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Primer

Aerodynamics of avian flight

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Much of the awe that humans have for the flight of birds derives from our earthbound habits and our bias toward emphasizing visual cues for interpreting processes in the world. Although we move through it and breathe it, air is vastly less dense than our bodies, so it is fanciful to imagine moving our limbs in a manner that would enable us to support our weight in the air. Moreover, air is invisible to us unless we use special tools to reveal its flow patterns. As evidence of our visual bias, contemplate a strong wind. You probably form a mental image of leaves moving on tree branches, or dust swirling about in a tornado, in both cases, solids moving in response to the force of the wind rather than the essence of the wind itself.

The complex wing and tail movements that enable bird flight were first revealed with the pioneering work of Muybridge and Marey in the late 19th century using time-sequenced photographs and, subsequently have been extensively studied by other researchers using high-speed film and video (Figure 1A). These techniques have demonstrated profound and dynamic morphing of flight surfaces due in part to aeroelastic deformation of flexible feathers and in part to actuation by the musculoskeletal system (see the primer on avian biomechanics by Biewener in this issue). Understanding the aerodynamics associated with this dynamic morphing is a major goal of modern research into bird flight and here we will begin to explore these aerodynamics.

Methods for studying aerodynamics of flying birds

The primary modern method for visualizing and measuring flow dynamics uses particle image velocimetry (Figure 1B). This requires seeding the air using micron-sized, neutrally-buoyant particles, illuminating the particles using pulses of laser light, and resolving time-based trajectories of the flow field using video. Particle image velocimetry grew from early work studying wake dynamics in flying birds by Magnan using smoke, Kokshaysky using sawdust, and Spedding and colleagues using helium-filled soap bubbles.

Another method for revealing aerodynamics of a flying bird instead measures pressure. This may involve placing differential pressure transducers between the shafts of feathers of the wings and tail and recording the pressure distribution on these flight surfaces. For this, the bird carries wires that transmit the analog signals to signal conditioners, amplifiers and computers. Alternatively, a new technique has a bird fly within an aerodynamic ‘force platform’ which is a chamber whose walls consist of extremely sensitive, low-mass, force plates. The force plates are like large microphones, measuring changes in pressure induced by the bird to the air as it flies.

Flow dynamics may also be modeled using computational fluid dynamics based on the Navier–Stokes equations and incorporating air density, viscosity, pressure and velocity to predict pressure distributions on flight surfaces. Sophisticated modern computational fluid dynamics incorporates three-dimensional morphing of the flight surfaces as resolved using high-resolution three-dimensional videography. This work has revealed the importance of wing morphing upon aerodynamics. A challenging yet promising future direction for computational fluid dynamics is to combine it with modeling of the material properties of flight feathers (Biewener, this issue) using finite element analysis. This type of combined modeling effort will improve insight into the functional significance of feedback cycles between elastic deformations of feathers (Figure 1B) that are induced by pressure distributions on the feathers and resultant aerodynamics due to the deformations.

Wake dynamics

As a wing or other flight surface produces lift with attached flow, the circulation around any two-dimensional slice of the airfoil is described according to the Kutta-Joukowski theorem as a line integral of tangential velocity on a closed loop surrounding the airfoil. Lift is also sometimes interpreted in terms of the Bernoulli Principle, with higher velocity (dynamic pressure) over the dorsal surface of the wing compared with that over the lower surface, and thus lower static pressure on the upper wing surface compared to the lower surface. This differential velocity also represents the bound circulation on the wing. Lift (differential pressure) is a product of this circulation, the speed of translation of the airfoil, and fluid

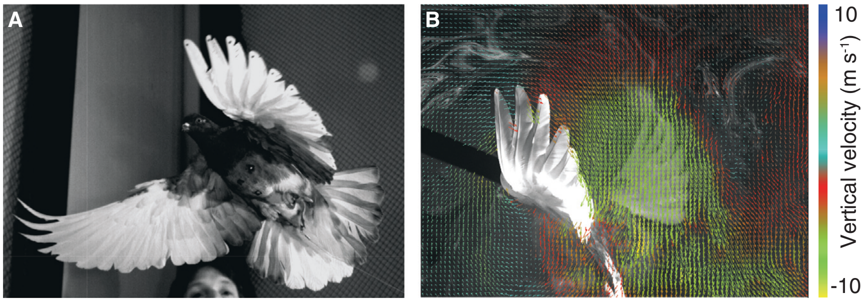

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Figure 1. Slow-speed flapping flight in a pigeon.
Current research into the aerodynamics of bird flight often uses high-speed video (A) to measure three-dimensional wing, body and tail movements (kinematics) including dynamic morphing of the flight surfaces due to aeroelastic deformation of the feathers such as the bent tips of the primary feathers in this pigeon. As humans are visually-oriented, we have a tendency to discount the magnitude of the velocity induced in the air by a bird as it flap its wings, but these velocities are revealed using particle image velocimetry, a laser-based system to measure flow. (B) This image is of a pigeon wing at mid-downstroke, and peak induced velocities in the near wake are ~10 m s^{-1}.

