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SYMPOSIUM

Unexpected Performance in Developing Birds

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Synopsis Birds are well known for their ability to fly, and flight-capable adult birds have many anatomical specializations for meeting the demands of aerial locomotion. Juvenile birds in altricial species typically acquire these specializations close to fledging and leave the nest with some flight capability. In contrast, juveniles in most precocial species begin navigating their environment with rudimentary anatomies and may not develop full-sized wings or musculoskeletal apparatuses for several months. This manuscript explores how juvenile birds achieve high levels of locomotor performance in the absence of flight specializations, by synthesizing work on two groups of precocial birds with very different developmental strategies. Galliforms like the Chukar Partridge (*Alectoris chukar*) have early wing development and are capable of flight within weeks. Compared with adults, juvenile chukars have less aerodynamically effective feathers and smaller muscles but compensate through anatomical, kinematic, and behavioral mechanisms. In contrast, waterfowl have delayed wing development and initially rely on leg-based locomotion. In Mallards (*Anas platyrhynchos*) and their domesticated derivatives, leg investment and performance peak early in ontogeny, but then decline when wings develop. Chukar and mallard juveniles thus rely on different mechanisms for negotiating their surroundings in the absence of flight specializations. In conjunction with work in other animals, these patterns indicate that juveniles with developing locomotor apparatuses can achieve surprisingly high levels of locomotor performance through a variety of compensatory mechanisms.

Introduction: flight and the avian body plan

Birds are perhaps best known for their ability to fly. Flapping, powered flight is the most physically demanding form of locomotion (Alexander 2002), and birds push its limits: hummingbirds (Trochilidae) hover, Bar-tailed Godwits (*Limosa lapponica*) migrate nonstop for 11 days and 8000+ miles (USGS), Bar-headed Geese (*Anser indicus*) cross the Himalayas (Scott et al. 2015), and Common Murres (*Uria aalge*) "fly" underwater to depths exceeding 500 feet. Exploits like these are possible because in many ways, the avian body plan is built around flight.

We have long known that flight-capable adult birds have a unique suite of anatomical features that are presumably adaptations or exaptations for flight (Fig. 1). The most conspicuous of these features are wings, which are made of pennaceous feathers that attach to the bones of the forelimb (see Hieronymus 2016) and overlap to produce an airfoil. In flying birds, the structure of these feathers visibly varies along the wing, with the degree of feather asymmetry increasing toward the wingtip such that the rachis (central shaft) lies progressively closer to one edge of the feather. This shift likely relates to feather orientation: distal (primary) feathers are arranged more perpendicularly to oncoming airflow, and having a rachis close to the feather's leading edge probably provides stability (Norberg 1984). Asymmetry is also associated with feather rotation about the rachis, which seems to reduce drag (Alexander 1982), delay stall (Klaassen van Oorschot et al. 2020), and open the wing like a venetian blind during the upstroke. Regardless of its position, the rachis clearly braces flight feathers against the aerodynamic and inertial forces associated with flapping (e.g., Bachmann

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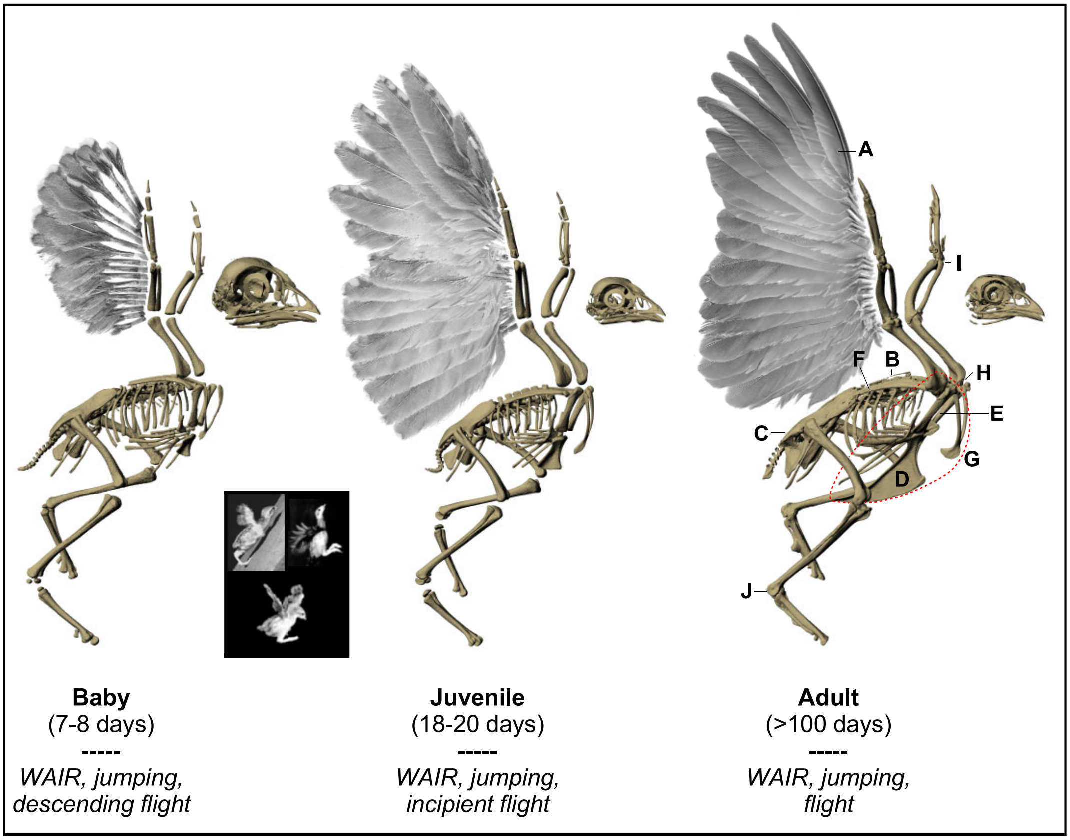

