Trends in
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Review

Waxing and Waning of Wings

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A major challenge to Darwinian evolution is explaining 'rudimentary' organs. This is particularly relevant to birds: rudimentary wings occur in fossils, as well as in developing, molting, and flight-impaired birds. Evidence shows that young birds flap small wings to improve locomotion and transition to flight. Although small wings also occur in adults, their potential role in locomotion is rarely considered. Here we describe the prevalence of rudimentary wings in extant birds, and how wings wax and wane on many timescales. This waxing and waning is integral to the avian clade and offers a rich arena for exploring links between form, function, performance, behavior, ecology, and evolution. Although our understanding is nascent, birds clearly show that rudimentary structures can enhance performance and survival.

Highlights

A major challenge to Darwinian evolution is to explain 'rudimentary' organs. This dilemma is especially relevant to birds: rudimentary wings occur in fossils, as well as in developing, molting, and flight-impaired birds.

Many studies show that immature birds flap their small, incipient wings to improve locomotion as they acquire flight capacity. Although similarly small wings occur in secondarily or temporarily flight-impaired birds, their role in locomotion has not been well studied.

Integrating studies on these different groups of birds demonstrates that rudimentary wings are ubiquitous across the avian clade, and that wings wax and wane on multiple timescales. Rudimentary wings improve locomotion and enhance survival during this process.

Although our understanding is still in its infancy, rudimentary structures may play important roles in many animal groups, both extant and long extinct.

Rudimentary Beginnings of Complex Organs

A major challenge to Darwinian evolution is explaining the 'rudimentary beginnings' [1] of 'organs of extreme perfection and complication' [2]. Although natural selection describes how small phenotypic differences might confer greater fitness and be favored, it did not satisfy many who questioned how small changes could result in large-scale ecological shifts. If morphology evolves slowly, through incremental adaptive stages, how do organisms acquire new and complex structures that seem to be useful only when fully assembled?

One of Darwin's critics was George Jackson Mivart, who asked: 'What use would half a wing offer any reptilian ancestor on its way to becoming a bird?' [1]. If wings evolved 'for' flight, a small wing would not be adaptive because it would not allow its owner to fly. Darwin attempted to address this dilemma in later editions of his book. Following his work and the discovery of the reptile-like early bird ***Archaeopteryx*** (see Glossary), discussions explored how progressively larger wings might have increased running speed or jump height (cursorial, AKA: ground-up, theories), or prolonged gliding (arboreal, AKA: trees-down, theories) [3]. These and other hypothetical scenarios dominated origin-of-flight debates throughout the 20th century. It was not until the relatively recent discoveries of dinosaurs with feathers and **'protowings'** [4,5] that half-wings became a reality and theory could be compared with the fossil record.

Diverse protowings are now documented by fossils [5]. How do we infer the function(s) of such structures and test hypothetical scenarios? Reconstructing the evolutionary beginnings of complex organs requires exploring how similar features function in extant organisms. This is the only way to establish biomechanical principles that underlie form–function relationships and extrapolate to fossils. However, few studies have empirically evaluated the utility of **rudimentary structures** among living organisms (but see [6–8]). Although rudimentary wings are common among extant birds – both in developing juveniles and in adults with reduced wings [9–11] – they are typically not examined from a locomotor perspective. When they are, findings may be dismissed under the premise that the birds studied are too derived to provide insight into extinct dinosaurs [12,13]. Nevertheless, evidence increasingly shows that, without incorporating rudimentary wings, our understanding of bird locomotion is incomplete and potentially misleading.

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Perspectives on rudimentary wing function have traditionally focused on evolutionary origins and the transition from no-wings to protowings to flight-capable wings [see [3,14,15] citations for evolutionary origins (>90 studies) and next section for development (~20 studies)]. Although undeniably important, this transition is only one of many that are intrinsic to birds. In reality, wings are constantly morphing, **waxing** and **waning** on **ontogenetic**, seasonal, and evolutionary timescales, across the **avian** clade [16] (Figure 1). This acquisition and loss of wings is a fundamental component of bird diversity and offers a powerful but underappreciated system for exploring relationships between form, function, performance, behavior, ecology, and evolutionary history. Most importantly, evidence suggests that transitional, rudimentary wings enhance survival during the waxing or waning process. Here we describe the widespread occurrence of rudimentary wings among extant birds, synthesize evidence on rudimentary wing use, and discuss how this information may enhance our understanding of birds on multiple timescales.

Waxing and Waning of Wings: Ontogenetic Timescales

What advantage is half a wing? Although originally viewed in an evolutionary context, Darwin's 'dilemma of incipient stages' [17] is equally relevant to developing organisms. Juveniles of many species rely on rudimentary structures that lack the specializations of adults and often resemble features of extinct relatives [3]. These juveniles thus reveal how transitional, incipient structures can function in ecological settings.

For example, most newly hatched birds are dependent on their legs, or on their parents [9], and often have rudimentary flight apparatuses even after leaving the nest (Figure 1A). It is often assumed that similarly rudimentary features precluded avian ancestors from powered flight and bird-like wingstrokes [14,18–20]. However, extant developing birds clearly show that incipient wings can have important locomotor functions. Evidence gathered over the past 20 years reveals several key insights into rudimentary wings:

- Cooperative Use of Wings and Legs Bridges Flightless to Flight-Capable Transitions
  Traditionally, wings and legs have been viewed independently: wings during aerial locomotion, legs during terrestrial [21]. However, wings and legs are often engaged cooperatively, especially in birds with proportionally small wings. Studies show that developing birds flap their incipient wings to (i) increase foot traction and ascend steep inclines [**wing-assisted incline running** (**WAIR**)], then control their aerial descent back down [e.g., ground birds (Galliformes), owls (Strigiformes), and raptors (Falconiformes)]; (ii) 'steam' across water, using their wings as oars and their legs as paddles [e.g., ducklings (Anseriformes)]; and/or (iii) increase jump height (e.g., ground birds) [22–25] (Figure 2, https://www.youtube.com/watch?v=3USAC-Ky25s). This **wing–leg cooperation** acts as a developmental bridge between leg- and wing-based locomotion, allowing juveniles to seamlessly transition from terrestrial to aerial environments in incremental functional stages [26,27]. For example, increases in wing size and performance allow developing birds to flap-run up increasingly steep obstacles, or jump higher, descend back down, and eventually fly [25,28,29]. Juvenile birds thereby demonstrate that developing wings are immediately functional because they assist the hind limbs and thus improve whole-body performance.
- A Whole-Body Perspective Is Necessary for Understanding Wing and Leg Performance
  Wings and legs appear to be influenced by **tradeoffs**. Across species, birds with higher wing investment (musculoskeletal mass) tend to have lower leg investment, and this affects wing versus leg performance and behavior [25]. Similarly, during ontogeny, juveniles with higher wing investment and performance have lower leg investment and performance, compared with either adults or other juveniles. Thus, tradeoffs likely influence both ontogenetic and

Glossary

***Archaeopteryx*:** a genus of feathered theropod from the late Jurassic (~150 million years ago) Solnhofen Limestone of Germany. It was originally found as a single feather but is now known from 12 specimens; one of the earliest theropods with bird-like wings.
Avian: the term is used here informally to refer to extant or recently extinct birds (Neornithes: Neognathae + Palaeognathae).
Molt: seasonal feather loss and renewal. In sequential molt, flight feathers are shed and regrown one at a time, or a few at a time. In simultaneous (also known as synchronous) molt, all, or nearly all, flight feathers are shed simultaneously.
Ontogeny: the growth and development of an organism.
Paedomorphosis: retention of juvenile characteristics into adulthood (decreased growth and development compared with the ancestral condition), as a result of delayed onset (postdisplacement), slower rates (neoteny), or a reduced ontogenetic period (progenesis).
Peramorphosis: increased growth and development compared with the ancestral condition as a result of earlier onset (predisplacement), faster rates (acceleration), or an extended ontogenetic period (hypermorphosis).
Power-to-mass ratio: the capacity to develop mechanical work per second (or any unit of time) relative to body mass; a high power-to-mass ratio equates to swift and maneuverable locomotion.
Protowing: an incipient forelimb apparatus with a wing-like architecture.
Rudimentary structures: structures that are small or simple compared with the maximal size or complexity observed among adults or relatives. These include (i) incipient, developing structures in juveniles (e.g., growing wings); (ii) incipient, evolving structures in extinct animals (e.g., protowings of fossils); and (iii) secondarily or temporarily reduced structures in adults (e.g., vestigial wings, molting wings) (after Mivart 1871 [1]).
Secondarily flightless: birds that have lost the ability to fly over evolutionary time (their ancestors once possessed flight capacity).
Semi-flightless: birds that have a reduced ability to fly compared with the ancestral condition.
Theropod-avian lineage: a group that includes extant birds and the lineage of

evolutionary trajectories in locomotion. However, tradeoffs are offset at the whole-body level when wings and legs are recruited cooperatively. For example, wing and leg performance show opposite developmental trajectories in Mallards (*Anas platyrhynchos*) and Indian Peafowl (*Pavo cristatus*), with legs developing at the expense of wings or vice versa (Figure 3A). However, whole-body performance is continuously enhanced during steaming [24] or wing-assisted jumping [25] (Figure 3B). These findings reiterate the importance of a whole-body perspective.

