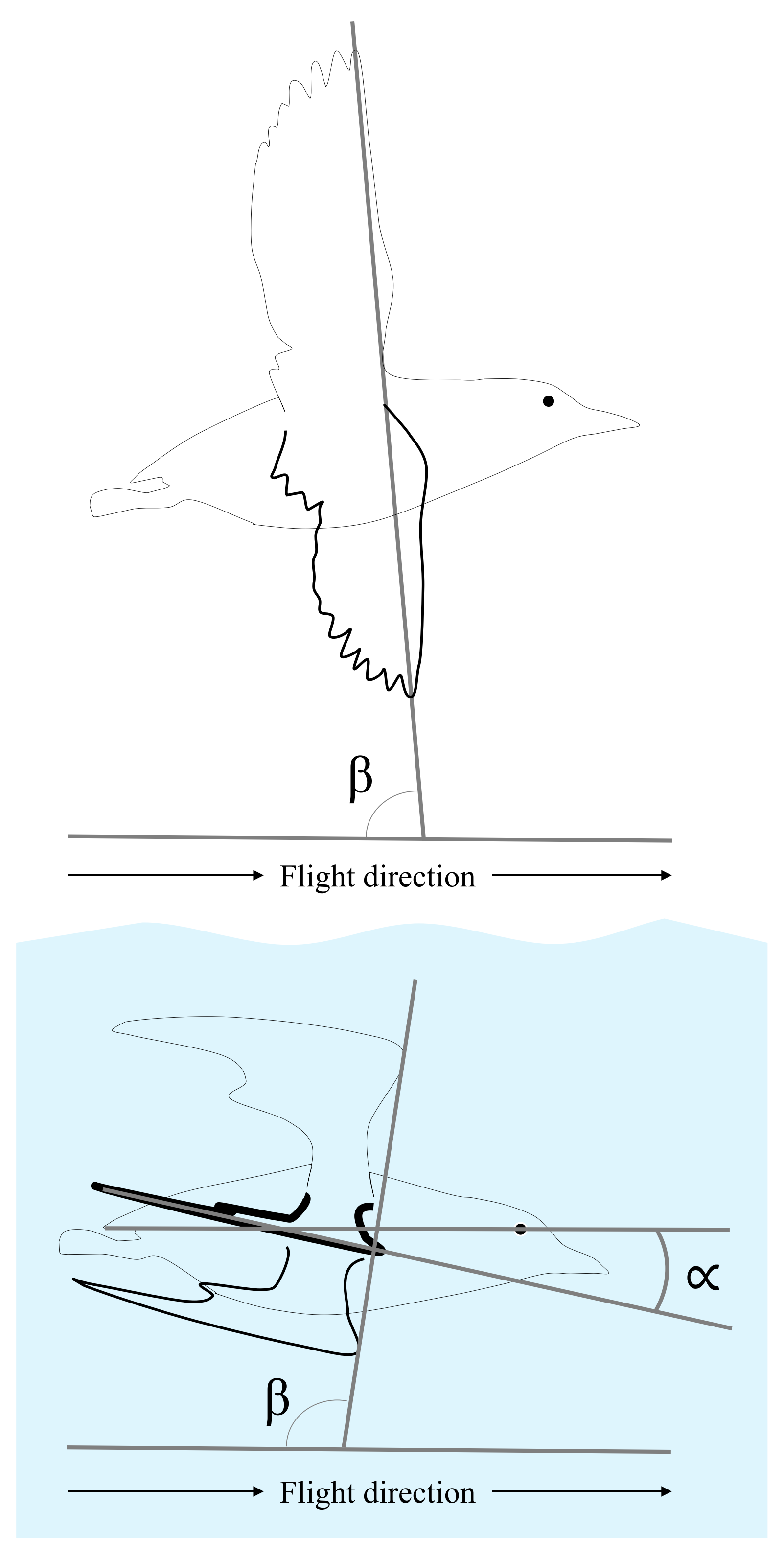

Figure 1. Measurements of stroke-plane angle (β) and chord angle (∝). The wings drawn with the thin black line indicate the position at the start of downstroke in air (top) and water (bottom, with blue shading). The wings drawn with the dashed line indicate the position at the end of downstroke in air and water. β was measured using the wingtip in aerial flight and the wrist in aquatic flight. ∝ was measured at mid-upstroke and mid-downstroke (wing drawn with thick black line) during aquatic flight.

We hypothesized that alcids maintain efficient *St* and consistent stroke velocities across air and water, which would allow this group to mitigate the costs of fluid generalism (***Figure 1***).

Results

Strouhal numbers (*St*) for horizontal aquatic flights averaged 0.18 ± 0.02 for common murres, 0.13 ± 0.01 for horned puffins, 0.15 ± 0.01 for pigeon guillemots, and 0.15 ± 0.02 for tufted puffins (***Figure 2***, blue points). *St* for descending aquatic flights were significantly greater than those for horizontal aquatic flights ($F_{1,27}$ = 145.6, η^2 = 0.729, p-value = 2.18e-12) with a relatively minor but significant interaction between species and the type of aquatic flight ($F_{3,27}$ = 3.59, η^2 = 0.054, p-value = 0.0264). Within-species *post hoc* tests indicated that all species exhibited greater *St* during descending aquatic flights relative to horizontal aquatic flights (p = 0.0478, 4.19e-04, 9.17e-07, 5.72e-07; for species in alphabetical order). *St* for descending aquatic flights averaged 0.24 ± 0.01 for flights of common murres, 0.21 ± 0.04 for horned puffins, 0.29 ± 0.06 for pigeon guillemots, and 0.29 ± 0.03 for tufted puffins (***Figure 2***, green points).

St for aerial flights based on the ground speed of the birds averaged 0.17 ± 0.02 for common murres, 0.22 ± 0.14 for horned puffins, 0.49 ± 0.06 for pigeon guillemots, and 0.27 ± 0.02 for tufted puffins (***Figure 2***, dark red points). Except for the flights of common murres, all birds appeared to be flying in considerable wind based on the size of the waves on the surface of the water. Thus, we also calculated *St* for aerial flights based on the airspeed characteristic of each species as reported in ***Spear and Ainley, 1997*** (see Materials and methods for details). When estimated from the range of measured cruising flight speeds, *St* for aerial flights ranged from 0.12 to 0.25 for flights of common murres, 0.13 to 0.27 for horned puffins, 0.18 to 0.27 for pigeon guillemots, and 0.16 to 0.25 for tufted puffins (***Figure 2***, light red lines).

Downstroke velocities were significantly greater during aerial flights than during aquatic flights for all four species (*t-Value* = 8.10, 11.5, 6.04, 25.9; *df* = 16.5, 19.0, 9.48, 16.5; p-values = 3.80e-07,

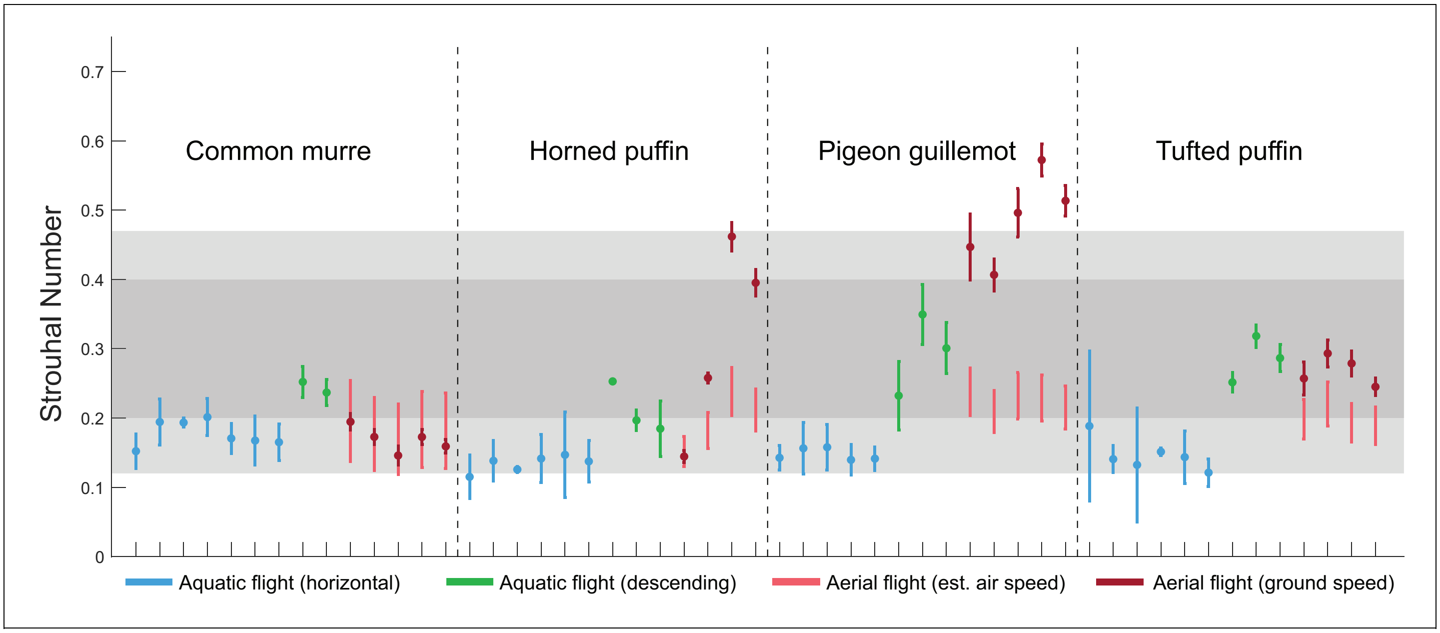

Figure 2. Strouhal numbers (*St*) of four species of alcid in aerial and aquatic flight. Each hatch mark on the x-axis indicates a unique flight. The darker shaded section indicates 0.2 < *St* < 0.4, in which propulsive efficiency is predicted to peak, and the lighter shaded region indicates 0.12 < *St* < 0.47, which is the range of St exhibited during cruising flight of strictly aerial birds reported in ***Taylor et al., 2003***. Points indicate *St* for horizontal aquatic flights (blue), descending aquatic flights (green), aerial flights based on ground speed (dark red), and aerial flights calculated using the range of cruising speeds of that species reported in the literature (light red). Each flight is represented by the mean *St* for that flight ± s.d., except for *St* calculated for aerial flights based on airspeed, for which we chose not to indicate a central tendency.

The online version of this article includes the following source data for figure 2:

Source data 1. Strouhal numbers of four species of alcid in aerial and aquatic flight.