Fig. 1 Flight and the avian body plan. Flight-capable adult birds are characterized by a suite of anatomical features that presumably are adaptations or exaptations for flight. Some of these structures are functionally intuitive, whereas others have no known or demonstrated function(s) but are considered aptations based on their presence in flight-capable birds and their absence in flightless birds and extinct theropods (lineage giving rise to birds). (A) Stiff, cohesive, and asymmetrical primary feathers presumably provide stability and reduce permeability for aerodynamic force production. Fused vertebrae likely stabilize the trunk while transferring wing- or leg-generated forces to the body (notarium, B), and/or absorb shock (synsacrum, C). A robust flight apparatus [e.g., keeled sternum (D), long and firmly articulated coracoids (E), long scapulae (F), and furcula (G)] permits the attachment and contraction of large, powerful muscles [e.g., pectoralis (dashed red line), supracoracoideus], while the triosseal canal (H) (not visible) allows the supracoracoideus muscle to function similarly to a pulley and elevate and rotate the wing during upstroke. Reduced and fused elements in the distal limbs, coupled with channelized joints (I, J), likely reduce weight and facilitate swift limb oscillation, help coordinate joint movements, and restrict joint motion to keep the wing in a planar orientation during downstroke, or the ankle confined to movements in the direction of motion. Unlike adult birds, developing birds lack many of these flight aptations: their wings are smaller and/or less aerodynamically effective, and their skeletons are more gracile and less constrained. Immature birds nevertheless recruit their rudimentary wings during a variety of locomotor behaviors [italicized text and inset: wing-assisted incline running (top left); wing-assisted jumping (top right); varying degrees of flight (bottom)] and achieve flight capacity long before flight aptations are fully acquired. *Legend and images of Chukar Partridges from Heers and Dial (2012) and Heers et al. (2018, 2021). Not to scale.*

et al. 2012). Support is also provided by overlap between feathers and microscopic barbicels (hooklets) that zip a feather together and help prevent air from passing through (Muller and Patone 1998; Heers et al. 2011; Dial et al. 2012). Flying birds thus have strong, overlapping feathers that become increasingly asymmetrical toward the wingtip and provide stability against oncoming airflow while reducing drag, excessive deformation, and permeability (Alexander 1982; Norberg 1984; Muller and Patone 1998; Nudds and Dyke 2010; Heers et al. 2011; Dial et al. 2012). The net result is a cohesive but morphable airfoil.

In addition to their distinctive wings, flying birds have a specialized musculoskeletal apparatus. Muscles that cross the elbow and wrist joints mainly fine-tune wing position and orientation and are relatively small (Dial 1992; Biewener 2011). In contrast, muscles crossing the shoulder joint power the flight stroke and are exceptionally large (∼12–43% body mass in volant birds; Hartman 1961). Like cursorial mammals, these muscles are concentrated near the body wall, which minimizes limb inertia and facilitates rapid oscillation. Unlike most animals, however, two muscles play a disproportionately important role in bird flight. The pectoralis muscle provides most of the power for downstroke. It originates on the keel and adjacent areas, inserts on the ventral surface of the deltopectoral crest on the proximal humerus, and begins contracting during late upstroke to decelerate the wing and then pull it downward (George and Berger 1966; Dial 1992; Biewener 2011; Heers et al. 2018). The upstroke is mainly powered by the supracoracoideus muscle. Like the pectoralis, the supracoracoideus is anchored to the keel, but instead sends a long tendon through the bony triosseal canal near the shoulder to insert on the dorsal surface of the deltopectoral crest. Consequently, when the supracoracoideus contracts toward the end of downstroke, it decelerates and then elevates and rotates the humerus (Poore et al. 1997). Together, these two muscles generate most of the power required for flight and are conspicuously large in flying birds.

The bone movements that result when flight muscles contract are quite complex and are carried out—often extremely rapidly [up to 50+ cycles per second (Greenewalt 1960)]—at specialized wing joints. Proximally, the shoulder joint allows birds to sweep their wings both above the back and below the belly while simultaneously rotating them. This extensive range of motion is the culmination of a major evolutionary shift in the position and orientation of the shoulder joint, which was posteroventrally oriented in basal theropods (dinosaur lineage giving rise to birds) and gradually shifted to the dorsolateral orientation of extant volant birds (Jenkins 1993). In contrast, the elbow and wrist joints have become more channelized in birds, such that the main movement is flexion–extension and other joint movements are somewhat restricted (Baier et al. 2013; Heers et al. 2016) due to interlocking articular surfaces and ligaments and tendons. Channelization of these distal wing joints presumably allows birds to achieve a stereotypic flight stroke without requiring extensive musculature along the wing (see Vazquez 1992, 1994). Joint morphology thus plays an important role in flapping flight.

In short, the avian body plan is highly specialized with a unique integument and extensively modified muscles and bones, which collectively meet the demands of flight. How do these features develop?

Ontogenetic origins of avian flight

Most hatchling birds cannot fly (Starck and Ricklefs 1998) and have rudimentary, somewhat "dinosaur-like" anatomies: small or non-existent wings, small flight muscles, and less specialized skeletons (Heers and Dial 2012). Qualitatively, we have long known that as birds develop, their wings and muscles get larger and their skeletons become more robust as they acquire flight capacity. But how anatomical specializations and flight capacity are acquired during ontogeny varies widely, along a spectrum that we are just beginning to explore with respect to locomotor development.

Toward one extreme of the spectrum, altricial birds hatch with their eyes closed, limited feathering and locomotor ability, and are entirely dependent on their parents (Starck and Ricklefs 1998; Ducatez and Field 2021). In spite of these helpless beginnings, altricial hatchlings develop rapidly and usually acquire large wings and at least some flight ability by the time they leave the nest around a few weeks of age (though this varies with predation rate; Martin et al. 2018). Altricial birds therefore typically fledge and begin flying when their anatomies are relatively adult-like, with specializations for flight.

In contrast, precocial birds hatch with their eyes open and fully covered in downy feathers, able to walk and forage (Starck and Ricklefs 1998; Ducatez and Field 2021). Unlike altricial birds, precocial birds leave the nest hours after hatching and long before acquiring flight adaptations and the ability to fly. How do these fledglings navigate their surroundings? Specifically, how do animals with rudimentary or transitional flight apparatuses locomote and survive without the anatomical specializations of flying adults? Such questions have long been debated by paleontologists but are equally relevant to many developing birds.

This manuscript explores how precocial birds negotiate their surroundings in the absence of conspicuous flight adaptations, using two case studies: galliforms (chicken-like ground birds) and anseriforms (waterfowl, including ducks and geese). Together, these two groups form a clade near the base of modern birds (e.g., Prum et al. 2015). Both groups have precocial development and relatively large legs, and in both groups, hatchlings begin walking and foraging shortly after hatching, relying on rudimentary anatomies.