- Rudimentary Wings Are Utilized during Transitional Behaviors in Particular Habitats
  The cooperative recruitment of wings and legs is a transitional behavior that is intermediate between leg-based locomotion (e.g., running) and wing-based locomotion (flight). Different transitional behaviors are used in different habitats. For example, ducklings bridge leg- and wing-based locomotion via aquatic behaviors such as steaming, where wings and legs are recruited simultaneously to increase swimming speed and avoid predators until flight is acquired [24]. Even nonaquatic juveniles such as Hoatzin (*Opisthocomus hoazin*) [30], songbirds (K.P.D. unpublished data; Passeriformes), and owls and raptors [juvenile (https://www.youtube.com/watch?v=d2c-PHB18fU) adult (https://www.youtube.com/watch?v=UMft3Ny7hFk)] may employ their wings to swim. Similarly, immature owls and ground birds can use inclined or branching substrates to flap-run, flap-walk, or flap-jump to elevated refuges [25,26,31,32]. Although quantitative studies are limited, observation suggests that developing birds with transitional anatomical features routinely use these transitional behaviors (steaming, WAIR, wing-assisted jumps) to negotiate habitats (e.g., aquatic, inclined, or branched substrates) that serve as stepping stones between leg- and wing-based locomotion and provide intermediate phenotypes with selective advantages.
- Predators Play a Key Role in Wing and Leg Development
  Immature birds are highly vulnerable to predation [9,33–36], and predation risk likely plays a crucial role in ontogeny. For example, developing birds appear to prioritize structures that enhance predator escape. Ducklings initially avoid predators by running or swimming and emphasize the hind limbs early in development [24], whereas peachicks are dependent on arboreal refuges and allocate more resources to their wings [25]. In both cases, however, incipient wings are used to enhance locomotion, by increasing swim speed or foot traction (during WAIR) and jump height. Predation risk also influences fledging time and developmental rate [37–39]. Across passerines, higher levels of nest predation are associated with earlier fledging. In species where young leave the nest earlier, wing development is prioritized over that of other structures, providing some aerodynamic capacity at, or soon after, fledging. Although these fledglings have less developed wings and poorer flight compared with species that fledge later, the risk of losing an entire brood to a nest predator appears to outweigh the risk of losing an individual fledgling to a ground predator [38]. In short, predation is an integral moderator of locomotor trajectories.
- Body Size Plays a Key Role in Wing Performance
  Body size has long been known to influence locomotion [40–42]. **Power-to-mass ratio**, or the rate of work standardized by body size, essentially measures the relative strength and quickness of the locomotor apparatus and is a key indicator of wing performance. Flight becomes more challenging in larger animals due to scaling constraints that cause relative force and/or power to decline with increasing body size [43–49]. Consequently, extant volant birds are relatively small (<15 kg; median = 38 g) compared with terrestrial vertebrates [50]. Similarly, developing birds acquire flight when they are small and wing loading (mass per unit wing area) is low [51]; flight performance then typically improves with increases in wing and muscle size (Figure 2A). However, some species outgrow their

extinct theropod dinosaurs that gave rise to them.
Tradeoff: a compromise between structures, conditions, or strategies in which one state increases at the expense of another.
Wane (waning): to decrease in relative size and/or complexity; in this case, a decrease in relative wing investment during development, molt, or evolution.
Wax (waxing): to increase in relative size and/or complexity; in this case, an increase in relative wing investment during development, molt recovery, or evolution.
Wing-assisted incline running (WAIR): a locomotor behavior in which wings are flapped to increase foot traction while ascending steep inclines; WAIR is particularly important for birds with developing or proportionally small wings (high wing loadings).
Wing–leg cooperation: locomotor behaviors involving the coactivation of hind limbs and winged forelimbs (rudimentary or fully formed wings); these include wing-assisted incline running (WAIR) or walking (a slower version of WAIR), wing-assisted jumping – launching from a terrestrial or arboreal substrate with assistance from flapping wings, and steaming – using the feet as paddles and the wings as oars to swim; steaming is commonplace in aquatic birds.

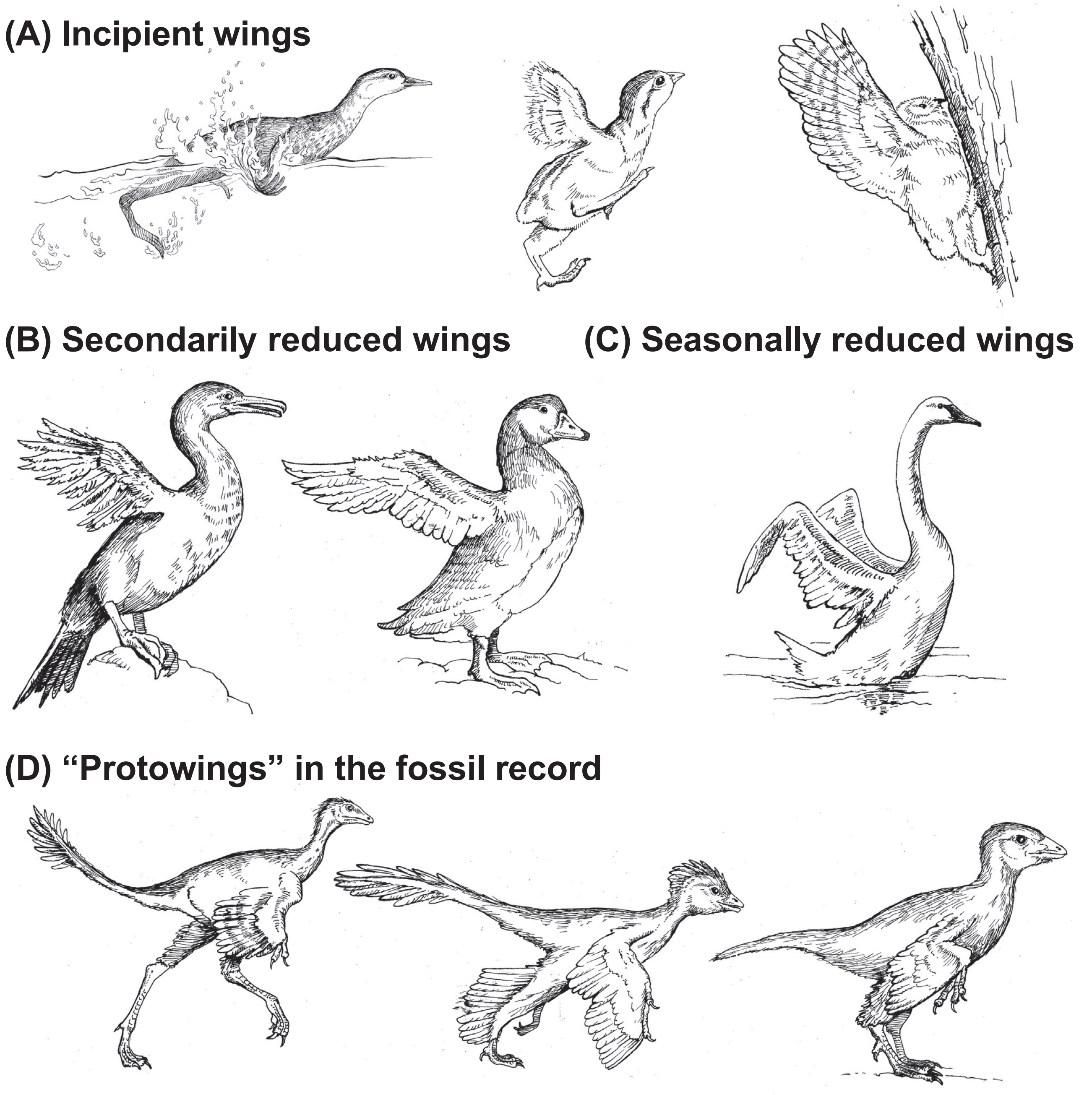

Figure 1. Rudimentary Wings. Rudimentary wings are widespread across the theropod-avian lineage, and are found (A) in all developing birds, (B) in secondarily flightless or semi-flightless birds, (C) in birds that molt their flight feathers simultaneously, and (D) among extinct theropods with 'protowings'. Although such structures are rarely examined empirically, studies clearly demonstrate that rudimentary wings can improve locomotor performance and enhance survival. From left to right: (A) Mallard duckling (*Anas platyrhynchos*), Chukar Partridge (*Alectoris chukar*), owlet Strigiformes); (B) Flightless Cormorant (*Phalacrocorax harrisi*), steamer-duck (*Tachyeres* sp.); (C) swan *(Cygnus* sp.); (D) *Caudipteryx*, *Anchiornis*, *Eosinopteryx*. Illustrations by Robert Petty.

wings as adults because increases in body mass outpace increases in wing area (Figure 2B). For example, in Indian Peafowl and Australian Brush-turkeys (*Alectura lathami*), wing performance of juveniles is greater than that of adults [25,52]. Similarly, Giant Coots