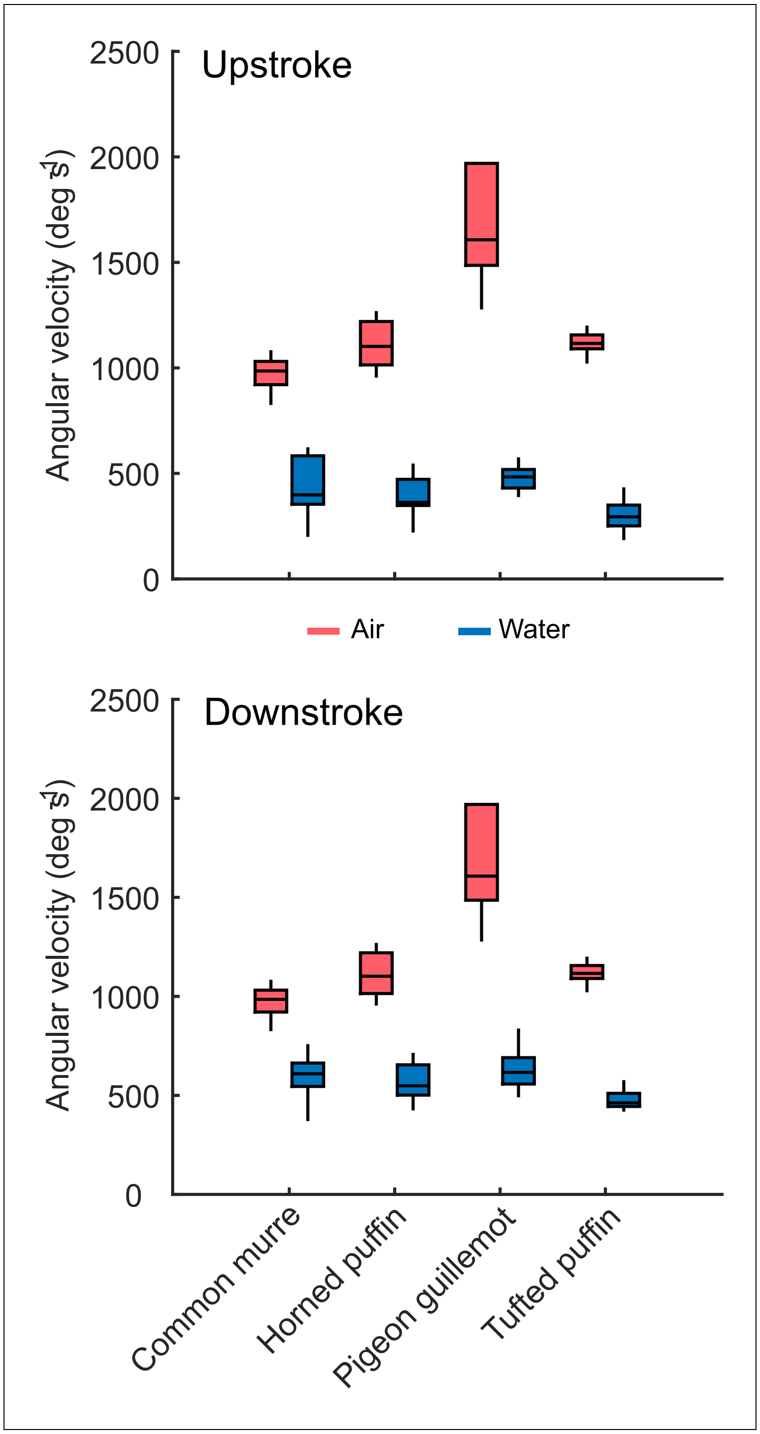

Figure 3. Stroke velocities of four species of alcid in aerial and aquatic flight. Stroke velocity was significantly greater during aerial flights (red) than during aquatic flights (blue) for each of the four species for both downstroke (t-Value = 8.10, 11.5, 6.04, 25.9; df = 16.5, 19.0, 9.48, 16.5; p-values = 3.80e-07, 5.19e-10, 1.55e-04, 8.56e-15; for species in alphabetical order) and upstroke (t-Value = 10.5, 16.0, 6.83, 26.4; df = 15.0, 18.8, 9.18, 16.1; p-values = 2.67e-08, 2.13e-12, 6.97e-05, 1.09e-14; for species in alphabetical order). The central line in each box marks the median, while the upper and lower margins of the box indicate the quartile range. The entire range of values lie between the whiskers.

The online version of this article includes the following source data for figure 3:

Source data 1. Stroke velocities of four species of alcid in aerial and aquatic flight.

5.19e-10, 1.55e-04, 8.56e-15; for species in alphabetical order; **Figure 3**). The same was true for upstroke velocities (*t-Value* = 10.5, 16.0, 6.83, 26.4; *df* = 15.0, 18.8, 9.18, 16.1; p-values = 2.67e-08, 2.13e-12, 6.97e-05, 1.09e-14; for species in alphabetical order; **Figure 3**). Wingbeat amplitudes were greater during aquatic flights across species ($F_{1,71}$ = 162.4, η^2 = 0.597, p-value<2.2e-16; **Figure 4**) with a relatively minor but significant interaction between species and fluid ($F_{3,71}$ = 3.52, η^2 = 0.039, p-value=0.019). Within-species *post hoc* tests indicated that all four species exhibited significantly greater wingbeat amplitudes during aquatic flight relative to aerial flight (p-values=1.93e-06,<1.0e-08, 3.29e-04, 2.36e-05). Stroke durations were often 2-3X greater in water as compared to air, as indicated by the differences in wingbeat frequency (**Figure 4**), leading to significant differences in stroke velocities between fluids.

When horizontal and descending aquatic flights are grouped together, stroke-plane angle (β) was significantly lower (the top of stroke plane is rotated more caudally) during aerial flights relative to aquatic flights ($F_{1,47}$ = 41.3, η^2 = 0.422, p = 6.14e-08; **Figure 5**). Across species, stroke-plane angle averaged 79 ± 7 deg for aerial flights, 92 ± 7 deg for horizontal aquatic flights, and 93 ± 12 deg for descending aquatic flights. Within aquatic flights, there was no significant relationship between stroke-plane angle and angle of descent ($F_{1,27}$ = 0.0755, η^2 = 0.002, p = 0.786; **Figure 5**).

There was a significant relationship between chord angle (α) and angle of descent for upstroke ($F_{1,30}$ = 55.7, η^2 = 0.458, p = 2.55e-08; **Figure 6**) and downstroke ($F_{1,27}$ = 8.17, η^2 = 0.122, p = 8.11e-03; **Figure 6**). However, a significant crossed interaction between species and angle of descent for downstroke chord angle ($F_{3,27}$ = 7.68, η^2 = 0.343, p = 7.26e-4), indicates that the main effect of angle of descent on chord angle during downstroke is uninterpretable (i.e. the response depends on the species; **Figure 6**). However, alcids significantly increased chord angle (thus, the degree of supination) during upstroke as a function of angle of descent.

Discussion

Alcids achieve efficient wake production based on *St* during both aerial flight (based on airspeed) and during aquatic flight. While *St* for horizontal aquatic flights often fell below *St* = 0.2 (**Figure 2**, blue points), all measured values overlapped with the range for the cruising aerial flight of strictly aerial birds reported in the literature (**Taylor et al., 2003**). Because stroke velocities were substantially different between air and water (**Figure 3**), the use of efficient *St* seems to come at a cost to the contractile efficiency of the primary flight muscles. Alternatively, aerial and aquatic flight may be powered by different sets of muscles, as discussed below.

We interpret the relatively low values of *St* during horizontal aquatic flight to be a consequence of buoyancy. While swimming horizontally, alcids must counteract buoyancy as it attempts to pull them toward their dorsal side. Buoyancy is especially strong at shallow depths, as air volumes compress with depth (**Wilson et al., 1992**). To compensate for buoyancy during horizontal aquatic flight, alcids in this study seemed to produce quick, low excursion wingbeats with near-horizontal chord angles (α) on the upstroke (**Figure 6**). Given that the upstroke produces negative heave (ventrally directed acceleration) in swimming alcids (**Watanuki et al., 2006**), these kinematics seem to be a strategy used to counteract the strong, dorsally oriented buoyancy experienced during horizontal swimming at shallow depths. In contrast, descending alcids must counteract buoyancy as it attempts to resist their forward motion and are, therefore, not required to produce negative heave via the upstroke. Still, all values of *St* for horizontal aquatic flight overlapped with the range reported for strictly aerial birds in aerial flight – 0.12 < *St* < 0.47 – (Figure 1), suggesting that alcids produce wakes of similar efficiency to their fully aerial relatives even while fighting buoyancy.

From previous research, the precise range of *St* values which confer optimal propulsive efficiency (the proportion of total mechanical energy expended that contributes to useful work) depends somewhat on the kinematics of the flapping foil, but departures from that range can have substantial effects (**Anderson et al., 1998**; **Read et al., 2003**). Data comparing *St* to propulsive efficiency in animals are limited, but **Rohr and Fish, 2004** report that a relatively minor shift in *St* in cetaceans (e.g. from 0.25 to 0.35 in *Pseudorca crassidens*) can reduce propulsive efficiency by 5–10% (**Rohr and Fish, 2004**). The paucity of data for animals swimming and flying outside the optimal range of *St* may be due to the challenge of eliciting inefficient kinematics from animals. Alternatively, because translational velocity is partially determined by wing excursion and frequency, the convergence of *St* on some range of values may be inevitable. The latter seems unlikely, however, as trout adhere to a