Among other vertebrates, juveniles are often able to compensate for their underdeveloped anatomies and achieve high levels of locomotor performance (Herrel and Gibb 2006). For example, in jackrabbits the gastrocnemius (calf) muscle has a greater mechanical advantage and proportionally higher force output in juveniles than adults, and juveniles are able to accelerate more rapidly (Carrier 1983, 1995). Hind limb bones also have proportionally higher second moments of area in young jackrabbits, which likely compensates for the lower mineralization of growing bone in juveniles that must be able to accelerate rapidly to avoid predators (Carrier 1983). Similar patterns have been observed in the leg bones of developing gulls (Carrier and Leon

1990). In guinea pigs (Trillmich et al. 2003) and some lizards (Marsh 1988), young have proportionally long hind limbs and proportionally higher running speeds than adults. Anatomical compensations thus play an important ontogenetic role in many species. Behavior probably does as well, because juveniles may try harder and perform closer to maximal levels (Irschick 2000). In short, compensatory mechanisms are likely prevalent in locomotor development, because many juveniles must feed and avoid predators early in ontogeny when they are handicapped by small size, naivete, and the immaturity of their growing tissues (Williams 1966; Wassersug and Sperry 1977; Ricklefs 1979; Martin 1995; Carrier 1996; Starck and Ricklefs 1998; Herrel and Gibb 2006; Jackson et al. 2009; Cheng and Martin 2012; Heers and Dial 2012). Do such mechanisms occur in galliforms and anseriforms?

Locomotor development in galliforms: early wing growth

Much of what is known about locomotor development in galliforms is based on the extensively studied Chukar Partridge (*Alectoris chukar*). Like many other galliforms, chukars hatch without pennaceous wing feathers but begin growing wings very early, within a week of hatching (Dial et al. 2006; Heers et al. 2011). However, their wings and other anatomical features are initially very rudimentary (Fig. 1). In fact, most anatomical changes are completed late in ontogeny (>40 days post-hatch), long after leaving the nest. Young chukars therefore navigate their environment with less specialized flight apparatuses for weeks. How do such juveniles locomote and survive?

Though wings are often associated with flight, a growing body of evidence shows that precocial juveniles do not “wait” for their wings to become flight-capable. In many species, immature birds use their wings before they can fly, typically to improve leg performance. For example, during wing-assisted incline running (herein “WAIR”) (Dial 2003; Dial et al. 2008), juveniles flap their developing wings to drive themselves into a substrate and increase foot traction to ascend steep inclines. Developing birds may also use their forelimbs to swim (Thomas 1996) or increase swimming speed (Dial and Carrier 2012), or to increase jump height and even make short flights (Heers and Dial 2015) (vide-os). Such behaviors demonstrate that many precocial birds—including chukars—begin using their wings and even flying long before they acquire the highly specialized anatomies of adults.

How do immature birds with developing flight apparatuses cope with anatomical limitations during these wing-based behaviors? Work over the past 20 years suggests that, like many precocial animals, chukars achieve surprisingly high levels of locomotor performance by compensating for their developing flight apparatuses.

Anatomical compensation

Feathers

7-8 day old “baby” chukars have small “protowings,” similar to some extinct theropod dinosaurs (Dial et al. 2006; Heers and Dial 2012) (Fig. 1). It is not until 18–20 days, in “juvenile” chukars, that wings reach adult-like proportions. These substantial changes in wing size are accompanied by conspicuous changes in feather structure: as they emerge, feathers become more unfurled, more asymmetrical, stiffer, and more cohesive due to increasing barbule overlap and hooklet density (Heers et al. 2011). Collectively, these changes are correlated with improvements in aerodynamic capacity (Fig. 2): 7–8 day old chukars produce aerodynamic forces that are ∼8% of their body weight during WAIR, compared to much higher forces produced by adults during WAIR or flight (Heers et al. 2011). Younger chukars also produce less lift per unit drag (less efficient). Together, these data demonstrate that compared with adults, younger chukars have rudimentary and less aerodynamically effective wings.

In spite of these handicaps, by the time they start flying at 18–20 days, juvenile chukars are able to partially compensate for their less effective feathers by having proportionally long feathers (Fig. 3; Heers et al. 2018). Coupled with their light bodies, this reduces wing loading (how much weight wings need to support) right at the age when chukars begin to fly (Jackson et al. 2009). In short, juveniles compensate for their less-effective feathers by growing big wings on little bodies.

Muscles

In addition to having less-effective feathers, young chukars have proportionally small flight muscles (Fig. 4). In adults, the pectoral muscles—which include the pectoralis and supracoracoideus—constitute ∼24% of body mass (Heers and Dial 2015). In developing chukars, these muscles are proportionally much smaller: ∼7% body mass in 7–8 day old baby chukars and ∼15% body mass in 18–20 day old juvenile chukars.

Musculoskeletal modeling suggests that 18–20 day old juvenile chukars can compensate for this limitation as well (Heers et al. 2018). Simulations of WAIR indicate that juvenile chukars have proportionally longer muscle moment arms, or greater muscle leverage, than adults: for most muscles spanning the shoulder joint, juvenile chukars have the greatest relative leverage in elevation–depression and protraction–retraction (Heers et al.

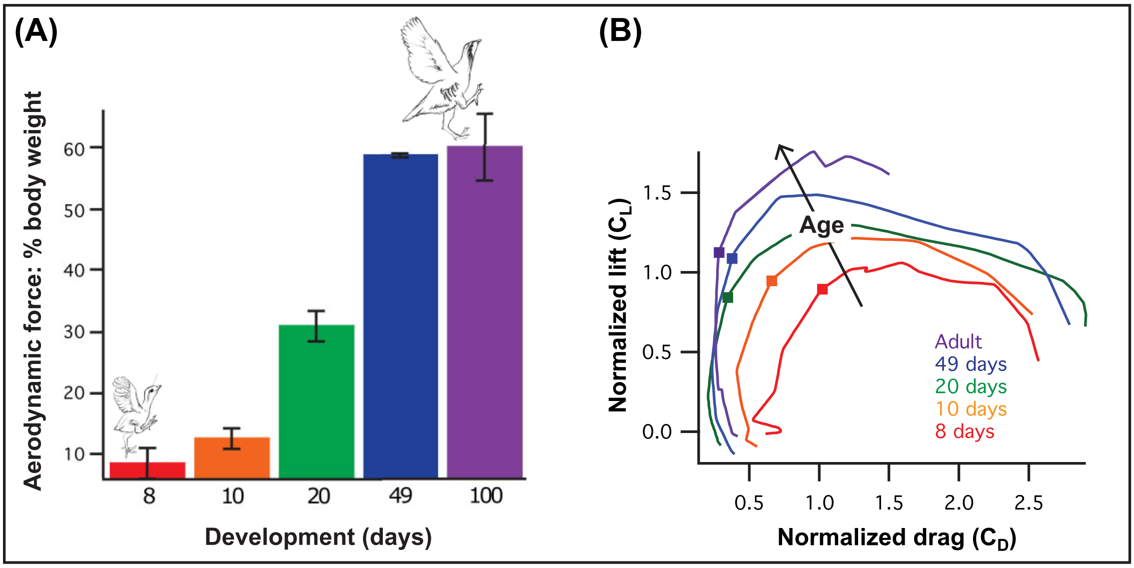

Fig. 2 Development of aerodynamic capacity in galliforms. (A) Aerodynamic force production and (B) lift-to-drag ratios increase through chukar ontogeny as the wings grow larger and feathers become more aerodynamically effective. *Drawings by Robert Petty; graphs from Heers et al. (2011, 2018).*