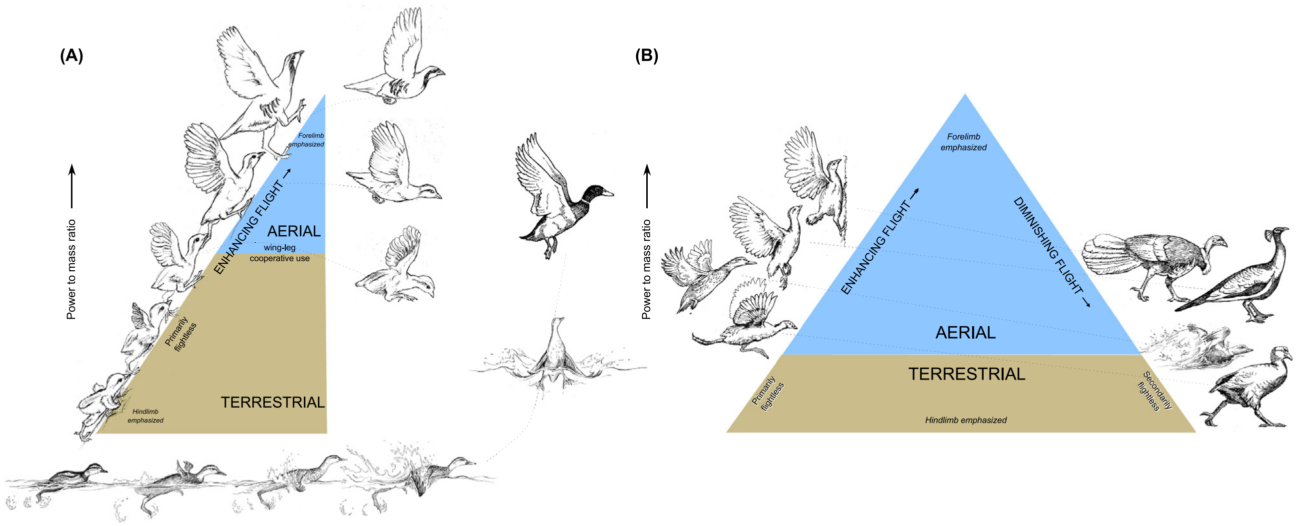

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Figure 2. Incipient Wings. This and all subsequent pyramids illustrate major parameters associated with the waxing and waning of wings: anatomy (more forelimb-dominated towards the top, more hindlimb-dominated towards the bottom), performance (power-to-mass ratio of wings, increasing towards the top), and habitat or substrate (brown indicates more terrestrial or aquatic, with leg-based locomotion; blue indicates more aerial, with wing-based locomotion). (A) Juvenile birds with small, incipient wings negotiate steep inclines or aquatic substrates by supplementing leg-based locomotion with their developing forelimbs. For example, immature Chukar Partridges (left side of pyramid) flap their wings to generate small aerodynamic forces that allow them to flap-run up steep obstacles by increasing foot traction. Improvements in aerodynamic performance allow chukars to flap-run up steeper inclines and eventually fly. Similarly, ducklings (below the pyramid) initially use their feet as paddles and their rudimentary, developing wings as oars to 'steam' across water, and later to fly. Whether terrestrial or aquatic, developing birds employ their wings to avoid predation, initially relying on transitional behaviors such as wing-assisted incline running (WAIR) or steaming, and later relying on powered flight – once the forelimbs mature enough to provide sufficient power for the body size of the animal. (B) Some species 'outgrow' their wings during ontogeny and exhibit reduced flight ability as adults due to increased wing loading and a reduced power-to-mass ratio. Giant Coots (*Fulica gigantea*; bottom), steamer-ducks (middle bottom), Indian Peafowl (*Pavo cristatus*; middle top), and Australian Brush-turkeys (*Alectura lathami*; top) all experience greater wing performance as juveniles than as adults – Giant Coots and some steamer-ducks can fly as juveniles but become flightless as adults, whereas peafowl and brush-turkey adults can still fly but are more leg-dependent than their immature counterparts. Illustrations by Robert Petty.

(*Fulica gigantea*) and some steamer-ducks (*Tachyeres* sp.) can fly as juveniles but must engage their wings and legs cooperatively as adults, by steaming [53,54]. Even large, flight-capable birds recruit their hindlimbs to take off (https://www.youtube.com/watch?v=vAuPH69ohZo). Body size is thus a key determinant of locomotion, and birds with proportionally small wings often rely heavily on wing–leg cooperation.

In summary, the rudimentary anatomical features observed in developing birds serve several important functions. Developing birds bridge flightless to flight-capable transitions, offset tradeoffs, compensate for low power, and often elude predators by recruiting their wings and legs cooperatively during transitional behaviors in habitats that act as stepping stones between leg- and wing-based locomotion. Collectively, these findings provide valuable insights into avian biology.

These insights can also be extrapolated to fossils via modeling techniques in which data from extant animals is used to explore function while accounting for anatomical differences between extant and extinct species ([55] for citations). Like developing birds, extinct theropods might have improved locomotor performance by engaging their legs and protowings cooperatively. Different scenarios (WAIR, wing-assisted running or leaping, four-winged gliding, etc.) can be tested by constructing models of fossils and determining whether the locomotor apparatus was consistent with the inferred behavior ([3,14,15] for citations of origin-of-flight scenarios). In short,

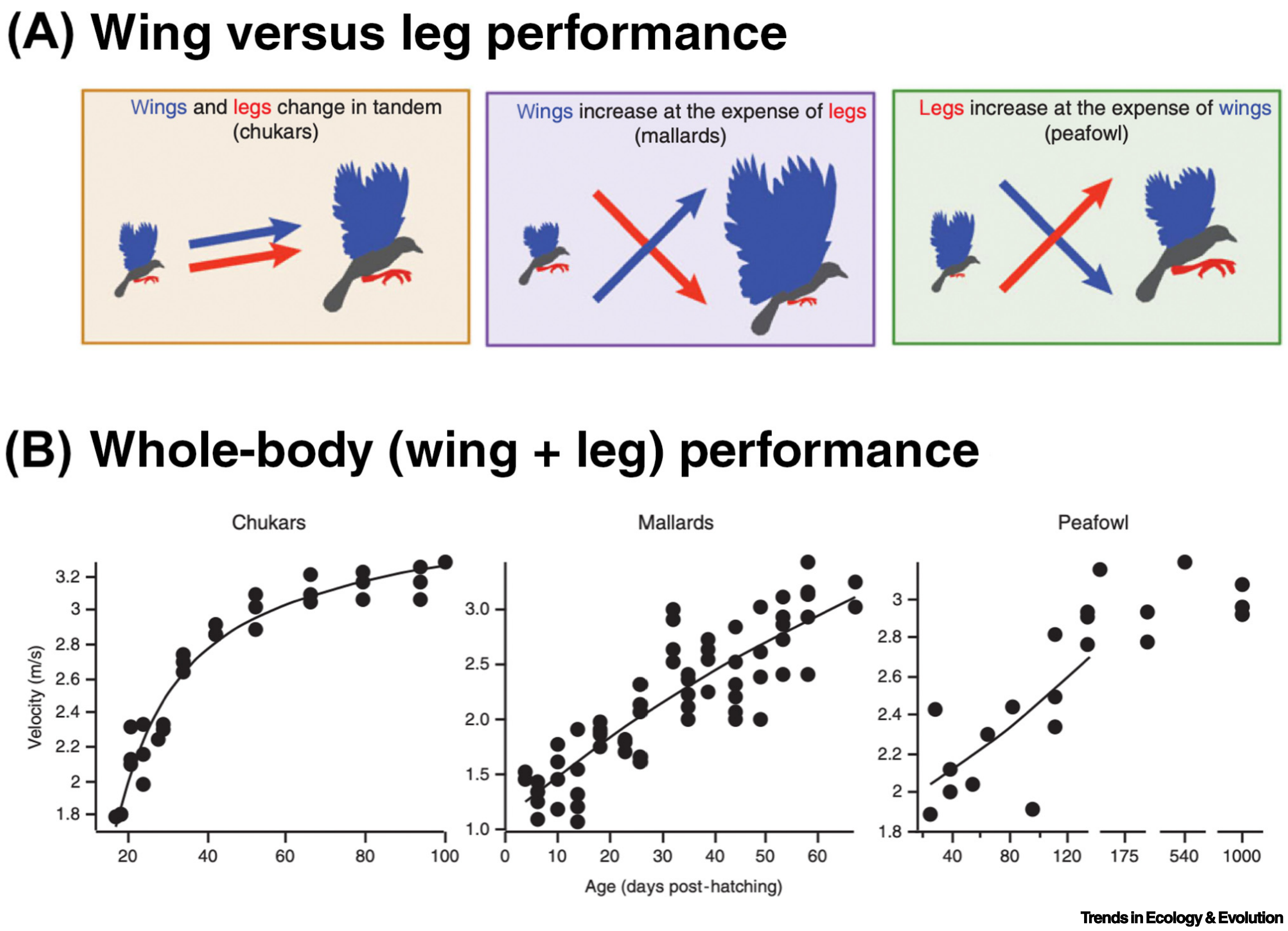

Figure 3. Tradeoffs between Wings and Legs. (A) Developing birds show different trajectories of wing versus leg growth and performance: in Chukar Partridges, wings and legs develop in tandem with moderate levels of performance, whereas in Mallards, wing performance increases at the expense of legs, and in Indian Peafowl the opposite occurs. (B) Despite such tradeoffs, whole-body performance improves when wings and legs are engaged cooperatively during behaviors such as vertical takeoff (chukars, peafowl) or steaming (ducks). Figure modified, with permission, from [25].

locomotor ontogeny has offered rich insight into form–function relationships and, in conjunction with work on other birds (see later), has the potential to greatly improve our understanding of the **theropod-avian lineage**.