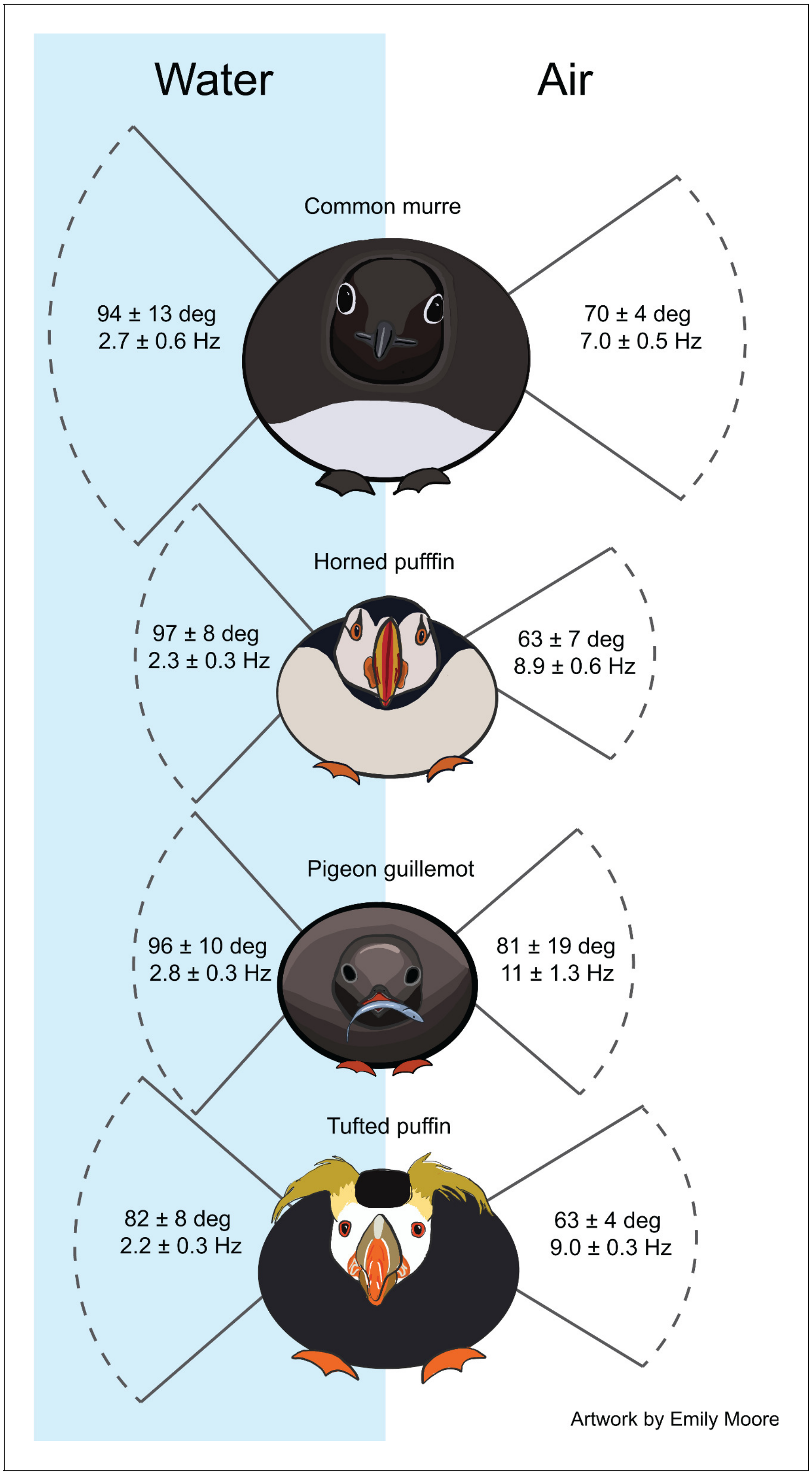

Figure 4. Wingbeat amplitude and frequency of four species of alcid in aerial and aquatic flight.

Artwork by Emily Moore

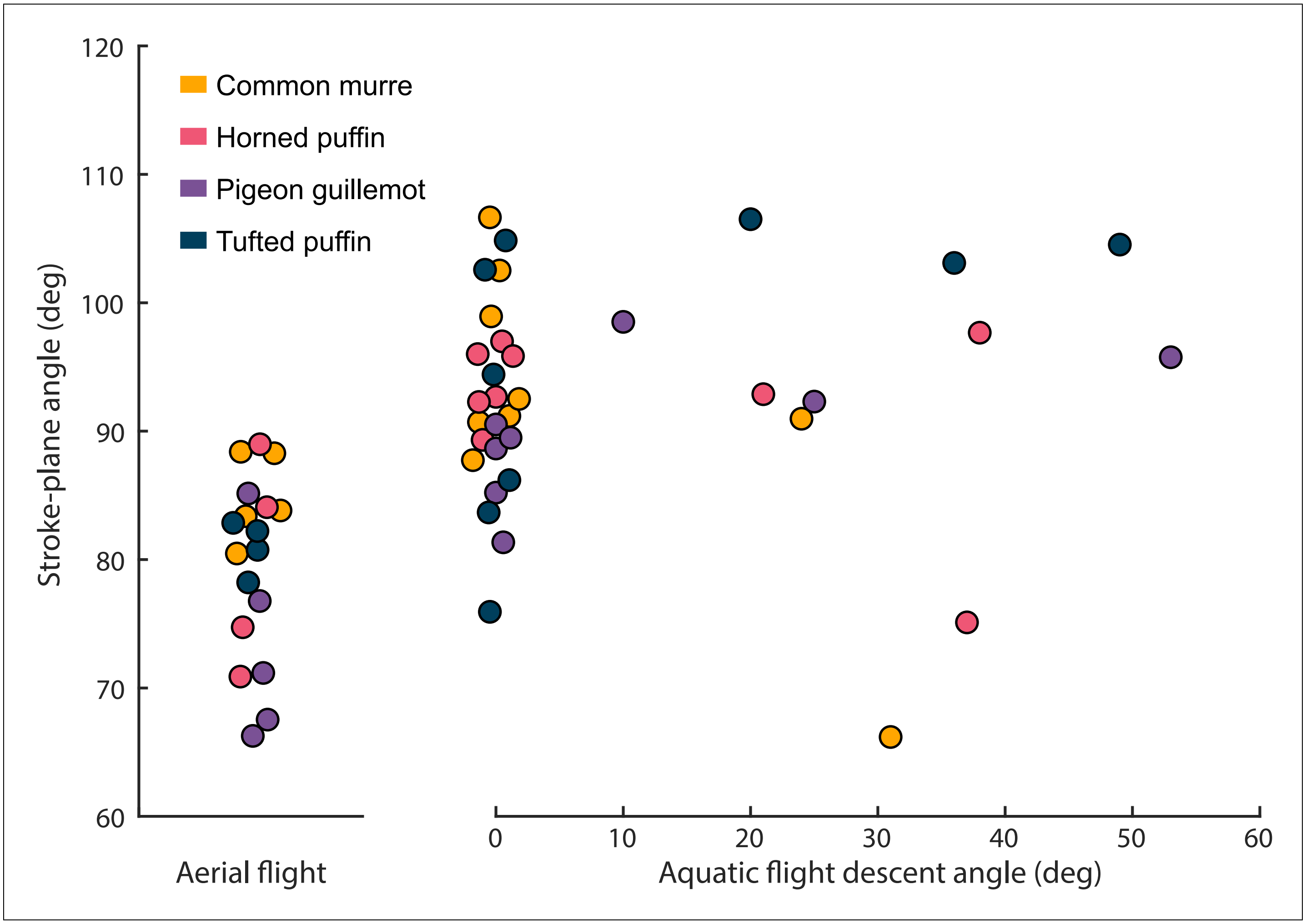

Figure 5. Stroke-plane angle (β) of four species of alcid in aerial and aquatic flight. β was significantly lower (the top of the stroke plane was rotated more caudally) during aerial flights relative to aquatic flights ($F_{1,47}$ = 41.3, η^2 = 0.422, p = 6.14e-08). Within aquatic flights, there was no consistent relationship between β and the angle of descent ($F_{1,27}$ = 0.0755, η^2 = 0.002, p = 0.786). Jitter was added to the points representing aerial flights and horizontal aquatic flights (descent angle = 0) to increase visibility.
The online version of this article includes the following source data for figure 5:

Source data 1. Stroke-plane angle of four species of alcid in aerial and aquatic flight.

narrow range of *St* despite experimentally-induced disruptions to their kinematics (***Nudds et al., 2014***).

One limitation of this study is that recordings of aquatic flight were made at shallow depths. However, previous work has indicated that velocity (***Lovvorn et al., 2004***; ***Watanuki and Sato, 2008***; ***Watanuki et al., 2006***), wingbeat frequency (***Watanuki et al., 2006***), and wing excursion (***Kikuchi et al., 2015***) of descending birds remain within a narrow range across depths, suggesting that our results apply to wild alcids. Average velocity and wingbeat frequency of common murres during swimming in this study were 1.63 m s^{-1} and 2.4 Hz, respectively, whereas ***Watanuki et al., 2006*** report 1.61 m s^{-1} and 2.6 Hz for wild birds (***Watanuki et al., 2006***).

In moving between air and water, alcids must cope with a dramatic shift to the forces exerted upon them. For example, a bird in aerial flight must counteract the downward pull of gravity, whereas the same bird in shallow water must counteract the upward pull of buoyancy. Recent work with robotics has revealed that a simple shift in stroke-plane angle (β, ***Figure 1***) can allow for both aerial and aquatic propulsion from the same wing (***Izraelevitz et al., 2018***). The authors of this study point to alcids as their inspiration for exploring stroke-plane angle in a hybrid, flapping wing, but, to