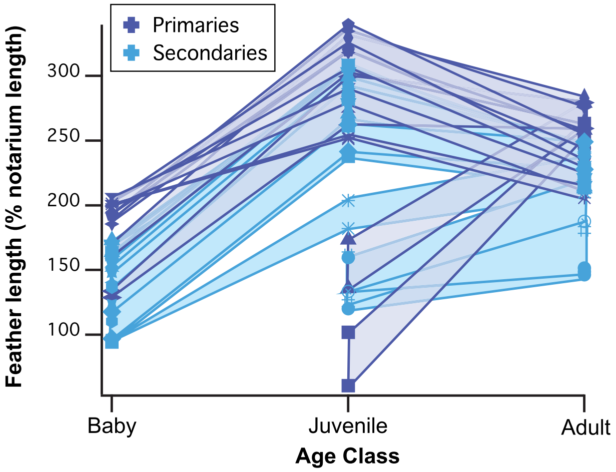

Fig. 3 Feather compensation in galliforms. Juvenile chukars partially compensate for their less aerodynamically effective feathers (Fig. 2) by having proportionally long feathers (although some feathers are just emerging: P8, P9, S1, S12, S13, and S14 are absent or very small in babies). *Figure modified from Heers et al. (2018).*

2018) (Fig. 5A). This greater leverage likely results from juveniles having proportionally longer and wider wing bones (Fig. 5B), which shifts muscles away from the wing joints and increases their leverage. Thus, like a small child sitting on a seesaw far from the fulcrum, juvenile chukars may compensate for their small muscles by increasing muscle leverage.

To what degree does having greater muscle leverage improve performance in juvenile chukars? Though this question cannot be answered precisely, simulations can again provide insight (Heers et al. 2018). When

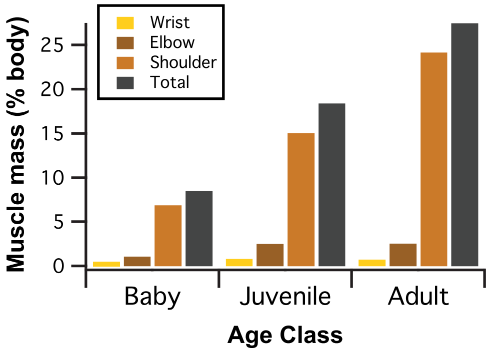

Fig. 4 Development of wing musculature in galliforms. When normalized by body mass, muscle mass increases through chukar ontogeny. These increases are most extreme for muscles that originate on the pectoral girdle and power shoulder movements. *Figure from Heers et al. (2018).*

WAIR is simulated using *in vivo* kinematics and aerodynamic force production, activations of the pectoralis and supracoracoideus muscles are low in all age classes (<0.5). When the same behavior is simulated in juvenile chukars using *in vivo* or adult kinematics and adult levels of aerodynamic force production (~60% body weight versus ~30% for *in vivo*), simulated muscle activations change slightly but remain low (Heers et al. 2018). These trends hold even when accounting for body size and inertial properties and suggest that the small muscles of juvenile chukars are effective enough to flap better, more adult-like wings. Given that wings grow faster than muscles, developing muscles may need to be pre-primed to flap larger wings, and this is likely possible partially because juvenile chukars compensate