Waxing and Waning of Wings: Seasonal Timescales

Rudimentary wings also occur in adult birds that are temporarily flightless due to **molting**. For example, many birds molt feathers sequentially (~one at a time), but some birds molt flight feathers simultaneously and become flightless for days [e.g., American Dippers (*Cinclus mexicanus*) [56]] to months [Eared Grebes (*Podiceps nigricollis*) [57]] (see Text S1 in the supplemental information online). These dramatic seasonal reductions in wing size and flight capacity occur across many taxa (Figure 4 and see Table S1 in the supplemental information online), and have been well studied in terms of body composition and resource allocation [58–60], activity budgets [61–64], habitat preferences [65–68], migratory patterns [57], and predation [67]. By contrast, how feather molt and recovery influence flight performance and behavior is largely unknown.

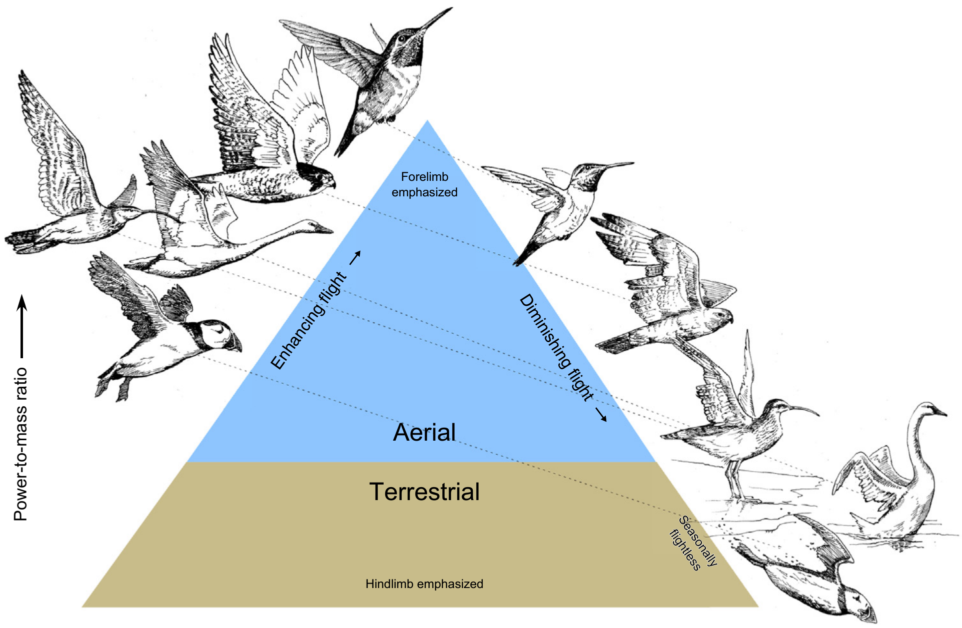

Figure 4. Seasonally Reduced Wings. All birds undergo annual or seasonal molts. Waxing and waning of wings thus occurs in ecological as well as evolutionary time. In species that molt all their flight feathers simultaneously, these changes are extreme but survivable because foraging and predator escape do not require aerial flight. Simultaneous molt and seasonal flightlessness is common and occurs across the avian clade – waterfowl (Anseriformes), cranes (Gruidae), rails (Rallidae), flamingos (Phoenicopteridae), grebes (Podicipedidae), wading birds (Scolopacidae), jacanas (Jacanidae), alcids (Alcidae), sunbirds (Heliornithidae), loons (Gaviidae), petrels and shearwaters (Procellariiformes), darters (Anhingidae), hornbills (Bucerotidae), and songbirds (Passeriformes) [56,68,78,79,82,90,127–147]. From bottom up: aquatic species such as alcids [puffin (*Fratercula* sp.)] become aerially flightless during simultaneous molt but are still capable of foraging underwater (aquatic flying) for prey. Swans are rendered flightless during wing molt but can reach submerged aquatic vegetation with their long necks and escape threat by using their hindlimbs to dive. Many waterfowl and shorebirds (e.g., Bristle-thighed Curlews, *Numenius tahitiensis*) fly to remote, predator-free locations to molt in safety. Although these represent extreme examples, even species that molt their flight feathers sequentially (i.e., they only lose a few feathers at a time), such as raptors (Falconiformes) and hummingbirds (Trochilidae), exhibit compromised flight ability during molt. Thus, wings wax and wane on seasonal timescales in all birds. Illustrations by Robert Petty.

Laboratory work suggests that molting wings are less effective but still functional because wing reductions can be at least partially compensated for, depending on the degree of feather loss [69–77]. In hawks (Falconiformes), passerines, and hummingbirds (Trochilidae) with sequential molts, feather loss has been associated with reductions in lift-to-drag ratio, flight speed, takeoff angle, maneuverability, and/or energetic efficiency. These effects are mitigated by weight loss, increases in flight muscle mass, changes in wing posture, and/or slow feather molting, to the extent that naturally molting birds may reduce activity and become more secretive but show very little reduction in flight performance. Birds that molt their flight feathers simultaneously clearly differ because flight capacity is severely impaired (lost) for a period of time. However, work with various water birds, hornbills (Bucerotidae), and passerines indicates that simultaneously molting birds similarly adopt strategies that compensate for feather loss and, in at least some cases, use their rudimentary wings for locomotion. These birds:

- Molt in a Safe Location where Aerial Flight Is Not Required
  Many birds migrate to secluded areas to shed their feathers, including wetlands and lakes, coastal waters, or remote islands [57,59,61,63,68,78–80]. These molting sites are often characterized by low predator abundance and offer alternative means of escape. For example, molting aquatic birds may run to water, swim into vegetation or deeper water, or dive to

avoid predation [59,63,65–68], and it is likely that rudimentary wings assist in these escapes by increasing swim speed (via steaming) or propelling divers [80].

- Adopt Secretive Behaviors that likely Reduce Predation Risk while Simultaneously Lowering Energy Expenditure

  These behaviors occur concomitantly with a reduction in [57,67,68,81,82]. Molting individuals typically become warier and may spend more time roosting, congregate in large flocks, shift to nocturnal foraging, or even delay post-molt migration to fly under the cover of longer nights.
- Reallocate Resources and Recruit the Hind Limbs.

  Just as shorebirds increase the size of digestive organs to refuel along migration routes (e.g., [83]), waterfowl adjust the size of their digestive organs throughout molt [57,84–86] (see Text S2 in the supplemental information online). In addition, wing molting is typically accompanied by atrophy of flight muscles, and this may reduce metabolic costs and provide protein for feather synthesis [57–60,87]. Many species partially compensate for this reduction through increases in leg muscle and use [57,58,60,84,86,88–91]. Nevertheless, rudimentary wings can play an important role in locomotion. For example, aquatic species such as alcids become aerially flightless during molt but still use their wings to forage underwater [80]. Similarly, many species begin to fly when their wings are still small, with as little as 62% feather regrowth [91–93]. Hind limb input is probably particularly important in these cases, for swimming to foraging sites or for initiating takeoff [94–97]. This reiterates the importance of wing–leg cooperation.
- Reacquire Flight through Temporary Mass Loss and/or Differential Organ Reabsorption

  Migratory birds are well known for reducing nonessential organs and reallocating mass to the heart and flight muscles (e.g., [83]). Molting birds often adopt a similar strategy, but to an extent that total body mass declines. Mass loss during molt may be a consequence of reduced foraging but may also shorten the flightless period: by reducing body mass and wing loading, power-to-mass ratios are improved and flight can be regained before feathers are fully regrown [64,91–93,98–100]. In species with long flightless periods (e.g., Eared Grebes), mass loss occurs long after feathers have regrown, but similarly reduces wing loading for migration [57]. Thus, small wings are used for locomotion in many recovering birds, and body size is a key moderator.

Many of these findings are consistent with strategies used by developing birds. For example, both developing and temporarily flight-impaired birds tend to be secretive and benefit from the safety provided by nests and parents or by remote molting locations. Like immature birds, molting birds are also highly leg-dependent and utilize unique modes of locomotion in carefully selected habitats. Developing birds rely on substrates that allow them to use their wings and legs cooperatively, whereas simultaneously molting birds elude predators by hiding, running, swimming, or diving, with varying contributions from the wings. Proportionally large legs and/or leg-based behaviors compensate for rudimentary wings, whereas increases in flight muscle are associated with decreases in leg muscle, and vice versa (tradeoffs). Total body mass also plays a key role in acquiring flight – mass loss allows many molting birds to fly when their wings are still small, just as developing birds become flight-capable when wing loading is low [51]. Collectively, these patterns suggest that simultaneously molting birds display many juvenile characteristics and behaviors.

Ultimately, temporary flightlessness is common and widespread, and molting birds bear many similarities to developing birds. Nevertheless, very few empirical data are available on wing function and locomotor performance as birds lose and regain their feathers. We know that the strategies deployed are sufficient because molting birds are able to compensate for wing loss with leg-dominated behaviors in selected habitats [68]. But how does locomotor performance and behavior vary with feather and muscle regrowth? Do molting birds adopt flapping behaviors similar to those observed among developing birds? Locomotion and survivorship are inextricably coupled [38], but these types of questions have not been explored.

Waxing and Waning of Wings: Evolutionary Timescales

We instinctively associate birds with flight, but not all birds fly well and some species have completely lost aerial flight [e.g., penguins (Sphenisciformes) and ostriches (Struthioniformes)]. **Secondary flightlessness** has evolved in many groups of birds, both extant (>15 families; see Table S2 in the supplementary information online) and long extinct (e.g., *Patagopteryx*, *Hesperornis*) [101,102]. In fact, only 2000 years ago there were many flightless species [11] that are now extinct as a result of hunting, habitat degradation, and/or introduced predators (see Text S3 in the supplementary information online for conservation implications). Our present-day paucity of flightless birds is not normal for the avian clade.