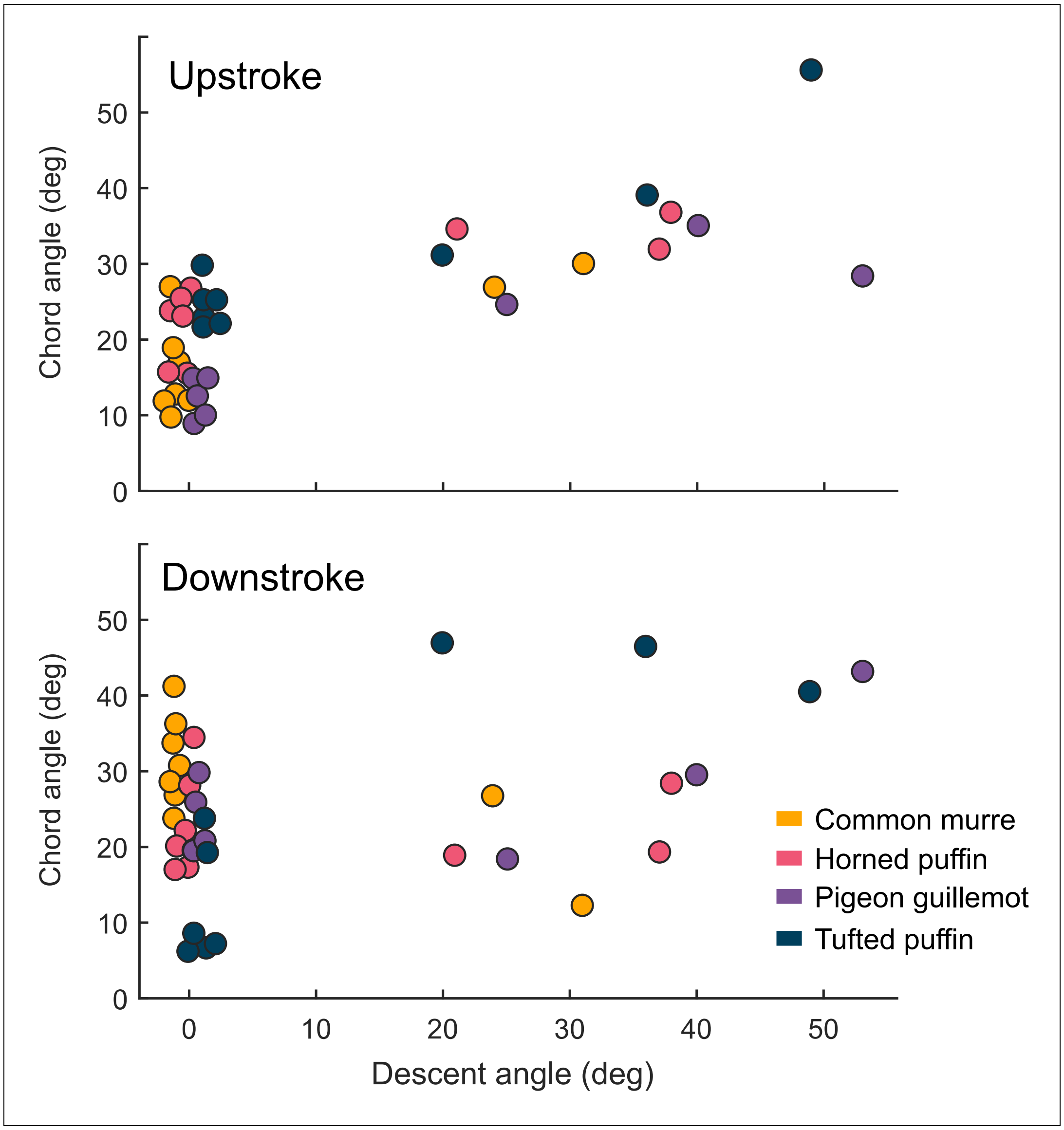

Figure 6. Chord angle (α) versus descent angle for aquatic flights of four species of alcids. α increased with the angle of descent for upstroke ($F_{1,30} = 55.7$, $\eta^2 = 0.458$, p = 2.55e-08) and downstroke ($F_{1,27} = 8.17$, $\eta^2 = 0.122$, p = 8.11e-03). However, a significant crossed interaction between species and angle of descent for downstroke chord angle ($F_{3,27} = 7.68$, $\eta^2 = 0.343$, p = 7.26e-4), indicates that the main effect of angle of descent on chord angle during downstroke is uninterpretable (i.e. the response depends on the species). Jitter was added to the points representing horizontal aquatic flights (descent angle = 0) to make all points visible.
The online version of this article includes the following source data for figure 6:

Source data 1. Chord angle versus descent angle for aquatic flights of four species of alcids.

our knowledge, our result is the first to confirm that β varies as predicted by ***Izraelevitz et al., 2018*** as dual-medium birds transition between air and water.

The stroke plane is rotated to a greater degree during aerial flight to values that are consistent with strictly aerial fliers (***Figure 5***; ***Tobalske et al., 1999***). In other words, during the aerial downstroke, while the wing is being depressed alcids also draw the wing forward. To reset the position, alcids elevate and retract the wing during the aerial upstroke. According to ***Izraelevitz et al., 2018***, this stroke-plane angle helps create the vertical force needed to counteract gravity in air. In water, wherein a bird is actually pulled up by buoyancy rather than down by gravity, the top of the stroke plane rotates cranially (***Figure 5***), allowing the bird to orient net force production to counteract drag

(**Izraelevitz et al., 2018**). Thus, alcids shift stroke-plane angle to cope with the shift in external forces between air and water.

We found no significant relationship between the angle of descent and stroke-plane angle, suggesting that – while stroke-plane angle varies between air and water – alcids do not seem to further modify β to fine-tune the direction of their force output (**Figure 5**). Instead, alcids appear to change the orientation of their force output during aquatic flight, at least in part, by increasing upstroke chord angle (α) with angle of descent (**Figure 6**).

While amplitude was greater in water for all species (**Figure 4**), as expected, stroke durations were dramatically shorter, causing stroke velocities in aerial flight to be ~2X faster than those during aquatic flight (**Figure 3**). The work of **Kikuchi et al., 2015** suggest a similar result for rhinoceros auklets; however, they report nearly equal wingbeat amplitudes across fluids (87 deg in water, 88 deg in air). Our results may differ because we measured wingbeat amplitude in different ways. **Kikuchi et al., 2015** relied on the vertical extent of the wingtip in aerial flight and the estimated half-wingspan. Based on our observations, the excursion of the wingtip may not be a reliable measure for inferring contractile velocity. This is because the distal feathers bend considerably during the end of each half-stroke in air, increasing the perceived wingbeat amplitude. This means that stroke velocity measured via the wingtip in aerial flight is not comparable to that measured at the wrist during aquatic flight.

Assuming stroke velocity is proportional to contractile velocity of the major wing muscles, the pectoralis and supracoracoideus, alcids either contract these muscles at inefficient velocities in one or both fluids or maintain a two-geared system – with one set of muscle fibers used for aquatic flight and another for aerial flight. This is because muscle fibers of a given fiber type and myosin isoform are most efficient over a narrow range of contractile velocities (**Goldspink, 1977**; **He et al., 2000**; **Reggiani et al., 1997**; **Rome et al., 1988**). Alcids have exceptionally long sterna, perhaps allowing for regional specializations in the pectoralis and supracoracoideus (**Hamilton, 2006**; **Kovacs and Meyers, 2000**; **Stettenheim, 1959**). Alternatively, Kovacs and Meyers indicate that the latissimus dorsi caudalis, which is enlarged in alcids, is positioned to retract the wing as occurs during the aquatic downstroke. Thus, alcids may rely on different muscles for powering the downstroke in each fluid (**Kovacs and Meyers, 2000**). Additionally, previous histology research has documented two, 'fast' fiber-types in the muscles (both with fast myosin but differing slightly in oxidative and glycolytic capacities) of Atlantic puffins (**Kovacs and Meyers, 2000**). These lines of evidence suggest the presence of a two-geared flight system, the number of myosin isoforms in these muscles in alcids or their contractile properties remain unknown.

By maintaining a two-geared system, alcids would avoid the costs of inefficient muscle contractions but would have increased aerial flight costs due to the additional mass of the 'aquatic gear' (**Ellington, 1984b**). In contrast, maintaining the 'aerial gear' may actually benefit aquatic performance, as muscle represents a vital oxygen storage site to diving animals (**Ponganis, 2015**). Consistent with this hypothesis, the metabolic rate of common murres is high in aerial flight but low in aquatic flight (**Elliott et al., 2013**). Future research should test whether the pectoralis and supracoracoideus muscles contract at different speeds in aerial and aquatic flight and explore in more detail the variation in myosin composition of those muscles to test for a two-geared system. It would be especially interesting to explore the presence of a two-geared system in dippers (genus *Cinclus*) – the only dual-medium passerine birds – given that passerines often express only one myosin isoform (**Rosser et al., 1996**).

Conclusion

Alcids cruised within the efficient range of *St* in both aerial flight and aquatic flight, suggesting that selection has optimized these species for locomotion in remarkably different fluids. However, alcids flapped their wings at two discrete sets of stroke velocities according to fluid medium, indicating that they either contract their muscles at inefficient velocities in one or both fluids or maintain a two-geared muscle system, with one set of muscle fibers used in air and another in water. In addition, stroke-plane (β) and chord (α) angles appear to be important in allowing alcids to shift the orientation of their force output between media and among descent angles in water. Future research should explore the potential of a two-geared muscle system in dual-medium birds by examining myosin isoforms in alcids and other species and test for functional and regional specializations in the flight apparatus across dual-medium birds.

Materials and methods

Study area and animals

Study animals were common murres (*Uria aalge,* Pontoppidan 1763), pigeon guillemots (*Cepphus Columba,* Pallas 1811), horned puffins (*Fratercula corniculata,* Naumann 1821), and tufted puffins (*Fratercula corniculate*, Pallas 1769).

Filming of aquatic flight was performed at the Alaska SeaLife Center in Seward, Alaska. The Alaska SeaLife Center contains an outdoor aviary exhibit with a large area for aerial flight (approximately 20 m wide X 20 m long X 8–10 m tall) over a 397,500-liter saltwater tank. The surface of the water measures approximately 10.5 m X 11 m and is approximately 6.5 m deep at its deepest point. The southern edge of the tank is inset with a large glass viewing window approximately 3.5 m wide which extends from ~2 m above the waterline to the floor of the tank. The glass of the viewing window varies from ~6.5 cm to ~25.0 cm thick from the waterline to the floor of the tank. At the time of this study, the exhibit contained 12 horned puffins, 10 tufted puffins, 4 pigeon guillemots, and 6 common murres. Individuals of each species of alcid regularly swam past the viewing window. Birds opted either to swim parallel to the water's surface and at depths of 0.5–3 m, presumably for transportation around the tank, or to descend to the bottom of the tank. Given the clear contrasts between these two behaviors, we differentiate between horizontal (trajectory <10 deg) and descending aquatic flight (trajectory $\geq$20 deg). The birds swam on their own volition and selected their own swimming speeds and descent angles.

Videos of aquatic flight of all four species were taken using a GoPro Hero6 Black (GoPro, Inc, San Mateo, California, USA) at 119.88 fps and a shutter speed of 1/480 s in the 'Linear View' mode (***Video 1***, bottom panel), which removes the 'fisheye' distortion common to action cameras (Tyson Hedrick, pers. comm.). The camera was positioned on a tripod and leveled using a bubble-type level embedded in the tripod. Because birds chose when and where to dive, swimming bouts were sampled opportunistically. The camera was triggered *via* a GoPro Smart Remote (GoPro, Inc, San Mateo, California, USA) when we noticed a bird about to initiate a dive or swim past the viewing window. The camera was positioned approximately 1 m below the waterline; thus, all analyzed dives were between 0 to 3 m deep.