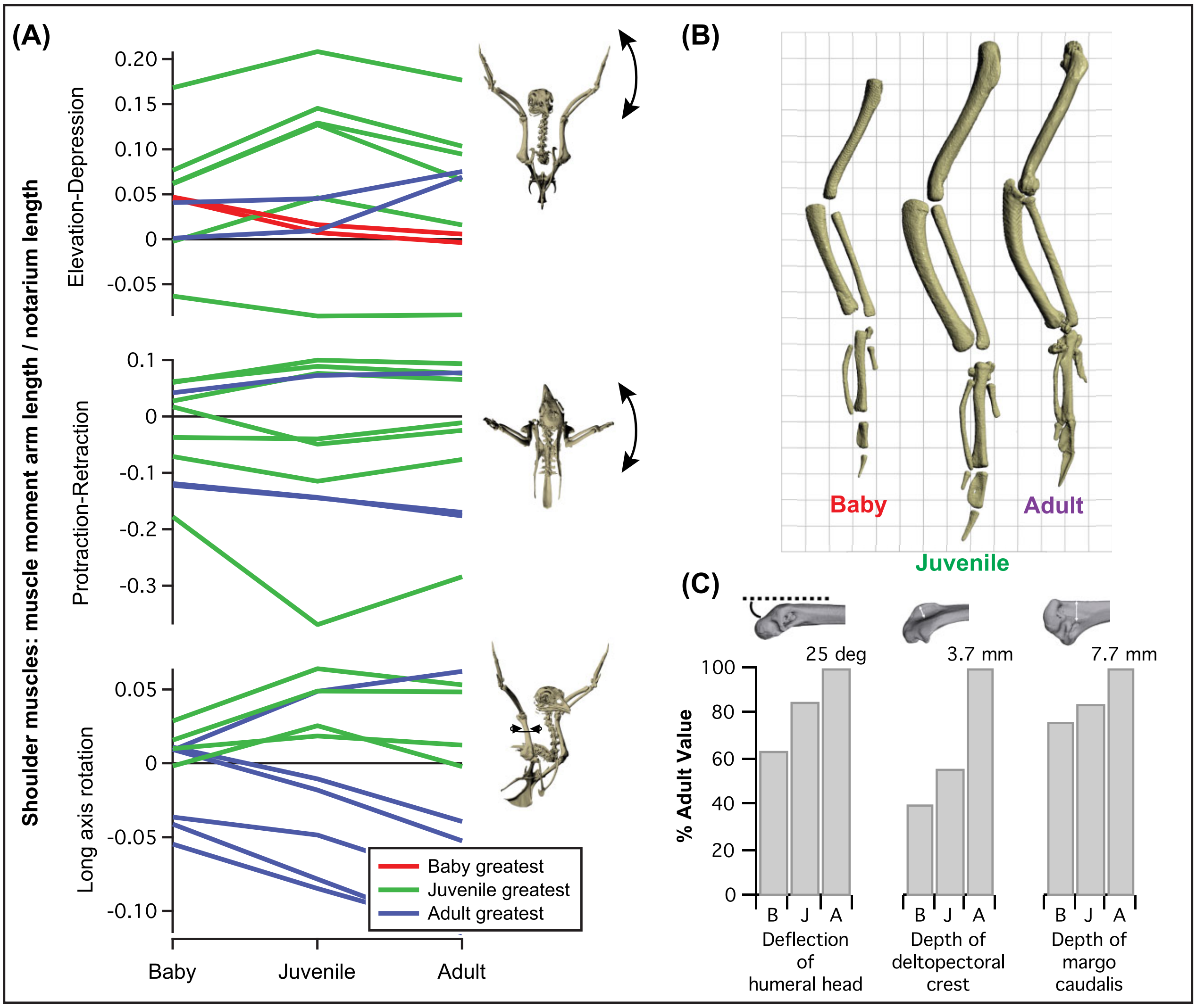

Fig. 5 Muscle leverage and compensation in galliforms. (A) When standardized by body length, muscle moment arm lengths generally increase through chukar ontogeny but show different developmental patterns depending on the direction of motion. Muscle leverage for elevation–depression and protraction–retraction tends to peak in juveniles, most likely due to their proportionally long forelimbs and deltopectoral crests (B). In contrast, leverage for long axis rotation tends to peak in adults, whose exaggerated muscle attachment sites help pull muscles away from the long axis of the humerus (C). *Each line represents the relative moment arm length (leverage) for one shoulder muscle about the z, y, or x axis, during maximal effort wing-assisted incline running (WAIR) in chukars. B = baby; J = juvenile; A = adult. Graphs and legend modified from Heers et al. (2018, 2021).*

for their small muscles with greater leverage (Heers et al. 2018).

Bones

As chukars mature and their muscles grow larger, the bones of the flight apparatus simultaneously become larger with more complex muscle attachment sites and joint surfaces (Fig. 1) (Heers et al. 2021). In addition, the furcula, coracoids, and sternum change orientation (Fig. 6). In 7–8 day old baby chukars, the angle between the coracoid and the scapula is obtuse, and the sternum is inclined away from the vertebral column. These features are also present in avian embryos, secondarily flightless birds (Livezey 1989, 2003, 2008), and various extinct theropods (Olson and Feduccia 1979; Feduccia 1986; Chatterjee and Templin 2003). As chukars mature, the scapulocoracoid angle decreases and the sternum becomes more parallel to the vertebral column, eventually resulting in a classic adult morphology. Bones therefore change substantially in size, complexity, and orientation during chukar development (Heers et al. 2021).

Intuitively, one might expect these extensive changes in skeletal anatomy to be associated with changes in muscle configurations and possibly functions—particularly for the pectoralis and supracoracoideus, which have origins on the pectoral girdle. However,

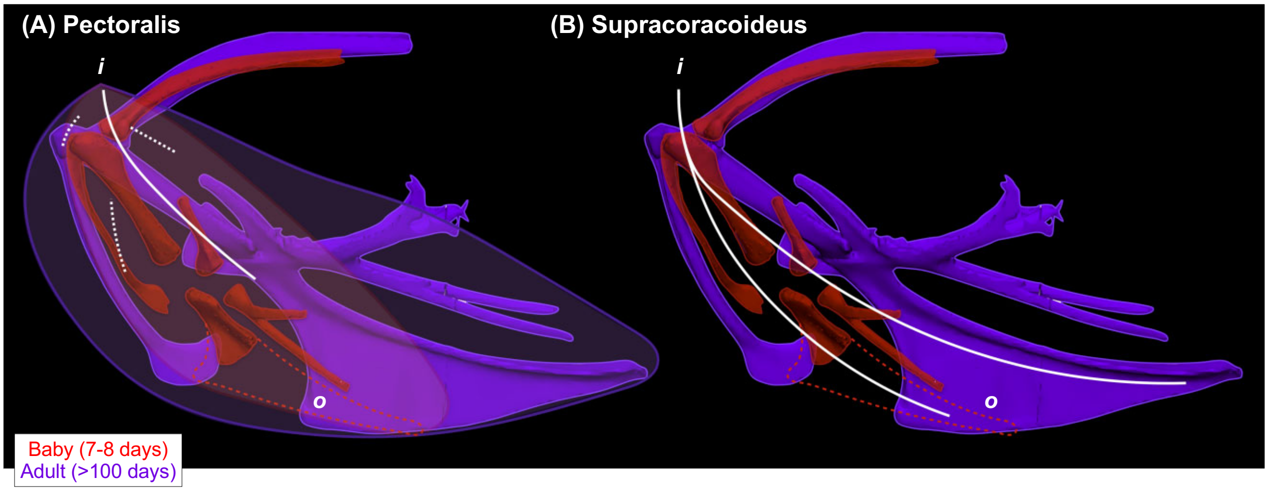

Fig. 6 Different skeletal configurations underlie similar muscle pathways. Despite underlying changes in skeletal morphology, the pectoralis (left) and supracoracoideus (right) maintain similar paths (indicated by white lines; o = origin, i = insertion) through chukar ontogeny because changes in one bone are offset by changes in others. As the coracoid (see Fig. 1 for bone labels) changes orientation and positions the growing sternum more caudally, the furcula and cranial portion of the keel expand and maintain the cranial origins of the supracoracoideus and especially the pectoralis. (A) Though the pectoralis has a very broad origin on multiple bones, the bulk of the muscle is concentrated cranially in adult birds, and muscle fibers converge near the shoulder joint, resulting in similar paths in babies and adults. (B) The supracoracoideus more closely tracks the sternum and coracoid but is constrained by the triosseal canal, causing muscle paths to similarly converge near the shoulder joint. *White lines show the path of the pectoralis (left; solid = central tendon, dashed = fibers) or the supracoracoideus tendon (right; passes medial to the shoulder joint through the triosseal canal, but shown so that the entire pathway is visible); red or purple lines show the approximate outline of the pectoralis muscle. Baby and adult aligned by the vertebral column, showing that (i) the glenoid does not change position, (ii) the scapula and furcula have similar orientations despite different coracoid orientations, and (iii) the keel in baby birds is functionally equivalent to the interosseous membrane between the sternum and furcula in adults. Figure and legend modified from Heers et al. (2021).*

these muscles maintain similar pathways throughout development (Fig. 6), because changes in one bone are offset by changes in others. For example, as the coracoid rotates (decreasing the scapulocoracoid angle) and displaces the growing sternum posteriorly, the furcula rotates slightly in the opposite direction and expands ventrally, while the anterior portion of the keel expands and the sternocoracoclavicular membrane fills in the remaining space that was originally occupied by the keel. Collectively, these changes expand muscle attachment sites and allow for increases in muscle mass without altering muscle function because muscle pathways converge near the shoulder joint and remain similar despite ontogenetic shifts in individual bones (Heers et al. 2021).