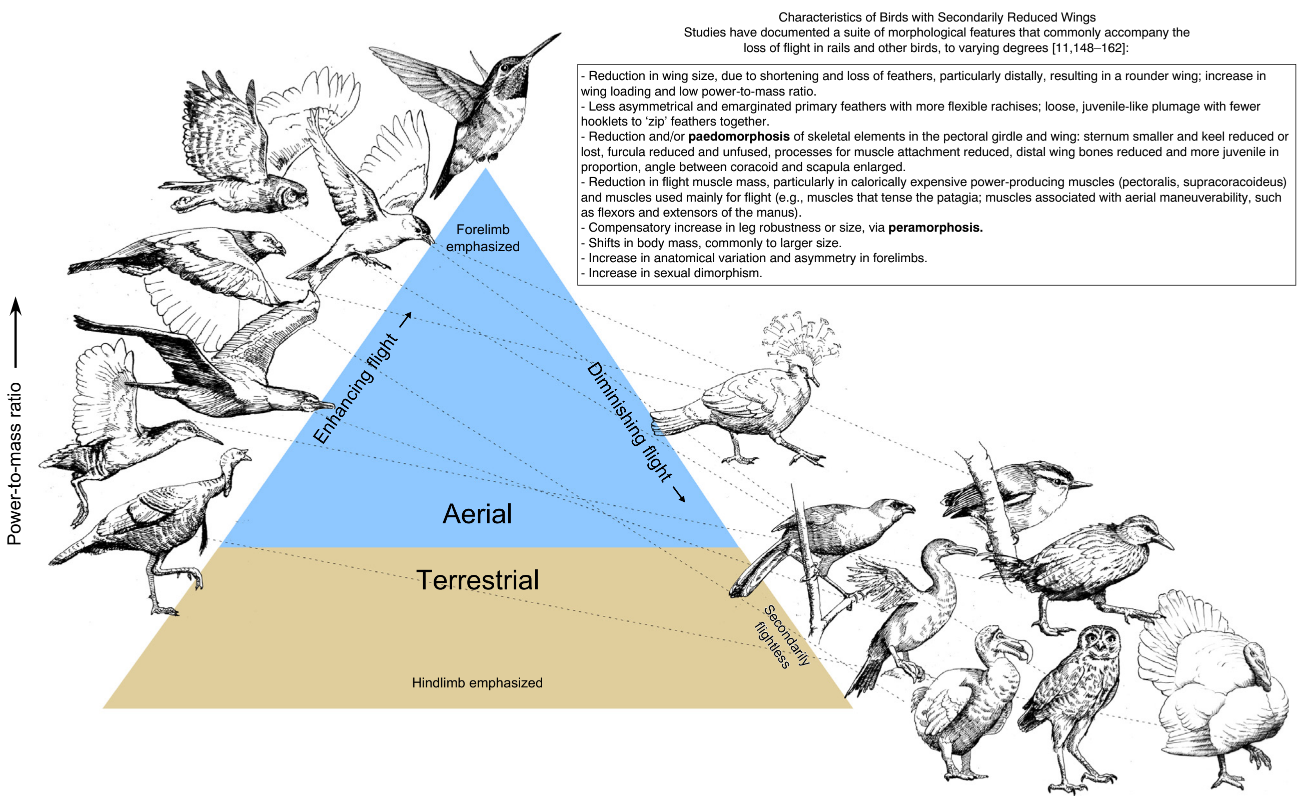

Figure 5. Secondarily Reduced Wings. Studies have documented a suite of morphological features that commonly accompany the loss of flight in rails and other birds, to varying degrees [11,148–162]. Some flightless birds possess most of these features, whereas others exhibit a mosaic of traits depending on their ecological requirements. For example, ostriches and rheas (Struthioniformes) retain long wing feathers for courtship display but have lost flight-muscle mass [10]. Penguins (Sphenisciformes) have done the reverse, losing the long flight feathers their ancestors must have possessed but augmenting the pectoral muscles that power underwater 'flight' [163,164]. Many living and recently extinct birds have extremely reduced wings compared with relatives that retain superior flight capacity. These secondarily flightless or semi-flightless birds occur in areas with reduced predation, year-round food supply, and moderate climate. For example, rails (Rallidae), cormorants (Phalacrocoracidae), pigeons (Columbidae), owls, and even passerines (Passeriformes) have become flightless or semi-flightless on remote, historically predator-free islands. Similarly, in the safety of their enclosures, several domesticated birds such as turkeys - have been bred for fast growth and large size, and, in the process, have outgrown their wings and lost flight. From bottom to top, left side then right: Wild Turkey (*Meleagris gallopavo*); King Rail (*Rallus elegans*); cormorant; Rock Pigeon (*Columba livia*); American Goldfinch (*Spinus tristis*); Great Horned Owl (*Bubo virginianus*); hummingbird; Dodo (*Raphus cucullatus*; extinct) of Mauritius; Giant Owl (*Ornimegalonyx* sp.; extinct) of Cuba; domesticated turkey; Flightless Cormorant - of the Galapagos Islands; Weka (*Gallirallus australis*), Kōkako (*Callaeas sp.*), and Rifleman (*Acanthisitta chloris*) of New Zealand; Victoria Crowned Pigeon (*Goura victoria*) of New Guinea. Illustrations by Robert Petty. See [11,148–162].

Despite such losses (or perhaps because of them), secondarily flightless birds have been well studied (see Text S4 in the supplementary information online). As previous authors have pointed out, these birds share many anatomical similarities with developing birds and extinct theropods (Figures 1A and 5) and, like immature and simultaneously molting birds, require safe habitats and food that can be acquired without flight. Thus, flightless birds are often leggy compared with their volant relatives. Leg-dominated, flightless birds have historically been successful – in some cases becoming apex predators [103–105] – and they are not the only birds with permanently reduced wings. Although we have traditionally categorized birds as flying or flightless, this binary terminology actually masks tremendous natural variation in anatomy and flight capacity. In many habitats, birds have reduced flight capacity compared with their relatives and are best characterized as **semi-flightless**.

Semi-flightless birds are rarely discussed and poorly studied, but are very common and widespread (Figure 5). For example, in North America, roadrunners (*Geococcyx* sp.; Cuculiformes) and Burrowing Owls *(Athene cunicularia)* have reduced wings and are more terrestrial than their relatives [106,107]. In the tropics, many birds are highly sedentary and forage mainly on foot through dense vegetation, flying only for short distances (<100 m) [108,109]. Similarly, the Rifleman *(Acanthisitta chloris*; Passeriformes*)* of New Zealand flutters briefly between trees to forage. In South America, the Giant Coot outgrows its wings during ontogeny and likely becomes flightless as an adult, instead using its wings to steam across water [53]. In short, there are many examples of birds with small wings and reduced flight. Although most have only been documented anecdotally (see Table S3 in the supplementary information online), two well-studied groups reveal several similarities with developing and simultaneously molting birds, and reiterate the utility of rudimentary structures:

- Steamer-ducks

  The steamer-ducks of South America have reduced but functional wings. This group shows high variation in flight capacity, across species, populations, sexes, and even within individuals – some birds may become flightless after molting or large meals, and many are likely flight-capable as juveniles but flightless as adults [54,110–112]. This mixed-flight capacity has also been reported in a rail (Rallidae) [113] and among seasonally flightless or migratory birds. Regardless of flight capacity, all steamer-ducks maintain robust pectoral muscles and recruit their wings and legs cooperatively to steam across water [54,114,115], similarly to juvenile ducks or alcids that use their molting wings to swim underwater.
- Island Birds

  Flightlessness is highly associated with islands, and recent evidence reveals that even island birds that are still capable of flight have evolved smaller flight muscles and longer legs than their continental relatives [97]. Such changes are more pronounced on islands with fewer predators, and seem to reflect a shift in investment from wings to legs. This 'avian island rule' applies to hundreds of species, including wing-dominated birds, suggesting that longer legs help to compensate for smaller wings during power-demanding behaviors such as takeoff, while reducing the energy requirements associated with maintaining large flight muscles [97]. In several respects semi-flightless island birds are thus similar to juvenile and perhaps simultaneously molting birds: they have proportionally smaller wings and larger legs, and rely on wing–leg cooperation.

In short, there are examples of birds with reduced wings all over the world and across the avian clade. These birds demonstrate that flight capacity is more of a gradation (flightless <–> semi-flightless <–> strong flight) than a dichotomous characteristic (flightless versus flight). Nevertheless, with few exceptions, wing contributions to locomotion in flightless or semi-flightless birds have not been explored (see Text S5 in the supplementary information online for a potential starting point). In the species that have been studied, reduced wings enhance locomotion. Collectively, developing, molting, and secondarily flight-impaired birds thus reveal that rudimentary structures can play important roles in locomotor behavior and performance.

Concluding Remarks

Developing birds with incipient wings and adult birds with temporarily or secondarily reduced wings collectively reveal that rudimentary wings are ubiquitous across the avian clade. Birds have often been categorized as flight-capable or flightless, but this binary terminology masks tremendous natural variation. In reality, flight capacity is a continuum (flightless <–> semi-flightless <–> strong flight), and rudimentary wings are more of a rule than an exception. This continuum offers a powerful but underappreciated system for exploring relationships between form, function, performance, behavior, ecology, and evolution, on multiple timescales.