Videos of common murres, horned puffins, and tufted puffins in aerial flight were recorded using a Red DSMC2 with a Helium 8K S35 sensor (Red Digital Cinema, Irvine, California, USA) at 29.97 or 59.94 fps and an auto shutter (***Video 1***, top panel). The camera was attached to a Cineflex gyro-stabilizated system (General Dynamics Global Imaging Technologies, General Dynamics Corporation, West Falls Church, Virginia, United States) mounted underneath a helicopter and recorded video of birds cruising over open water in Kachemak Bay, Alaska. Videos of pigeon guillemots in *aerial flight* were recorded from land at Monterey Bay, California using a Fastec Ts5 (Fastec Imaging, San Diego, California, USA) at 239.76 fps and a shutter speed of 1/960 s. The birds flew on their own volition and selected their own speeds.

Kinematic analyses

We performed kinematic analyses using MATLAB (2018a & b, MathWorks, Inc, Natick, Massachusetts, USA) using the DLTdv6 digitization tool described in ***Hedrick, 2008*** with additional analyses performed using MATLAB and IGOR Pro (v. 6.01, Wavemetrics, Inc, Beaverton, OR). Over 45,000 points were hand-digitized for this study.

Video 1. Aerial and aquatic flight of the Common murre, *Uria aalge*.
https://elifesciences.org/articles/55774#video1

Flights perpendicular to the camera view

We gathered data on wing excursion, wingbeat frequency (Hz), bird-centered chord angle ($\propto$) and stroke-plane angle (β), and translational velocity (body lengths s^{-1}) from flights of birds made perpendicular to the camera view (***Figure 1***). We were stringent in this assessment, selecting less than 5% of all video recordings for analysis. Still, due to the nature of the cosine law, even if birds were swimming 20˚ off from perpendicular it would only impact our estimates of relevant kinematic parameters by about 6%. Because animals are only expected to exhibit efficient *St* during cruising locomotion, the flight velocity of each animal was first visualized to ensure that the animal did not consistently accelerate or decelerate during a flight prior to its inclusion in our dataset.

For both aerial and aquatic flights, we digitized the eye, tip of the tail, and either the wrist (aquatic flight) or wingtip (aerial flight). The digitized points were analyzed in MATLAB using a custom script. For aquatic flights, the code first computed the angle between the bird's mean path and the waterline. If the bird was descending (trajectory >20 deg from horizontal), the code rotated, *via* a 2D Euler-angle rotation matrix, the digitized points about that angle so that the x- and y-axes were parallel and perpendicular to the bird's swimming direction, respectively. For horizontal aerial and aquatic flights (trajectory <10 deg from horizontal), we assumed that the x- and y-axes were aligned with the bird's direction and, therefore, did not transform the digitized points.

To convert the linear variables to a consistent set of units, we used the body length of the bird in each frame, as determined by the distance between the eye and the distal tip of the tail in each frame. This method of calibration accounts for variability in the distance between the camera and the bird as well as any distortion of the image created as the light passed from the water to the camera. We chose to use the entire length of the body for calibration, rather than some smaller anatomical length (e.g. culmen), as both the eye and tail were highly conspicuous in all frames of the recorded videos. Visual inspection of the aquatic data revealed pronounced head movement (relative to the body) in sync with the wingbeat cycle (i.e. body length varied with position in the stroke cycle) (***Lapsansky and Tobalske, 2019***). Because of this, we smoothed the raw body-length data using the 'smoothingspline' method of fitting in MATLAB and a smoothing parameter of 1e-04 to account for the head movement of the bird. To account for digitization error of the anatomical landmarks themselves, we smoothed the kinematic data using the same 'smoothingspline' method of fitting in MATLAB using a smoothing parameter of 0.01, based on ***Clifton and Biewener, 2018***.

For aerial flights, we computed wing excursion based on the elevation of the wingtip, relative to the average elevation of the eye and tail, and the wingbeat frequency as the number of complete wingbeats divided by the total duration of those wingbeats for each flight. Bird-centered stroke-plane angle was calculated as the angle between the vector describing the path of the wingtip between its minimum and maximum elevation relative to the direction the bird was traveling (***Figure 1***). We were unable to measure airspeed of alcids in aerial flight without disturbing their motion. Luckily, however, flight speeds of three of these species and their relatives have previously recorded in the wild (***Spear and Ainley, 1997***). ***Spear and Ainley, 1997*** categorized alcids as medium (tufted puffins, pigeon guillemots, and rhinoceros auklets) and large (common murres) (***Spear and Ainley, 1997***). To capture the full range of airspeeds exhibited by each species, we assumed alcids to have flown at the mean airspeed observed for birds of that size class flying in a crosswind ±1.96 * standard deviation of that measure (i.e. 95% prediction interval). Thus, we assumed medium alcids in our study (tufted puffins, pigeon guillemots, and horned puffins) to have flown at airspeeds between 13.95 $m\ s^{-1}$ and 18.65 $m\ s^{-1}$ and large alcids (common murres) to have flown at airspeeds between 13.32 $m\ s^{-1}$ and 24.68 $m\ s^{-1}$. We also computed *St* based on ground speed by comparing the movement of flying alcids to stationary objects (e.g. rocks, floating debris, standing waves) in each video. We did not measure chord angle for aerial flights given the low frame rates of our aerial videos for three species. Each perpendicular aerial flight (totaling n = 18) is represented by between 4 and 46 complete wingbeats (median: 15).

For aquatic flights, wing excursion was calculated as the difference between the maximum and minimum elevation of the wrist for a given wingbeat, relative to the average elevation of the eye and tail. If anything, this is a slight underestimate of wing excursion, as the hand-wing sometimes appeared to exhibit slightly greater excursions than the wrist ($\leq$10%). However, we chose to digitize the wrist as it was consistently visible in all videos. Frequency was the inverse of the duration of each wingbeat. Chord angle was the angle at mid-stroke between the position vector running from the wingtip to the wrist and that running from the tail to the eye. Stroke-plane angle was calculated as the angle between the bird-centered position vector describing the path of the wrist between its minimum and maximum elevation relative to the direction the bird was traveling. For aquatic flights, used the position of the tail to calculate velocity, as our previous work has demonstrated that the head is an unreliable indicator of overall body motion in swimming alcids (**Lapsansky and Tobalske, 2019**). Details of the velocity calculation, including how we corrected for the effects of pitching in our calculation, are described in more detail in **Lapsansky and Tobalske, 2019**. The velocity due to pitching of the body was typically <5% of the translational velocity. Each perpendicular aquatic flight (n = 35; 24 horizontal and 11 descending) is represented by the values for between 1 and 6 complete wingbeats (median: 3).

To convert the final wing excursion and velocity data from body lengths to meters (for ease of comparison), we measured the length of the culmen relative to the length of the body (eye-to-tail) of 15 individuals of each species engaged in aerial flight in high-resolution images gathered from the Macaulay Library at the Cornell Lab of Ornithology. We used these data to convert from body lengths to meters for individuals in our study. The average culmen length used in this analysis (averaged from values in the Birds of North America online **Rodewald, 2015**), calculated species-specific body length, and the asset numbers for the photographs are included in the supplement (***Supplementary file 1***). Given that *St* is dimensionless, our method of converting to metric units only affects our calculations of *St* based on the airspeed reported in **Spear and Ainley, 1997**.

In addition to comparing *St* of alcids to the theoretical efficient range of $0.2 < St < 0.4$, we also compare these data to the range for birds in cruising flight ($0.12 < St < 0.47$) reported in **Taylor et al., 2003**.

Flights parallel to the camera view

Stroke velocity (deg s^{-1}) was calculated from flights made parallel to the camera view. Thus, flights were selected for analysis when birds appeared to fly horizontally and straight at or straight away from the camera (±10 deg). For all flights (n = 80), we digitized the wrist and the shoulder of each bird at the maximum and minimum elevation of each wingbeat to calculate wingbeat amplitude (deg). Stroke velocity was computed as the change in angle (deg) over the duration (sec) of the stroke. For aquatic flights, this computation was performed on a stroke-by-stroke basis. For aerial flights of common murres, horned puffins, and tufted puffins, the relatively slow frame rate meant that computing the duration of each individual stroke would provide only a coarse measurement of stroke duration. Thus, we opted to compute stroke duration for flights of these species as 0.5 * the inverse of the wingbeat frequency of that flight. We validated this approximation by computing stroke duration via both methods for the aerial flight of pigeon guillemots, finding no significant differences between the two calculations (Upstroke: *t-Stat* = 1.67, *Cohen's d* = 0.037, p=0.10, *n* = 70 half-strokes; Downstroke: *t-Stat* = 0.71, p=0.48, *Cohen's d* = 0.019, *n* = 70 half-strokes; paired t-tests). While the frame rate was relatively low for aerial flights of common murres, horned puffins, and tufted puffins (29.97 or 59.94 fps), the long exposure of the video (auto-shutter) made it relatively easy to locate the top and bottom of each stroke, as the wing briefly pauses before the turnaround. Each parallel aquatic flight is represented by between 2 and 11 complete wingbeats (median: 4) and each parallel aerial flight by between 3 and 18 complete wingbeats (median: 12).

Data visualization and statistical analyses

We plotted data using the Gramm Toolbox from **Morel, 2018** in MATLAB and edited plots for visibility in Adobe Illustrator version 24.1.3 (Adobe Inc, San Jose, California, USA). Statistical analyses were performed using R version 3.6.3 (R Foundation for Statistical Computing, Vienna, Austria). To investigate the effect of each fluid (i.e. air or water) and type of aquatic flight (i.e. horizontal or descending) on *St* and kinematic parameters we built linear models (function *lm* in package 'stats') (e.g. *ln(KinematicVariable)~Species * Fluid*) and assessed the significance of the fixed effects using a type I ANOVA (function *anova* in package 'stats'). If the interaction between species and fluid was found to be insignificant, it was removed from the model and the model was fit again with only the main effects. To ensure normality and homoscedasticity of the residuals for each model, we log-transformed numerical data and systematically checked the diagnostic plots. We tested for the presence of outliers after each model fit using the function 'outlierTest' from the R package *car* and excluded significant outliers from analyses (**Fox and Weisberg, 2019**). We report eta-squared (η^2) calculated by the function *eta_sq* from the R package 'sjstats' (**Lüdecke, 2020**). Pairwise *post hoc* tests (for within-species differences between air and water) were performed using the *TukeyHSD* function in R and p-values for each within species comparison are reported in alphabetical order by species name.

The stroke velocity data displayed a significant departure from homoscedasticity due to unequal variances among species. Thus, we tested for differences in stroke velocities (both upstroke and downstroke) within each species using the R function *t.test* (with *var.equal = FALSE*) and a Bonferroni-corrected critical p-value of 0.0125 (p=0.05/4 species) to account for multiple testing.