Taken together, these data show that developing chukars can partially compensate for their rudimentary feathers and muscles and maintain muscle function as their bones grow and shift.

Kinematic and behavioral compensation

In addition to compensating anatomically, there is also evidence that developing chukars compensate kinematically and behaviorally. Using x-ray videos to quantify three-dimensional joint movements reveals that overall flapping kinematics (movements) are similar across ages during WAIR (Heers et al. 2016). However, flapping kinematics are not identical, and ontogenetic differences seem to be compensatory in at least three ways.

First, immature chukars deploy a greater level of effort at a given behavior than adults. During WAIR on a 65° incline, younger chukars use a greater stroke amplitude, which sweeps their wings through a greater arc of motion. During the downstroke, younger chukars also keep their wrists more extended, and thereby maximize their wing surface area (Heers et al. 2016). These ontogenetic differences are comparable to a human swimming with versus without fins. Adult chukars have large, effective wings that generate sufficient force for WAIR without being fully spread or flapped, just as fins allow a swimmer to move rapidly with relatively little effort. In contrast, younger chukars must flap their smaller and/or less aerodynamically effective wings more vigorously, just as a barefoot swimmer must kick more vigorously to keep pace with a person wearing fins. Young chukars also often use their wings and legs cooperatively [e.g., WAIR (Dial 2003), wing-assisted jumping (Heers and Dial 2015)] and compensate by recruiting all four limbs.

Although these behavioral compensations improve performance, they do not eliminate performance

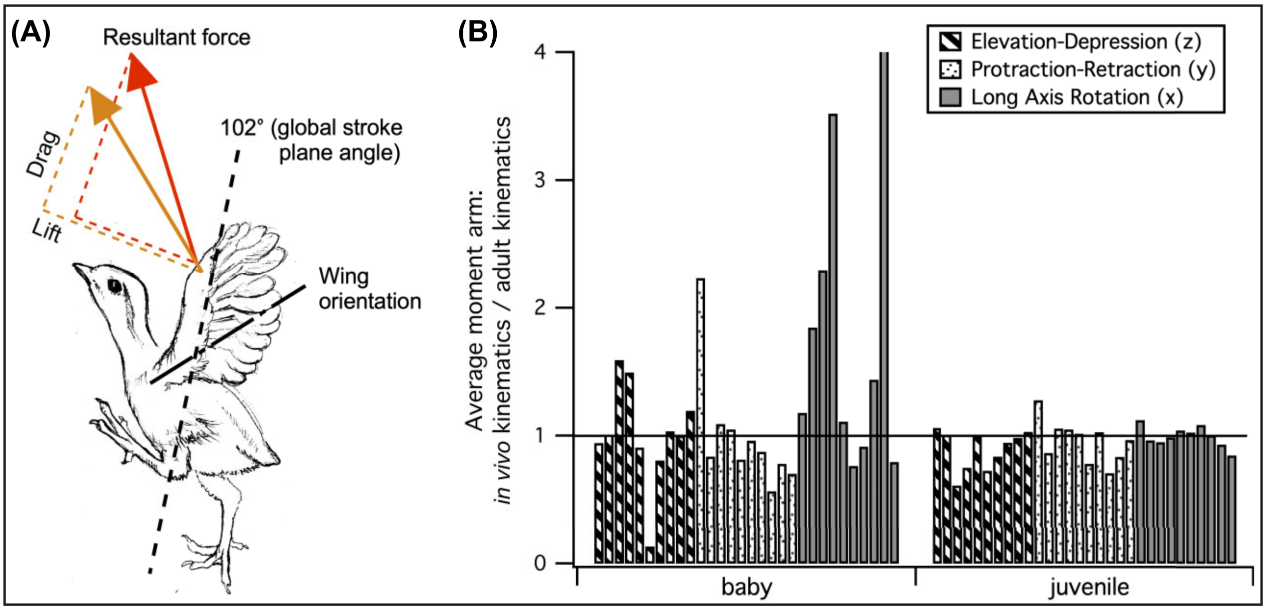

Fig. 7 Kinematic compensation in galliforms. In spite of changes in skeletal morphology, flapping kinematics during maximal effort wing-assisted incline running are very similar in immature and adult chukars (Heers et al. 2016). (A) Kinematic differences that do exist may improve wing performance in baby chukars: 8 (upper arrow) and 10 (lower arrow) day old chukars have a more vertical global stroke plane (flapping) angle than older birds, which helps compensate for their draggy wings by orienting drag in a direction that contributes substantially to weight support (Jackson et al. 2009; Heers et al. 2011). (B) Kinematic differences may also help improve muscle leverage for long axis rotation in baby chukars (Fig. 5), whose humeri lack the exaggerated muscle attachment sites of adults (7 out of 10 muscles have greater leverage for long axis rotation during *in vivo* than adult kinematics, compared to 4 out of 10 for elevation–depression and 3 out of 10 for protraction–retraction). In juveniles, muscle leverage for long axis rotation during *in vivo* and adult kinematics is more similar (5 out of 10 muscles have greater leverage for long axis rotation during *in vivo* than adult kinematics, but differences are not as substantial; 4 out of 10 are greater for elevation–depression and 5 out of 10 are greater for protraction–retraction). *Each bar represents the average moment arm of one muscle during in vivo kinematics divided by its average moment arm during adult kinematics; pectoralis and supracoracoideus are the first and second bars, respectively, for each grouping. Figure and legend modified from Heers et al. (2021); drawing by Robert Petty.*

differences between immature and adult chukars. This is partially because younger chukars still have more draggy wings that produce less lift per unit drag (Fig. 2) (Heers et al. 2011). However, 7–8 day old baby chukars compensate in a second way: in addition to flapping more vigorously, they also flap their wings more vertically during WAIR, which directs drag more vertically and helps support body weight (Fig. 7A). The youngest chukars with the most draggy wings therefore compensate for higher levels of drag production by directing drag more vertically to help support body weight (Heers et al. 2011).