In extant birds, rudimentary wings improve locomotor performance and enhance survival. Birds that have small wings with low power-to-mass ratios bridge flightless to flight-capable transitions, compensate for tradeoffs between wings and legs, and often elude predators by recruiting their wings and legs cooperatively during transitional behaviors in carefully selected habitats. Although sparsely studied and sometimes considered 'useless', rudimentary wings are often crucial for survival and can have selective value without flight capability.

Rudimentary, waxing or waning wings have probably been prevalent among birds since their beginning ~150 million years ago. Early winged fossils show substantial variation in wing and leg proportions, and secondary wing reductions are known for several groups [116–120]. This diversity is not present in all flying animals. Bats (Chiroptera), for example, show far less variation in limb proportions and behavior (there are no flightless bats), presumably because their legs are incorporated into their flight apparatus rather than functioning as a separate locomotor module [121]. Modularity thus facilitates the waxing and waning of wings among birds and likely contributes to diversity on short and long timescales.

Collectively, this evidence indicates that rudimentary structures can be functional, and are perhaps an intrinsic component of many clades (e.g., birds, fish, insects, amphibians, marsupials [122–126]). Among birds, we predict that small wings and reduced flight are much more common than has been appreciated, particularly among groups that have well-developed legs or live in habitats where sustained flight may not be necessary for escape or foraging (e.g., near water, in dense vegetation, or in remote locations). We also predict that birds with reduced wings not only have juvenile morphologies, but also display juvenile or basal behaviors involving the cooperative use of all four limbs. Although our understanding is still in its infancy (see Outstanding Questions), rudimentary structures likely enhance survival on multiple timescales in birds and many other animals – both extant and long extinct.

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Declaration of Interests

The authors declare no conflicts of interest.

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References

1. Mivart, S.G.J. (1871) *On the Genesis of Species*, Appleton
2. Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, Murray
3. Heers, A.M. and Dial, K.P. (2012) From extant to extinct: locomotor ontogeny and the evolution of avian flight. *Trends Ecol. Evol.* 27, 296–305
4. Qiang, J. *et al.* (1998) Two feathered dinosaurs from northeastern China. *Nature* 393, 753–761
5. Foth, C., Rauhut, O.W.M., eds (2020) *The Evolution of Feathers*, Springer
6. Fong, D.W. *et al.* (1995) Vestigialization and loss of nonfunctional characters. *Annu. Rev. Ecol. Evol. Syst.* 26, 249–268
7. Senter, P. and Moch, J.G. (2015) A critical survey of vestigial structures in the postcranial skeletons of extant mammals. *PeerJ* 3, e1439
8. Smith, H.F. and Wright, W. (2018) Vestigial organ. In *Encyclopedia of Animal Cognition and Behavior* (Vonk, J. and Shackelford, T., eds), pp. 1–6, Springer International Publishing
9. Starck, J.M., Ricklefs, R.E., eds (1998) *Avian Growth and Development: Evolution Within the Altricial-Precocial Spectrum*, Oxford University Press
10. Roots, C. (2006) *Flightless Birds*, Greenwood Press
11. Livezey, B.C. (2003) *Evolution of Flightlessness in Rails (Gruiformes: Rallidae): Phylogenetic, Ecomorphological, and Ontogenetic Perspectives*, American Ornithologists' Union
12. Feduccia, A. *et al.* (2005) Do feathered dinosaurs exist? Testing the hypothesis on neontological and paleontological evidence. *J. Morphol.* 266, 125–166
13. Novas, F.E. *et al.* (2020) Pectoral girdle morphology in early-diverging paravians and living ratites: implications for the origin of flight. *Bull. Am. Mus. Nat. Hist.* 440, 345–353
14. Dececchi, T.A. *et al.* (2016) The wings before the bird: an evaluation of flapping-based locomotory hypotheses in bird antecedents. *PeerJ* 4, e2159
15. Pittman, M. and Xu, X. (2020) Pennaraptoran theropod dinosaurs: past progress and new frontiers. *Bull. Am. Mus. Nat. Hist.* 440, 1–355
16. Dial, K.P. (2017) Waxing and waning of wings during molt, growth, and secondary loss of flight in birds. In *Proceedings of the Society for Integrative and Comparative Biology 2017 Annual Meeting, A83-1*
17. Gould, S.J. (1985) Not necessarily a wing. *Nat. Hist.* 94, 12–25
18. Bock, W. (1986) The arboreal origin of avian flight. *Mem. Calif. Acad. Sci.* 8, 57–72
19. Vazquez, R.J. (1992) Functional osteology of the avian wrist and the evolution of flapping flight. *J. Morphol.* 211, 259–268
20. Nudds, R.L. and Dyke, G.J. (2010) Narrow primary feather rachises in *Confuciusornis* and *Archaeopteryx* suggest poor flight ability. *Science* 328, 887–889
21. Butler, P.J. (1991) Exercise in birds. *J. Exp. Biol.* 160, 233–262
22. Dial, K.P. (2003) Wing-assisted incline running and the evolution of flight. *Science* 299, 402–404
23. Dial, K.P. *et al.* (2008) A fundamental avian wing-stroke provides a new perspective on the evolution of flight. *Nature* 451, 985–989
24. Dial, T.R. and Carrier, D.R. (2012) Precocial hindlimbs and altricial forelimbs: partitioning ontogenetic strategies in mallard ducks (*Anas platyrhynchos*). *J. Exp. Biol.* 215, 3703–3710
25. Heers, A.M. and Dial, K.P. (2015) Wings versus legs in the avian bauplan: development and evolution of alternative locomotor strategies. *Evolution* 69, 305–320
26. Dial, K.P. *et al.* (2015) Ontogenetic and evolutionary transformations: the ecological significance of rudimentary structures. In *Great Transformations in Vertebrate Evolution* (Dial, K.P. *et al.*, eds), pp. 283–301, University of Chicago Press
27. Heers, A.M. *et al.* (2016) Flapping before flight: high resolution, three-dimensional skeletal kinematics of wings and legs during avian development. *PLoS One* 11, e0153446
28. Tobalske, B.W. and Dial, K.P. (2007) Aerodynamics of wing-assisted incline running in birds. *J. Exp. Biol.* 210, 1742–1751
29. Heers, A.M. *et al.* (2011) Ontogeny of lift and drag production in ground birds. *J. Exp. Biol.* 214, 717–725
30. Thomas, B.T. (1996) Family Opisthocomidae (Hoatzin). In *Handbook of the Birds of the World. Vol. 3: Hoatzin to Auks* (Del Hoyo, J. *et al*., eds), pp. 24–33, Lynx Edicions
31. Marks, J.S. (1982) Night stalkers along the Snake. *I Wildl.* 3, 18–21
32. Marks, J.S. (1986) Nest-site characteristics and reproductive success of long-eared owls in Southwestern Idaho. *Wilson Bull.* 98, 547–560
33. Martin, T.E. (1995) Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol. Monogr.* 65, 101–127
34. Carrier, D.R. (1996) Ontogenetic limits on locomotor performance. *Physiol. Zool.* 69, 467–488
35. Herrel, A. and Gibb, A.C. (2006) Ontogeny of performance in vertebrates. *Physiol. Biochem. Zool.* 79, 1–6
36. Robinson, A.C. *et al.* (2009) Chukar seasonal survival and probable causes of mortality. *J. Wildl. Manag.* 73, 89–97
37. Cheng, Y.-R. and Martin, T.E. (2012) Nest predation risk and growth strategies of passerine species: grow fast or develop traits to escape risk? *Am. Nat.* 180, 285–295
38. Martin, T.E. *et al.* (2018) Age and performance at fledging are a cause and consequence of juvenile mortality between life stages. *Sci. Adv.* 4, eaar1988
39. Jones, T.M. and Ward, M.P. (2020) Pre- to post-fledging carryover effects and the adaptive significance of variation in wing development for juvenile songbirds. *J. Anim. Ecol.* 89, 2235–2245
40. McMahon, T.A. *et al.* (1983) *On Size and Life*, Scientific American Library
41. Biewener, A. (1989) Scaling body support in mammals: limb posture and muscle mechanics. *Science* 245, 45–48
42. Dial, K.P. *et al.* (2008) Allometry of behavior. *Trends Ecol. Evol.* 23, 394–401
43. Hill, A.V. (1950) The dimensions of animals and their muscular dynamics. *Sci. Prog.* 38, 209–230
44. Pennycuick, C.J. (1975) Mechanics of flight. *J. Avian Biol.* 5, 1–75
45. Marden, J.H. (1987) Maximum lift production during takeoff in flying animals. *J. Exp. Biol.* 130, 235–258
46. Marden, J.H. (1994) From damselflies to pterosaurs: how burst and sustainable flight performance scale with size. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 266, 1077–1084
47. Tobalske, B.W. and Dial, K.P. (2000) Effects of body size on take-off flight performance in the Phasianidae (Aves). *J. Exp. Biol.* 203, 3319–3332
48. Altshuler, D.L. *et al.* (2010) Allometry of hummingbird lifting performance. *J. Exp. Biol.* 213, 725–734
49. Jackson, B.E. and Dial, K.P. (2011) Scaling of mechanical power output during burst escape flight in the Corvidae. *J. Exp. Biol.* 214, 452–461
50. Blackburn, T.M. and Gaston, K.J. (1994) The distribution of body sizes of the world's bird species. *Oikos* 70, 127–130
51. Jackson, B.E. *et al.* (2009) Precocial development of locomotor performance in a ground-dwelling bird (*Alectoris chukar*): negotiating a three-dimensional terrestrial environment. *Proc. R. Soc. B* 276, 3457–3466
52. Dial, K.P. and Jackson, B.E. (2011) When hatchlings outperform adults: locomotor development in Australian brush turkeys (*Alectura lathami*, Galliformes). *Proc. R. Soc. B* 278, 1610–1616