For all statistical analyses, we treated flights as independent and used the average value of the kinematic parameter exhibited for that flight for testing (rather than analyzing each wingbeat as independent). For *St*, we propagated the standard deviation in wing excursion through to calculate the standard deviation in *St*. We report means ± s.d. unless otherwise specified.

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Additional information

Competing interests

Daniel Zatz: is affiliated with ZatzWorks Inc. The author has no financial interests to declare. The other authors declare that no competing interests exist.

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Author contributions

Anthony B Lapsansky, Conceptualization, Data curation, Formal analysis, Investigation, Visualization, Methodology, Writing - original draft, Project administration; Daniel Zatz, Resources, Data curation, Investigation, Writing - review and editing; Bret W Tobalske, Conceptualization, Resources, Supervision, Methodology, Writing - review and editing

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Ethics

Animal experimentation: All work was approved by the University of Montana's Institutional Animal Care and Use Committee (AUP 004-19BTDBS-020419). Work at the Alaska SeaLife Center was performed with approval from the animal husbandry and research staff.

Decision letter and Author response

Decision letter https://doi.org/10.7554/eLife.55774.sa1
Author response https://doi.org/10.7554/eLife.55774.sa2

Additional files

Supplementary files

- Supplementary file 1. Average culmen length, asset numbers, and calculated body length during flight for each of four species of alcid. Calculated body lengths were used to convert from units of species-specific body length to metric units. Average culmen length was calculated as the mean of all values present in the *Birds of North America* entry (***Rodewald, 2015***) for adult birds (males and females) of that species. Multiple birds were digitized in some photographs. See Materials and methods for details.

- Transparent reporting form

Data availability

All data are available at the following link: https://github.com/alapsansky/Lapsansky_Zatz_Tobalske_eLife_2020 (copy archived at https://github.com/elifesciences-publications/Lapsansky_Zatz_Tobalske_eLife_2020).

The following datasets were generated:

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Chapter 5

Aquatic locomotion in non-aquatic birds

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Abstract:

We report that non-aquatic birds can locomote effectively underwater. European starlings and house sparrows use both their feet and wings for submerged swimming and rise to the surface at twice the speed that they would if propelled by buoyancy alone. Despite a lack of selection for submerged swimming or experience, the kinematic patterns of submerged swimming in non-aquatic birds closely resembles those of semi-aquatic species like puffins, shearwaters, and dippers. Non-aquatic birds generate hydrodynamic lift with their wings and utilize unsteady aspects of fluid flow (leading-edge vortices) to enhance lift production. Our results alter current understanding of the evolution of aquatic lifestyles in vertebrates and inform the development of engineered systems.

Body:

Vertebrate lineages have repeatedly re-invaded water (e.g., cetaceans, pinnipeds, sirenians), but because water is 800 times denser and 60 times more viscous than air (Denny, 1993), reliance on aquatic environments has typically co-evolved with largescale morphological and physiological modifications for locomotion (Fish, 2016; Houssaye and Fish, 2016). Thus, how terrestrial clades adopt aquatic habits despite lacking adaptations for aquatic locomotion poses a conundrum. For this reason, it has been hypothesized that aquatic lineages must first pass-through stages of relatively inefficient aquatic locomotion – allowing them to become “pre-adapted” to movement in water – before developing more efficient patterns of force production (Fish, 2016).

We set out to explore whether surface-based aquatic locomotion [surface swimming] could serve as an evolutionary steppingstone to submerged aquatic locomotion [submerged swimming] (Fish, 2016), using non-aquatic birds as a study system. Surface swimming is widespread across birds. In aquatic taxa, surface swimming is used as part of a strategy to obtain food from water. Non-aquatic species, on the other hand, contact water only rarely in the process of escaping predators or obtaining food near the surface, and use their wings and feet to reach land after becoming entrapped by the weight of the water and surface tension (Abourachid et al., 2019; Fish, 2016; Heers, 2018). We hypothesized that surface swimming in non-aquatic birds would utilize the lower wingbeat frequencies, higher wingbeat amplitudes, and folded-wing postures relative to aerial flight found in the submerged swimming of semi-aquatic birds (Lapsansky et al., 2020). This could allow a surface-swimming population to become pre-adapted to submerged swimming, as selection would favor morphological modifications for more effective and efficient movement on the surface, which could then facilitate the re-invasion of water.

Instead, we discovered that at least two species of non-aquatic birds, *Passer domesticus* [House sparrow] and *Sturnus vulgaris* [European starling], can locomote effectively underwater despite a lack of training, experience, or sustained selection. This was true for all 29 individuals [16 starlings and 12 sparrows], including individuals of two life-stages [8 adult starlings and 8 juvenile starlings], and resulted in zero perceivable injuries. Birds used both their wings and feet for submerged swimming, with the wings providing the majority of thrust, similar to dippers, shearwaters, and seaducks (Chapter 1).

To constitute aquatic locomotion, animals must reach the surface more quickly through their kinematics than they would due to buoyancy. To determine if the wing- and foot-motion of non-aquatic birds could be considered aquatic locomotion, birds (n = 20) were placed by a researcher <0.35 m underwater in a 3000 L tank to simulate a fall into water from height. Each individual was dipped three times on a given day, with 5 starlings also dipped on three separate days to estimate a training effect. Because both species are invasive in North America (where these experiments were conducted), birds were then euthanized as per USDA guidelines and then re-dipped to determine the degree to which buoyancy alone could explain the motion of each individual. Based on analysis of three-dimensional (3D) videography (Hedrick, 2008; Mathis et al., 2018), birds reached the surface more quickly (Figure 1, n = 8 starlings) and achieved higher vertical velocities (Figure 2, n = 8 starlings) owing to the kinematics of their wings and feet. Individuals achieved similar submergence times and vertical velocities on day 1 as on days 2 and 3 (n = 5), indicating that there was no detectable effect of experience.

In species which use their wings for locomotion in both air and water (e.g., puffins, dippers, seaducks), submerged swimming is achieved with lower wingbeat frequencies, higher wingbeat amplitudes, and reduced stroke velocities (Heath et al., 2006; Lapsansky et al., 2020; Richman and Lovvorn, 2008; Watanuki, 2006) relative to aerial flight. We found that the same is true of non-aquatic birds. Figure 3 shows wingbeat amplitude (A) and frequency (B) of European starlings (n = 8) in submerged swimming relative to in ascending flight (n = 5) and flight in a wind tunnel (Tobalske, 1995). Wingbeat amplitude is high in water and similar to that exhibited during ascending flight in air (Figure 3A). Wingbeat frequency is similar across flight conditions but substantially lower (~60% less) in water. As a result, stroke velocity is significantly lower in water than in air for non-aquatic birds, similar to true semi-aquatic birds (Lapsansky et al., 2020) (Figure 4).

Additionally, all species which use their wings for locomotion in both air and water partially fold their wing underwater, exhibiting a flexed-wing posture, which decreases both wing length and area relative to in air. Previous authors have suggested that this posture either increases hydrodynamic efficiency by lowering drag (Rayner, 1986; Siddall and Kovač, 2014) or is enforced by structural limitations of the avian wing (Fish, 2016; Lock et al., 2012) – which is under selection to be both large and light for flight (Ellington, 1984). We found that sparrows and starlings also exhibit this flexed-wing posture in water (Figure 5).

To determine the mechanism of force production underlying the aquatic locomotion of non-aquatic birds, we used Particle Image Velocimetry (PIV) to visualize the fluid structures produced by their wings. Vertebrates are expected to transition through evolutionary time from forms which swim via drag-based mechanisms to forms capable of swimming via more efficient and effective lift-based mechanisms with increasing specialization to water (Fish, 1996; Fish, 2016). Drag is defined as a force which acts parallel to the direction of fluid flow about a propulsor (e.g. the feet or wings), whereas lift is defined as a force which acts perpendicular to the direction of fluid flow about a propulsor (Denny, 1993). Owing to their lack of specialization to water, we expected non-aquatic birds would swim via drag forces.

Instead, we found evidence that non-aquatic birds produce force in water through both lift and drag. During the downstroke, the wing is swept both ventrally and cranially. Near the root of the wing, this leaves a starting and ending vortex which translate approximately perpendicular to the path of the wing, indicative of lift-based force production (Figure 6A) and similar to the wake produced by birds during slow flight in air (Provini et al., 2012). At the wingtip, however, the deformation of the primary feathers during downstroke – caused by the high density of water – results in the formation of a pair of counter-rotating vortices which translate parallel to the path of the feathers (Figure 6B), indicative of drag-based force production. The deformation of the feathers, along with the presence of bubbles shed from the wing, complicate the flow structure relative to aerial flight. However, data from the trefftz plane – the wake of the bird as viewed head-on – indicate that both wings shed bound circulation at the end of downstroke (Figure 6C). As well, there is some evidence to suggest that the flexed-wing posture allows the formation of a leading-edge vortex (Figure 6D), which would facilitate lift-production at the high angles of attack utilized during submerged swimming.

Our results indicate that the re-invasion of water could occur without the steppingstone of surface swimming or largescale modifications to avian morphology. Non-aquatic birds of two species are capable of effective submerged swimming despite zero training or experience. Furthermore, these animals are capable of using their wings to generate lift forces underwater. Thus, the submerged swimming of non-adapted species has traits characteristic of specialized aquatic vertebrates, indicating that birds need not pass through stages of relatively inefficient aquatic locomotion before developing more efficient patterns of force production (Fish, 2016). This is likely made possible by the fact that fluid locomotion is an ancestral trait in birds. Unlike the ancestors of aquatic mammals, the avian bauplan is the result of selection for lift production in air, allowing lift production in water without modification to morphological structures. This could explain why some diving birds display only minor morphological modifications relative to non-aquatic species (e.g., dippers, shearwaters), whereas most diving mammals are heavily modified relative to their terrestrial ancestors (Fish, 2016). Finally, non-aquatic birds have not faced selection for efficient aquatic locomotion. Thus, that non-aquatic birds partially fold their wings, reduce wingbeat frequency, and reduce stroke velocity for submerged swimming – patterns characteristic of all volant, wing-propelled diving birds – suggests that these kinematics are not the result of selection for efficient submerged swimming (Rayner, 1986; Siddall and Kovač, 2014), but are instead enforced by structural limitations of the avian wing system (Fish, 2016; Lock et al., 2012). Engineered systems, which can utilize stronger materials and generate higher power, therefore, need not replicate these patterns to effectively locomote in both air and water (Izraelevitz et al., 2018). Key sights for adaptation in wing-propelled diving lineages are likely an increased rigidity of the feathers to reduce bending and the tuning of muscle fibers to the slower contractile velocities exhibited in water (Lapsansky et al., 2020).