Finally, baby chukars appear to use subtle differences in flapping kinematics to optimize muscle leverage (Heers et al. 2021). In adult chukars, the humerus has a deflected head and exaggerated muscle attachment sites, which pull muscles away from the shoulder joint and increase their leverage for long axis rotation (Fig. 5C). 18-20 day old juvenile chukars have less complex but proportionally longer and wider humeri (Fig. 5B), which helps compensate for their simpler bones and smaller muscles by increasing muscle leverage for elevation–depression and protraction–retraction. Baby chukars have the smallest and simplest humeri and thus cannot compensate anatomically like juveniles. Instead, baby chukars seem to compensate kinematically. Simulations of WAIR show that when average muscle moment arms during *in vivo* flapping kinematics are compared to those during adult kinematics, shoulder muscles have similar leverage during *in vivo* and adult kinematics for all joint movements in juveniles and similar leverages for elevation–depression and protraction–retraction in babies (Fig. 7B). However, for long axis rotation, 70% of the shoulder muscles in baby chukars have greater leverage during *in vivo* than adult kinematics, suggesting that subtle differences in how baby chukars flap their wings improve muscle leverage for long axis rotation—possibly to compensate for their less complex humeri.

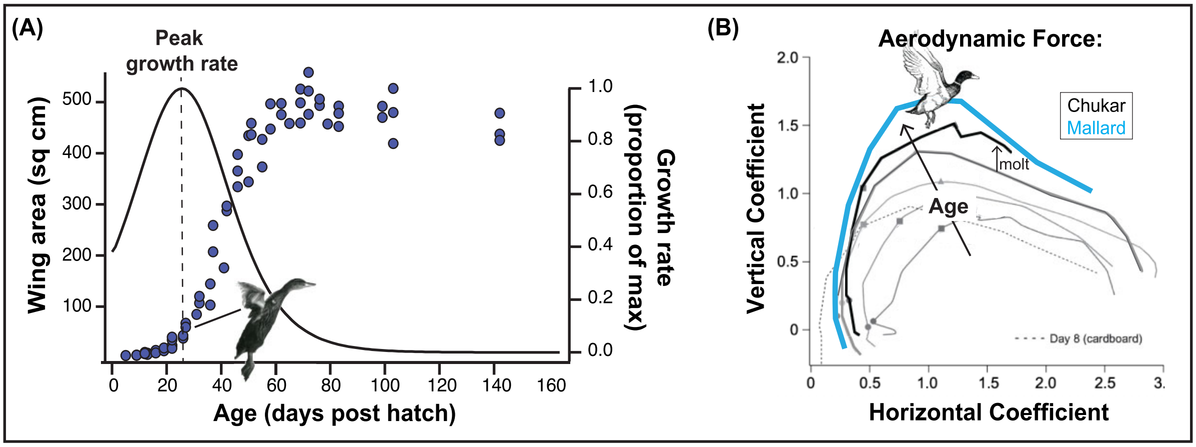

Fig. 8 Wing growth and performance in anseriforms. (A) In mallards, wing growth is delayed until body growth begins to slow. (B) Delayed wing development may permit the growth of higher quality wings: whereas chukars do not achieve peak wing performance until their lower quality juvenile feathers are molted and replaced with higher quality adult feathers, at ∼60 days post-hatch, mallards grow high-quality feathers and achieve high performance at the same age without molting. *Data in (A) from Heers et al., in preparation; (B) modified from Dial et al. (2012); drawing by Robert Petty.*

Summary of locomotor development in chukars

In summary, immature chukars begin using their wings and even flying when they have rudimentary flight apparatuses: small wings and/or less aerodynamically effective feathers, small muscles, and less complex bones with smaller muscle attachment sites and different orientations. However, like other precocial juveniles, evidence suggests that chukars can at least partially compensate for their less specialized anatomy in multiple ways:

(1) behaviorally, by using their wings and legs cooperatively and increasing their level of effort;
(2) kinematically, by flapping such that drag supports body weight and muscle leverage is optimized (baby chukars);
(3) anatomically, by offsetting changes in the orientation of one bone with changes in others and acquiring proportionally long feathers and muscle moment arms by the time they start to fly (juvenile chukars).

Yet this is merely one strategy adopted by chukars—and likely other galliforms—that grow and use their wings early in development. Preliminary work reveals that ducks take a very different approach.

Preliminary findings on locomotor development in anseriforms: delayed wing growth

In contrast to galliforms, ducks and many other aquatic birds have delayed wing development. For example, previous (Dial and Carrier 2012; Dial et al. 2012) and ongoing (Heers et al., in preparation) work shows that Mallards (*Anas platyrhynchos*) and their domesticated relatives do not begin growing pennaceous wing feathers until approximately one month of age (Fig. 8A). This delay may allow ducks to grow longer wings better suited for migration. For example, evidence suggests that trade-offs between tissue growth rate and functional maturity are important determinants of development (Ricklefs 1979; Ricklefs et al. 1994). Structures used early in ontogeny (early maturation) may have constrained growth trajectories and retain relatively juvenile-like morphologies into adulthood (Frazzetta 1975), whereas structures used later in ontogeny may be freed to grow rapidly and develop in ways that are incompatible with early use in juveniles. In mallards, the bones of the forelimb maintain high, possibly maximal growth rates through ontogeny, resulting in a long and narrow “endurance” wing (Dial and Carrier 2012). Presumably, this type of wing could not be grown any faster and would not be well suited to the short, explosive flights observed in early flying juveniles like chukars, which have shorter wings that they maintain, along with their powerful but brief style of flight, into adulthood. Delayed wing development might also permit growth of higher quality wing feathers because feather growth begins after body growth slows, which could allow for greater investment in wing feathers. Chukars do not achieve peak wing performance until their juvenile feathers are molted and replaced with higher quality adult feathers, at ∼60 days post-hatch (Heers et al. 2011). In contrast, mallards grow high-quality feathers and achieve high performance at the same age without molting (Fig. 8B) (Dial et al. 2012). Multiple lines of evidence therefore suggest that delayed