53. Fjeldsa, J. (1981) Biological notes on the giant coot *Fulica gigantea*. *Ibis* 123, 423–437
54. Livezey, B.C. and Humphrey, P.S. (1986) Flightlessness in steamer-ducks (Anatidae: *Tachyeres*): its morphological bases and probable evolution. *Evolution* 40, 540–558
55. Pittman, M. *et al.* (2020) Methods of studying early theropod flight. *Bull. Am. Mus. Nat. Hist.* 440, 277–294
56. Price, F.E. and Bock, C.E. (1983) Population ecology of the dipper (*Cinclus mexicanus*) in the Front Range of Colorado. *Stud. Avian Biol.* 7, 1–84
57. Jehl, J.R. (1997) Cyclical changes in body composition in the annual cycle and migration of the eared grebe *Podiceps nigricollis*. *J. Avian Biol.* 28, 132–142
58. Young, D.A. and Boag, D.A. (1982) Changes in physical condition of male mallards (*Anas platyrhynchos*) during moult. *Can. J. Zool.* 60, 3220–3226
59. Hohman, W.L. (1993) Body composition dynamics of ruddy ducks during wing moult. *Can. J. Zool.* 71, 2224–2228
60. Portugal, S.J. *et al.* (2009) Testing the use/disuse hypothesis: pectoral and leg muscle changes in captive barnacle geese *Branta leucopsis* during wing moult. *J. Exp. Biol.* 212, 2403–2410
61. Austin, J.E. (1987) Activities of postbreeding lesser scaup in Southwestern Manitoba. *Wilson Bull.* 99, 448–456
62. Thompson, J.E. (1992) *The Nutritional Ecology of Molting Male Canvasbacks (Aythya valisineria) in Central Alberta*, University of Missouri
63. Frimer, O. (1994) The behaviour of moulting king eiders *Somateria spectabilis*. *Wildfowl* 45, 176–187
64. Adams, P.A. *et al.* (2000) Time-activity budgets of harlequin ducks molting in the Gannet Islands, Labrador. *Condor* 102, 703–708
65. Kortegaard, L. (1974) An ecological outline of a moulting area of Teal, Vejlerne, Denmark. *Wildfowl* 25, 134–142
66. Derksen, D.V. *et al.* (1982) Habitat ecology of Pacific black brant and other geese moulting near Teshekpuk Lake, Alaska. *Wildfowl* 33, 39–57
67. Kahlert, J. *et al.* (1996) Nocturnal feeding in moulting greylag geese *Anser anser* – an anti-predator response? *Ardea* 84, 15–22
68. Fox, A.D. *et al.* (2014) Waterfowl habitat use and selection during the remigial moult period in the northern hemisphere. *Wildfowl (Special Issue)* 131–168
69. Tucker, V.A. (1991) The effect of molting on the gliding performance of a Harris' hawk (*Parabuteo unicinctus*). *Auk* 108, 108–113
70. Slagsvold, T. and Dale, S. (1996) Disappearance of female pied flycatchers in relation to breeding stage and experimentally induced molt. *Ecology* 77, 461–471
71. Chai, P. (1997) Hummingbird hovering energetics during moult of primary flight feathers. *J. Exp. Biol.* 200, 1527
72. Swaddle, J.P. and Witter, M.S. (1997) The effects of molt on the flight performance, body mass, and behavior of European starlings (*Sturnus vulgaris*): an experimental approach. *Can. J. Zool.* 75, 1135–1146
73. Chai, P. and Dudley, R. (1999) Maximum flight performance of hummingbirds: capacities, constraints, and trade-offs. *Am. Nat.* 153, 398–411
74. Lind, J. (2001) Escape flight in moulting tree sparrows (*Passer montanus*). *Funct. Ecol.* 15, 29–35
75. Lind, J. and Jakobsson, S. (2001) Body building and concurrent mass loss: flight adaptations in tree sparrows. *Proc. R. Soc. B* 268, 1915–1919
76. Hedenström, A. (2003) Flying with holey wings. *J. Avian Biol.* 34, 324–327
77. KleinHeerenbrink, M. and Hedenström, A. (2017) Wake analysis of drag components in gliding flight of a jackdaw (*Corvus monedula*) during moult. *Interface Focus* 7, 20160081
78. Marks, J.S. (1993) Molt of bristle-thighed curlews in the northwestern Hawaiian islands. *Auk* 110, 573–587
79. Marks, J.S. and Redmond, R.L. (1994) Migration of bristle-thighed curlews on Laysan Island: timing, behavior and estimated flight range. *Condor* 96, 316–330
80. Bridge, E.S. (2004) The effects of intense wing molt on diving in alcids and potential influences on the evolution of molt patterns. *J. Exp. Biol.* 207, 3003
81. Bailey, R.O. (1982) *The Postbreeding Ecology of the Redhead Duck (Aythya Americana) on Long Island Bay, Lake Winnepegosis, Manitoba*, McDonald College of McGill University
82. Folk, M.J. *et al.* (2008) Feather molt of nonmigratory whooping cranes in Florida. *N. Am. Crane Workshop Proc.* 164, 128–132
83. Piersma, T. *et al.* (1999) Rapid changes in the size of different functional organ and muscle groups during refueling in a long-distance migrating shorebird. *Physiol. Biochem. Zool.* 72, 405–415
84. Ankney, C.D. (1984) Nutrient reserve dynamics of breeding and molting brant. *Auk* 101, 361–370
85. DuBowy, P.J. (1985) Seasonal organ dynamics in post-breeding male blue-winged teal and northern shovelers. *Comp. Biochem. Physiol. A Physiol.* 82, 899–906
86. Fox, A.D. and Kahlert, J. (2005) Changes in body mass and organ size during wing moult in non-breeding greylag geese *Anser*. *J. Avian Biol.* 36, 538–548
87. Guillemette, M. *et al.* (2007) Flightlessness and the energetic cost of wing molt in a large sea duck. *Ecology* 88, 2936–2945
88. Ankney, C.D. (1979) Does the wing molt cause nutritional stress in lesser snow geese? *Auk* 96, 68–72
89. Holly, R.G. *et al.* (1980) Stretch-induced growth in chicken wing muscles: a new model of stretch hypertrophy. *Am. J. Physiol. Cell Physiol.* 238, C62–C71
90. Gaunt, A.S. *et al.* (1990) Rapid atrophy and hypertrophy of an avian flight muscle. *Auk* 107, 649–659
91. Brown, R.E. and Saunders, D.K. (1998) Regulated changes in body mass and muscle mass in molting blue-winged teal for an early return to flight. *Can. J. Zool.* 76, 26–32
92. Panek, M. and Majewski, P. (1990) Remex growth and body mass of mallards during wing molt. *Auk* 107, 255–259
93. Taylor, E.J. (1995) Molt of black brant (*Branta bernicla nigricans*) on the Arctic Coastal Plain, Alaska. *Auk* 112, 904–919
94. Earls, K.D. (2000) Kinematics and mechanics of ground take-off in the starling *Sturnis vulgaris* and the quail *Coturnix*. *J. Exp. Biol.* 203, 725–739
95. Tobalske, B.W. *et al.* (2004) Take-off mechanics in hummingbirds (Trochilidae). *J. Exp. Biol.* 207, 1345–1352
96. Provini, P. and Abourachid, A. (2018) Whole-body 3D kinematics of bird take-off: key role of the legs to propel the trunk. *Sci. Nat.* 105, 12
97. Wright, N.A. *et al.* (2016) Predictable evolution toward flightlessness in volant island birds. *Proc. Natl. Acad. Sci.* 113, 4765–4770
98. Douthwaite, R.J. (1976) Weight changes and wing moult in the red-billed teal. *Wildfowl* 27, 123–127
99. Owen, M. and Ogilvie, M.A. (1979) Wing molt and weights of barnacle geese in Spitsbergen. *Condor* 81, 42–52
100. Sjoberg, K. (1988) The flightless period of free-living male teal *Anas crecca* in Northern Sweden. *Ibis* 130, 164–171
101. Marsh, O.C. (1880) Odontornithes: a monograph on the extinct toothed birds of North America. *Prof. Paper Engineer. Dept U.S. Army* 18, 1–201
102. Alvarenga, H.M.F. and Bonaparte, J.F. (1992) A new flightless landbird from the Cretaceous of Patagonia. *Los Angeles County Museum Nat. Hist. Sci. Ser.* 36, 51–64
103. Dingus, L. and Rowe, T. (1998) *The Mistaken Extinction: Dinosaur Evolution and the Origin of Birds*, WH Freeman
104. Chiappe, L.M., Witmer, L.M., eds (2002) *Mesozoic Birds: Above the Heads of Dinosaurs*, University of California Press
105. Chiappe, L.M. (2007) *Glorified Dinosaurs: The Origin and Early Evolution of Birds*, Wiley-Liss
106. Sibley, D.A. (2009) *The Sibley Guide to Bird Life and Behavior*, Alfred A. Knopf Inc.
107. Engels, W.L. (1938) Cursorial adaptations in birds. Limb proportions in the skeleton of *Geococcyx*. *J. Morphol.* 63, 207–217
108. Moore, R.P. *et al.* (2008) Experimental evidence for extreme dispersal limitation in tropical forest birds. *Ecol. Lett.* 11, 960–968
109. Karr, J.R. (1971) Ecological, behavioral, and distributional notes on some Central Panamá Birds. *Condor* 73, 107–111