Methods:

Birds were obtained from licensed pest control specialists. Birds were placed by a researcher <0.35 m underwater in a 3000 L tank to simulate a fall into water from height.

An initial set of birds (n = 8 juvenile starlings & 12 adult sparrows) were videoed underwater at 500 fps using two high-speed cameras [Phantom Miro eX4, Fastec Imaging, San Diego, California & FASTCAM 1024 PCI, Photron, Toyko, Japan] recording through a plexiglass window in the side of the tank. Because our initial goal was to record surface swimming, three-dimensional reconstructions based on these camera views had low accuracy in the dimension parallel to the camera view, as the cameras were placed close to one another. Thus, we only report data for the two planes which were perpendicular to the camera view for this set of birds. To resolve the kinematics of submerged swimming more accurately, a second set of birds (n = 8 adult starlings) were videoed at 120 fps using four GoPro Hero cameras [GoPro Inc., San Mateo, California] placed in the water and orthogonal to one another.

Ascending aerial flight (n = 5) was videoed at 500 fps using three high-speed cameras [FASTCAM SA3, FASTCAM NOVA S6, and FASTCAM Mini AX100, Photron, Toyko, Japan] attached to an aluminum cage [3.5 m long X 1.25 m wide X 1 m tall] placed over the water tank. Birds were released by a researcher and ascended within the flight cage.

The three-dimensional space was calibrated in MATLAB [Mathworks, Natick, Massachusetts] using EasyWand (Theriault et al., 2014) with points digitized by DLTdv8 (Hedrick, 2008). Distortion coefficients for each camera with an aquatic view were determined using the camera calibration application available in MATLAB. Videos from the initial set of birds were digitized using DeepLabCut (Mathis et al., 2018) and converted to the format required by DLTdv8 using a script written by Brandon Jackson and made available on GitHub (Jackson et al., 2016). These data were then refined by hand. Videos from the second set of starlings (adults recorded via submerged Go Pro cameras) were digitized directly by hand in DLTdv8.

To accurately represent both body position and velocity (Figures 1 & 2), 6 points on the head were digitized for each individual in the initial set of birds (bill base, apex of head, back of head, chin, eye, neck). The position and velocity of the eye was then determined based on the initial position of the eye and the average displacement of all 6 points to account for periods in which the eye was not visible. Wingbeat amplitude, frequency, and stroke velocity (Figures 3 & 4) were calculated for the second set of birds based on the position of the wrist relative to the shoulder, as in Lapsansky et al. (2020). Wingbeat amplitude, frequency, and wingspan of starlings flying in a wind tunnel were taken from the data originally presented in Tobalske (1995). Wingspan of birds in submerged swimming was calculated as the total distance between the tip of the 10th primary feather on each wing (Figure 5). Measurements for a given run were averaged and the average used in subsequent analyses and figures.

Particle Image Velocimetry (Figure 6) was accomplished using a Dual-Cavity Diode Pumped Solid State, High Repetition Rate Laser [LaVision, Göttingen, Germany] firing at 100 or 150 Hz with video recorded using a Mini AX100 high-speed camera [Photron, Toyko, Japan]. The laser was position above the water and created a plane of light perpendicular to the camera, which recorded through a plexiglass window in the tank. The water was seeded with glass beads to enhance flow visualization. Birds were placed by a researcher <0.35 m underwater with their backs to the laser source to reduce the risk of eye injury. Flow processing was performed using DaVis 10 [LaVision, Göttingen, Germany] and corrected for distortion using a Type 22 calibration Plate [LaVision, Göttingen, Germany].

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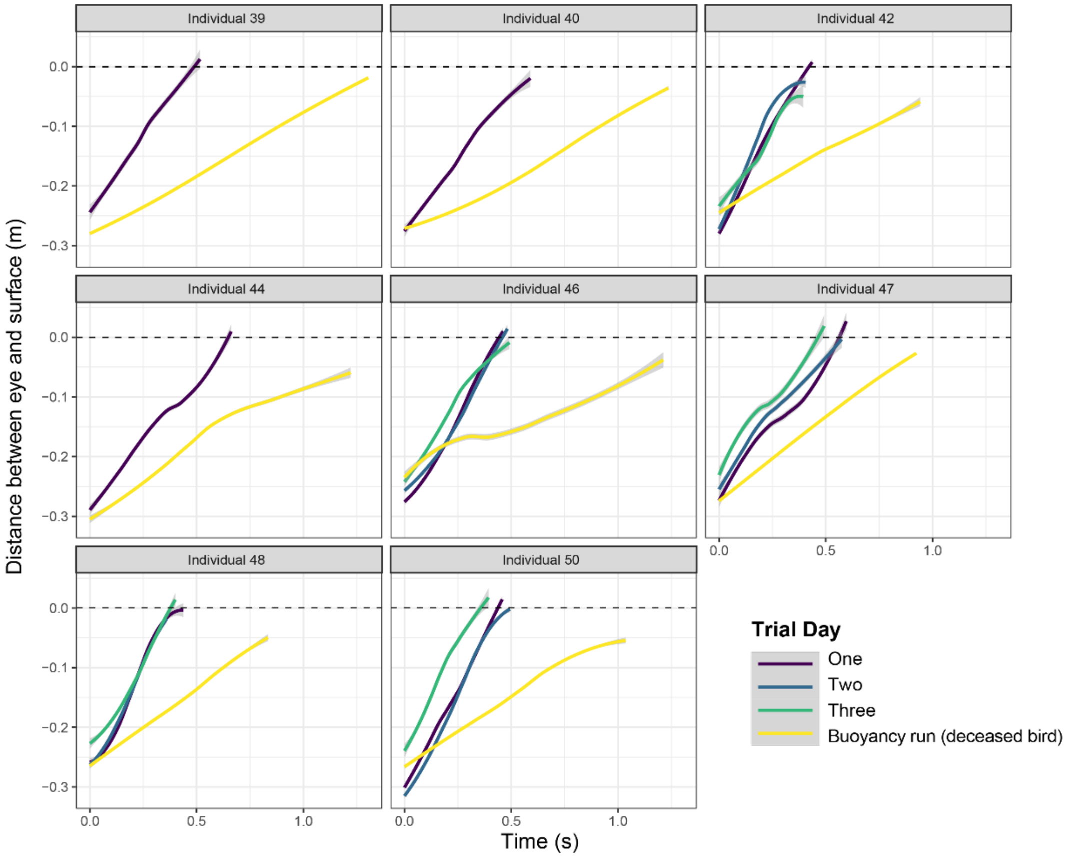

Figure 1: Paths of European starlings (n = 8) engaged in submerged swimming. All birds reached the surface of the water more quickly owing to their wing and leg movements, with no detectable effect of experience.

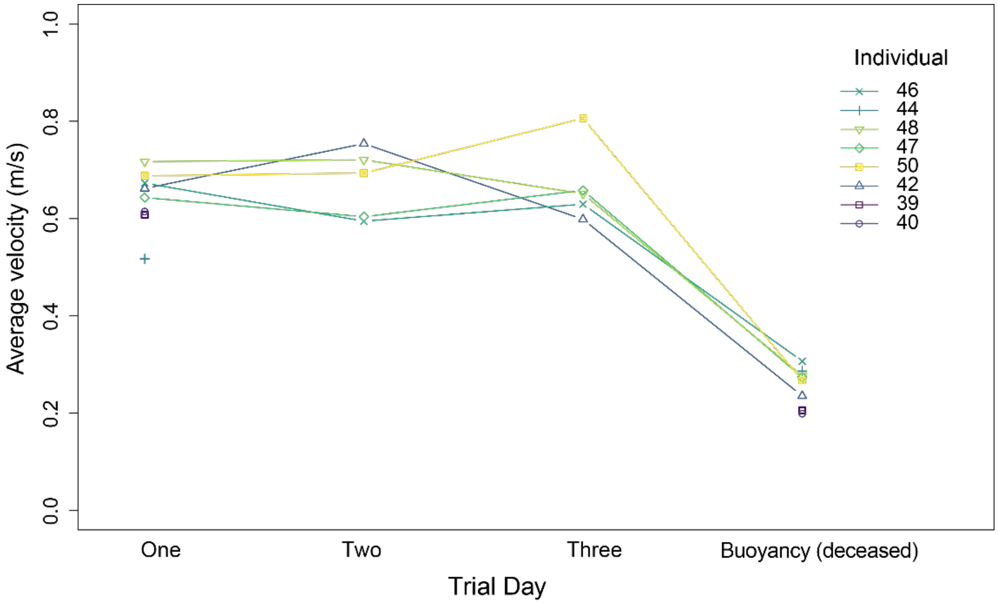

Figure 2: Average vertical velocity of European starlings (n = 8) versus trial day. All birds achieved higher velocities owing to their wing and leg movements, with no detectable effect of experience on velocity.

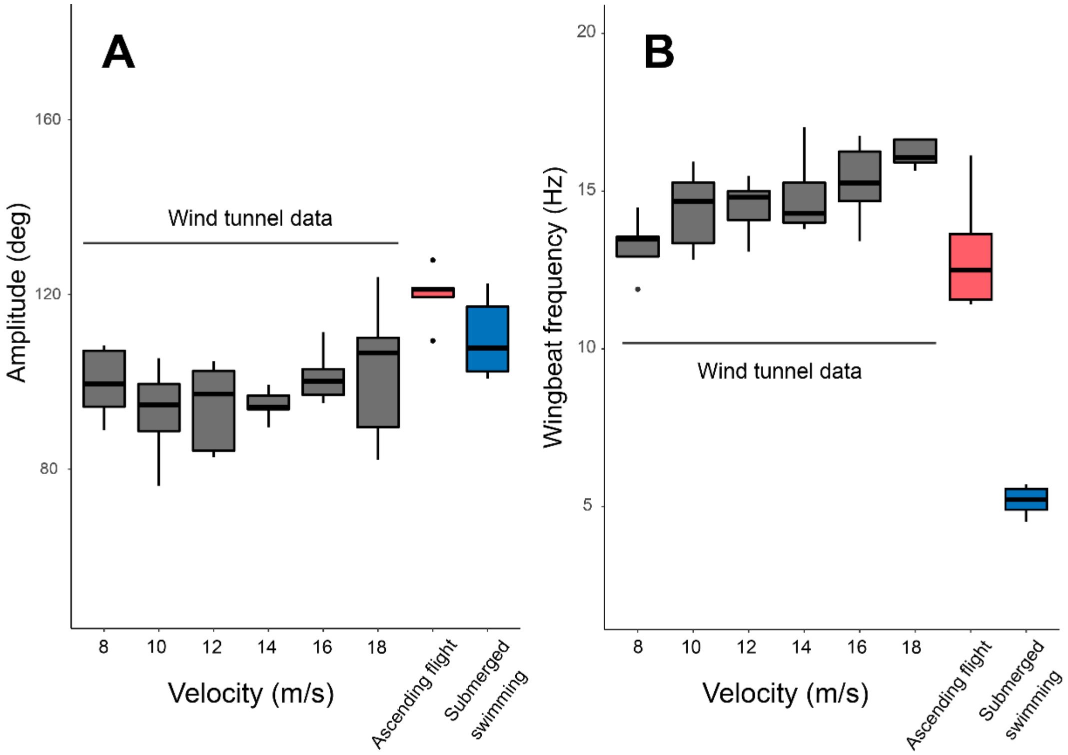

Figure 3: Wingbeat amplitude (A) and frequency (B) of European starlings during flight in air and water. Wind tunnel data are from Tobalske (1995).