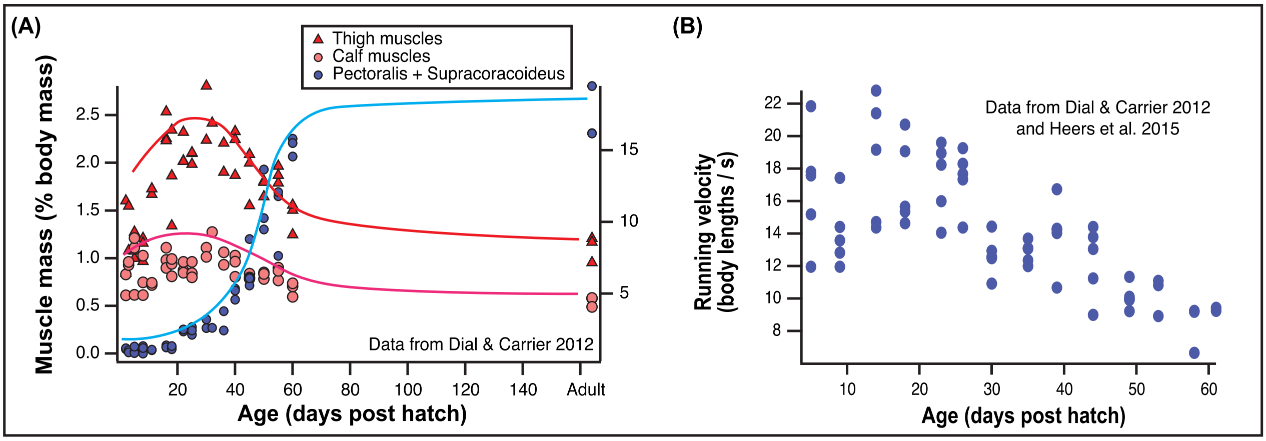

Fig. 9 Leg growth and performance in anseriforms. (A) In mallards, leg investment (e.g., muscle mass) increases rapidly, peaks early in ontogeny, and then decreases as the wings (e.g., pectoralis and supracoracoideus muscles) begin to develop. (B) High levels of leg investment are correlated with high leg performance: ducklings run rapidly and, at some stages, outperform adults (both absolutely and relatively). *Data from Dial and Carrier (2012) and Heers and Dial (2015).*

wing development allows birds to grow more specialized wings.

As flight-capable adults, mallards rely on their wings not only to migrate but also to avoid predators. Ducklings, of course, must also avoid predators. Given that mallards do not use their wings much prior to the onset of wing growth, they cannot be using the compensatory mechanisms of developing chukars. How then do ducklings negotiate their environment?

Studies show that flight-incapable ducklings invest heavily in their hind limbs. In mallards (Dial and Carrier 2012) and domesticated ducks (Heers et al., in preparation), leg muscle mass increases rapidly, peaks between 20 and 40 days post-hatch, and then declines—both absolutely and proportionally to body mass—as the wings begin to develop and play an increasingly prominent role in locomotion (Fig. 9A). Similarly, leg bone width increases rapidly early in ontogeny and then plateaus or even declines slightly (Dial and Carrier 2012), indicating that older ducks resorb some leg bone as well. Ducklings therefore invest heavily, but temporarily, in their hind limbs.

These high levels of leg investment are correlated with high leg performance in juvenile mallards. Absolute running velocity peaks between 25 and 45 days post-hatch (Dial and Carrier 2012), and relative running velocity (standardized by body length) peaks even earlier (Heers and Dial 2015) (Fig. 9B). Thus, at some ages, ducklings can outrun their parents. Once their wing feathers begin growing, like chukars, ducklings initially use their wings to supplement their legs, but mainly to increase swimming speed (Dial and Carrier 2012) by "steaming" (using the feet like paddles and the wings like oars). Ducklings are therefore revealing another approach to navigating the environment with a developing flight apparatus.

Conclusions

Galliforms and anseriforms illustrate two different strategies of locomotor development in precocial birds. Chukars have early wing development and use and grow lower quality feathers rapidly while compensating for their rudimentary flight apparatuses in multiple ways. Behaviorally, developing chukars compensate by recruiting their wings and legs cooperatively (Dial 2003; Dial et al. 2015; Heers and Dial 2015) and increasing their level of effort (Heers et al. 2016). 7-8 day old baby chukars also compensate kinematically—by using movements that reorient drag and optimize muscle leverage (Heers et al. 2011, 2021)—whereas older, incipiently flight-capable juvenile chukars compensate anatomically with proportionally long feathers and muscle moment arms (Heers et al. 2018). In contrast, mallards grow long wings with higher quality feathers (Dial et al. 2012) after body growth slows and, in the meantime, compensate by investing heavily but temporarily in their legs as ducklings (Dial and Carrier 2012; Heers et al., in preparation). Why these different strategies?

A growing body of evidence suggests that vulnerable, developing vertebrates invest most heavily in anatomical structures that aid in predator escape (Martin 1995; Carrier 1996; Starck and Ricklefs 1998; Herrel and Gibb 2006; Dial et al. 2015; Heers and Dial 2015). Ducklings can avoid predators by running to water or swimming and emphasize the hind limbs in this relatively two-dimensional setting. Chukars and other galliforms often use their wings and legs cooperatively to get off the ground and avoid terrestrial predators, and emphasize the forelimbs and hind limbs more equally in early ontogeny (Heers and Dial 2015). Galliforms that roost in trees take this to an even greater extreme, investing so heavily in their wings as hatchlings that juvenile peafowl (*Pavo cristatus*) (Heers and Dial 2015) and brushturkeys (*Alectura lathami*) (Dial and Jackson 2011) have greater wing performance than adults. In short, birds use a variety of strategies that emphasize the wings and legs to different degrees at different points in ontogeny, and this variation is likely related to predator avoidance and refuge location (Heers and Dial 2015).

Though this manuscript has focused on galliforms and anseriforms, the avian clade shows extraordinary diversity in anatomy, locomotion, developmental mode, and habitat—and how these factors influence locomotor development is still largely unknown. Navigating the environment with developing or rudimentary structures is a challenge that extends far beyond developing birds: rudimentary or transitional features lie at the core of evolutionary theory (Darwin 1859; Mivart 1871), are extensively discussed in paleontology (Heilmann 1926; Ostrom 1974; Gunnell 2002; Shubin et al. 2006; Feo et al. 2015; Xu et al. 2017), and are widespread in precocial juveniles and animals with vestigial structures. Yet the functional attributes of such features remain poorly understood. Studying young animals with rudimentary precursors to complex structures can therefore provide insight into multiple fields and a wide variety of organisms, both living and extinct. Though we are just beginning to explore the diversity of locomotor development in birds, one thing is clear: precocial birds—and juveniles in many other animal groups—can compensate for their rudimentary, developing anatomies in a variety of ways, and achieve unexpected levels of locomotor performance.

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Conflict of interest

I declare that I have no conflicts of interest.

Data availability

All data is available in graphical form or in previous publications.

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