110. Humphrey, P.S. and Livezey, B.C. (1982) Flightlessness in flying steamer-ducks. *Auk* 99, 368–372
111. Livezey, B.C. and Humphrey, P.S. (1983) Mechanics of steaming in steamer-ducks. *Auk* 100, 485–488
112. Fulton, T.L. *et al.* (2012) Multiple losses of flight and recent speciation in steamer ducks. *Proc. R. Soc. B* 279, 2339–2346
113. Feduccia, A. (1980) *The Age of Birds*, Harvard University Press
114. Cunningham, R.O. (1871) On some points in the anatomy of the steamer duck (*Micropterus cinereus*). *Trans. Zool. Soc. London* 7, 493–501
115. Lowe, P.R. (1934) On the evidence for the existence of two species of steamer duck (*Tachyeres*), and primary and secondary flightlessness in birds. *Ibis* 76, 467–495
116. Godefroit, P. *et al.* (2013) Reduced plumage and flight ability of a new Jurassic paravian theropod from China. *Nat. Commun.* 4, 1394
117. Wellnhofer, P. (2009) *Archaeopteryx: The Icon of Evolution*, Pfeil Verlag
118. Xu, X. *et al.* (2003) Four-winged dinosaurs from China. *Nature* 421, 335–340
119. Martin, L.D. and Tate, J. (1976) The skeleton of *Baptornis advenus* (Aves: Hesperornithiformes). In *Collected Papers in Avian Paleontology Honoring the 90th Birthday of Alexander Wetmore* (Olson, S.L., ed.), pp. 35–66, Smithsonian Institution Press
120. Xu, X. *et al.* (2015) A bizarre Jurassic maniraptoran theropod with preserved evidence of membranous wings. *Nature* 521, 70–73
121. Gatesy, S.M. and Dial, K.P. (1996) Locomotor modules and the evolution of avian flight. *Evolution* 50, 331–340
122. Standen, E.M. *et al.* (2014) Developmental plasticity and the origin of tetrapods. *Nature* 513, 54–58
123. Marden, J.H. and Kramer, M.G. (1994) Surface-skimming stoneflies: a possible intermediate stage in insect flight evolution. *Science* 266, 427–430
124. Landberg, T. and Azizi, E. (2010) Ontogeny of escape swimming performance in the spotted salamander. *Funct. Ecol.* 24, 576–587
125. Clack, J.A. (2011) The fin to limb transition: new data, interpretations, and hypotheses from paleontology and developmental biology. *Annu. Rev. Earth Planet. Sci.* 37, 163–179
126. Smith, K.K. (2006) Craniofacial development in marsupial mammals: Developmental origins of evolutionary change. *Dev. Dyn.* 235, 1181–1193
127. Moreau, E. (1937) The comparative breeding biology of the African hornbills (Bucerotidæ). *Proc. Zool. Soc. A* A107, 331–346
128. Salomonsen, F. (1950) *The Birds of Greenland*, Ejnar Munksgaard
129. Marshall, A.J. and Serventy, D.L. (1956) Moult adaptation in relation to long-distance migration in petrels. *Nature* 177, 943
130. Owre, O.T. (1967) Adaptations for locomotion and feeding in the *Anhinga* and the double-crested cormorant. *Ornithol. Monogr.* 6, 1–138
131. Woolfenden, G.E. (1967) Selection for a delayed simultaneous wing molt in loons (Gaviidae). *Wilson Bull.* 79, 416–420
132. Haukioja, E. (1971) Flightlessness in some moulting passerines in Northern Europe. *Ornis Fenn* 48, 101–116
133. Green, G.H. and Summers, R.W. (1975) Snow bunting moult in Northeast Greenland. *Bird Study* 22, 9–17
134. Sileo, L. *et al.* (1977) Plumages and primary moult in lesser flamingos. *Wildfowl* 28, 139–142
135. Bradstreet, M.S.W. (1982) Pelagic feeding ecology of dovekies, *Alle*, in Lancaster Sound and Western Baffin Bay. *Arctic* 35, 126–140
136. Storer, R.W. and Jehl, J.R. (1985) Moult patterns and moult migration in the black-necked grebe *Podiceps nigricollis*. *Ornis Scand.* 16, 253–260
137. Piersma, T. (1987) Population turnover in groups of wing-moulting waterbirds: the use of a natural marker in great crested grebes. *Wildfowl* 38, 37–45
138. Piersma, T. (1988) The annual molt cycle of great crested grebes. *Ardea* 76, 82–95
139. Espino-Barros, R. and Baldassarre, G.A. (1989) Activity and habitat-use patterns of breeding Caribbean flamingos in Yucatan, Mexico. *Condor* 91, 585–591
140. Jehl, J.R. (1990) Aspects of the molt migration. In *Bird Migration* (Gwinner, E., ed.), pp. 102–113, Springer-Verlag
141. Taylor, B. (1998) *Rails: A Guide to the Rails, Crakes, Gallinules and Coots of the World*, Yale University Press
142. Thompson, C.W. *et al.* (1998) An unusual sequence of flight-feather molt in common murres and its evolutionary implications. *Auk* 115, 653–669
143. Studer-Thiersch, A. (2000) What 19 years of observation on captive greater flamingos suggests about adaptations to breeding under irregular conditions. *Waterbirds* 23, 150–159
144. Bridge, E.S. (2006) Influences of morphology and behavior on wing-molt strategies in seabirds. *Mar. Ornithol.* 34, 7–19
145. Nesbitt, S.A. and Schwikert, S.T. (2008) Timing of molt in Florida sandhill cranes. *N. Am. Crane Workshop Proc.* 192, 125–127
146. Howell, S.N.G. (2010) *Molt in North American Birds* (1st edn), Houghton Mifflin Harcourt
147. Stanback, M. *et al.* (2018) The simultaneous moult of female hornbills is not triggered by the darkness of their nest cavity. *Ostrich* 89, 373–375
148. Lowe, P.R. (1928) A description of *Atlantisia rogersi*, the diminutive and flightless rail of inaccessible island (Southern Atlantic), with some notes on flightless rails. *Ibis* 70, 99–131
149. Snow, B.K. (1966) Obervations on the behaviour and ecology of the flightless cormorant *Nannopterum harrisi*. *Ibis* 108, 265–280
150. Olson, S.L. and Wetmore, A. (1976) Preliminary diagnoses of two extraordinary new genera of birds from Pleistocene deposits in the Hawaiian Islands. *Proc. Biol. Soc. Wash.* 89, 247–258
151. Olson, S.L. and Steadman, D.W. (1977) A new genus of flightless ibis (Threskiornithidae) and other fossil birds from cave deposits in Jamaica. *Proc. Biol. Soc. Wash.* 90, 447–457
152. James, H.F. and Olson, S.L. (1983) Flightless birds. *Nat. Hist.* 92, 30–41
153. Livezey, B.C. (1988) Morphometrics of flightlessness in the Alcidae. *Auk* 105, 681–698
154. Livezey, B.C. (1989) Phylogenetic relationships and incipient flightlessness of the extinct Auckland Islands merganser. *Wilson Bull.* 101, 410–435
155. Livezey, B.C. (1990) Evolutionary morphology of flightlessness in the Auckland Islands teal. *Condor* 92, 639–673
156. Livezey, B.C. (1992) Morphological corollaries and ecological implications of flightlessness in the kakapo (Psittaciformes: *Strigops habroptilus*). *J. Morphol.* 213, 105–145
157. Livezey, B.C. (2008) Flightlessness in the Galápagos cormorant (*Compsohalieus* [*Nannopterum*] *harrisi*): heterochrony, gigantism and specialization. *Zool. J. Linnean Soc.* 105, 155–224
158. McCall, R.a. *et al.* (1998) The role of wing length in the evolution of avian flightlessness. *Evol. Ecol.* 12, 569–580
159. Cubo, J. and Arthur, W. (2000) Patterns of correlated character evolution in flightless birds: a phylogenetic approach. *Evol. Ecol.* 14, 693–702
160. Maxwell, E.E. and Larsson, H.C.E. (2007) Osteology and myology of the wing of the emu (*Dromaius novaehollandiae*), and its bearing on the evolution of vestigial structures. *J. Morphol.* 268, 423–441
161. Longrich, N.R. and Olson, S.L. (2011) The bizarre wing of the Jamaican flightless ibis *Xenicibis xympithecus*: a unique vertebrate adaptation. *Proc. R. Soc. B* 278, 2333–2337
162. Gaspar, J. *et al.* (2020) Convergent morphological responses to loss of flight in rails (Aves: Rallidae). *Ecol. Evol.* 10, 6186–6207
163. Bannasch, R. (1994) Functional anatomy of the 'flight' apparatus in penguins. In *Mechanics and Physiology of Animal Swimming* (Maddock, L. *et al.*, eds), pp. 163–192, Cambridge University Press
164. Kovacs, C.E. and Meyers, R.A. (2000) Anatomy and histochemistry of flight muscles in a wing-propelled diving bird, the Atlantic puffin, *Fratercula arctica*. *J. Morphol.* 244, 109–125