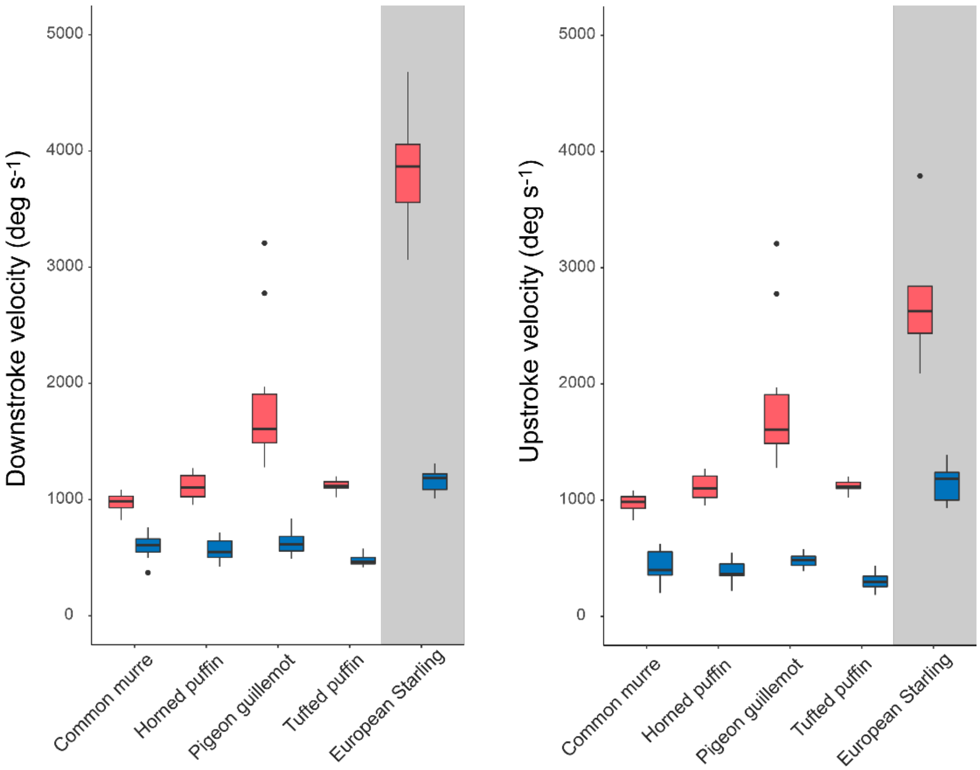

Figure 4: Stroke velocity of European starlings during flight in air and water. Data from alcids are replotted from Lapsansky et al. (2020).

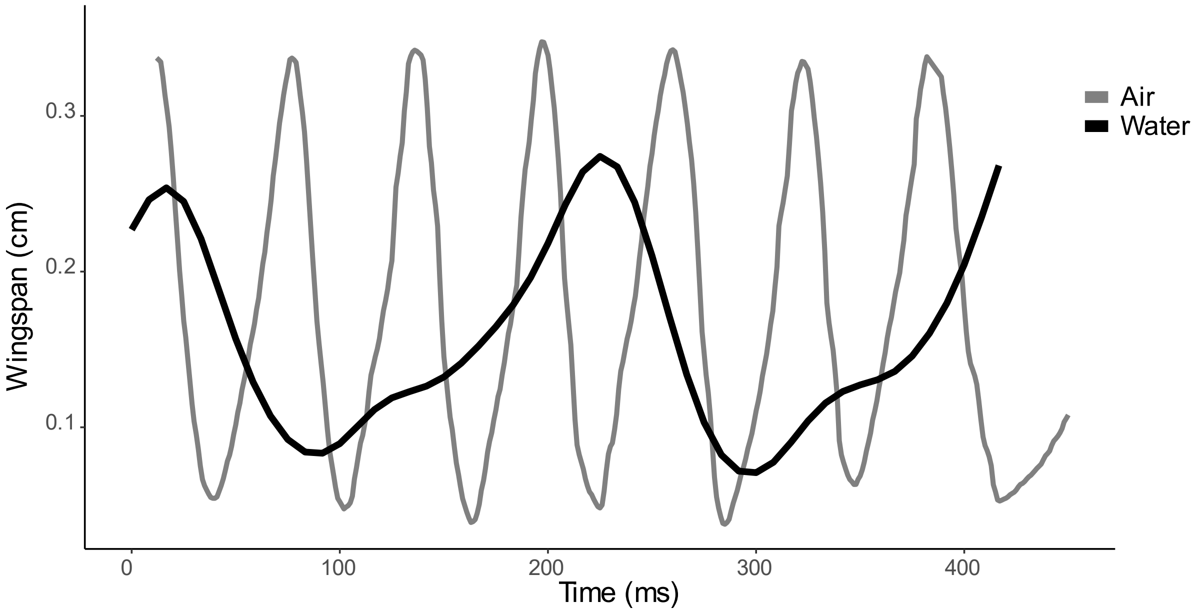

Figure 5: Example wingspan of a European starling locomoting in air versus in water. Data for air are from Tobalske (1995). Wingspan was measured as the distance between the tips of the 10th primaries on each wing.

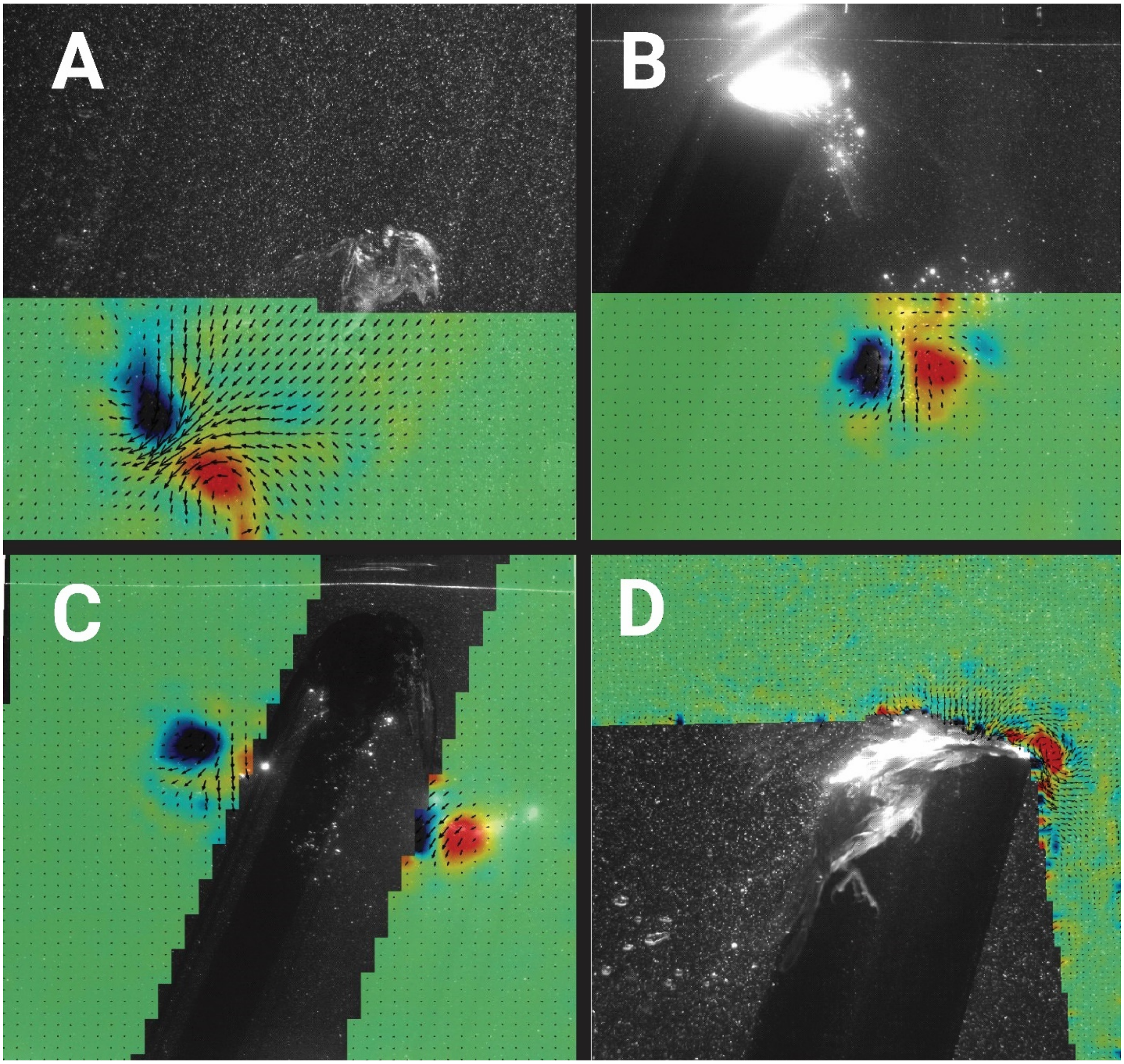

Figure 6: Flow visualization of non-aquatic birds. (A) Lift-based wake structure produced by the downstroke of a house sparrow. (B) Drag-based wake structure produced by the downstroke of a European starling. (C) Bound circulation shed from the wings of a European starling following downstroke. (D) Leading-edge vortex formation on the wing of a house sparrow in mid-downstroke.