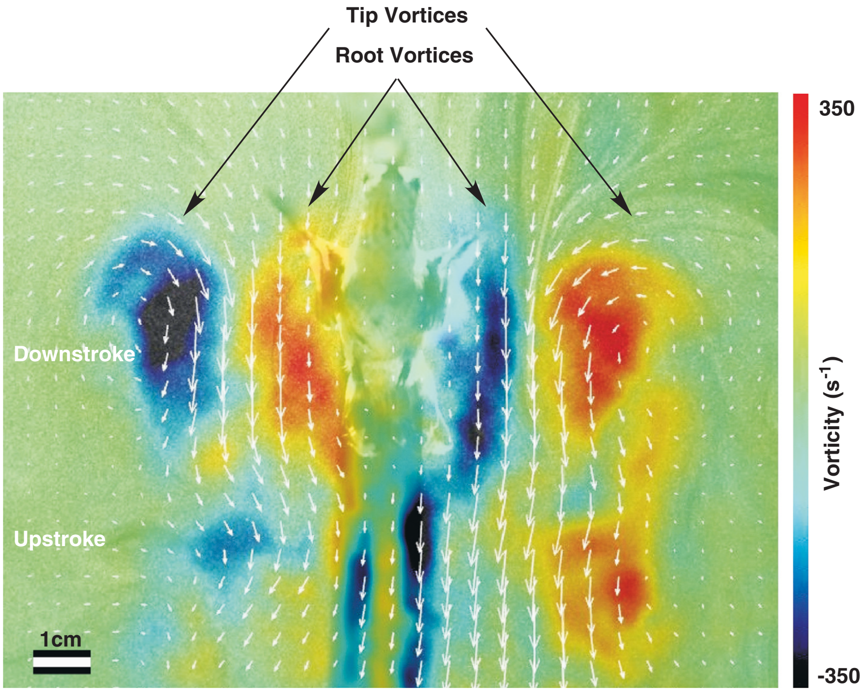

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Figure 2. Wake of hovering hummingbird from particle image velocimetry.
This image samples the frontal plane of a hovering hummingbird with velocity vectors (m s^{-1}) and vorticity (s^{-1}), representing rotational velocity about an axis extending perpendicular from the plane of the image. The bird is also in the background, in the first third of upstroke, which means the wings recently passed through the sample plane leaving a signal of downstroke. The lower part of the image shows the wake of a previous upstroke. Vortices are shed into the wake from the wingtips and the roots of the wing. Vorticity integrated with respect to area (m^2) yields circulation (m^2 s^{-1}), and the circulation in the wake is equal to the average circulation about the wing during the instant the wing passed through the sample plane.

density. In an imaginary world with wings of infinite span and uniform three-dimensional shape, each unit span of the wing would have the same circulation, and, while accelerating the air, no energy would be lost due to vortex shedding in the wake. How efficient!

In the real world, however, wings have roots where they attach to the body and tips where they end. Moreover, they have complex three-dimensional shapes. These realities cause circulation to vary along the wing, and, as a consequence, vorticity is shed into the wake. The simplest way to describe the wake is as having a closed-loop shape, with a starting vortex formed as the wing starts producing lift, an ending vortex formed when lift production stops, and both connected as a loop via root and tip vortices (Figure 2). Such closed-loop vortices would persist indefinitely except for decay due to air viscosity.

Tip vortices, and to a lesser extent root vortices, are useful for researchers as they represent the equivalent of a ‘wing print’ in the air because they are a record of wing forces (Figure 2). The circulation in the tip vortex is approximately equivalent to the average circulation on the whole wing at the instant the vortex was shed into the wake, and this has been used to reveal that patterns of lift production vary according to flight speed and wing shape. In all birds, the downstroke is presently understood to produce more lift than upstroke. Hummingbirds (Figure 2) are unique in their ability to sustain hovering, and their ability to produce substantial lift during upstroke, which contributes to this ability. A variety of species, mostly (but not exclusively) with relatively pointed wings, produce some lift during upstroke of slow flight and transition to more uniform lift production during cruising flight. Other species, usually with rounded wings, tend to produce lift only during downstroke, regardless of flight speed. Understanding the ecological and evolutionary significance of these patterns awaits new, comparative research.

To the bird (or other flier), these root and tip vortices represent a constraint upon span efficiency, which is maximal when the lift distribution on the wing induces uniform downwash velocity. Many birds have emarginate primary feathers that bend and twist relatively independently from the proximal wing. Recent research has confirmed that the individual primaries produce individual tip vortices. This has long been hypothesized to improve span efficiency by elevating and dispersing the portion of the wing shedding the tip vorticity. The upturned winglets widely utilized in modern aircraft are functionally equivalent. However, the limited evidence to date is equivocal for improved span efficiency due to feather emargination, independent bending of feather ‘winglets’. This general issue merits additional study given how widespread emarginate primaries are in birds.

Wings for weight support and thrust

The pressure distribution about the flapping wings of a bird simultaneously provides weight support and thrust (Figure 3A). Often it is mistakenly stated that lift and thrust are separate. This issue is potentially confusing because we may be more familiar with airplanes, where the wings provide weight support and propellers (or jet engines) separately provide thrust. Helicopters blend the two functions into the responsibility of their main rotors. A gliding bird produces weight support only with its wings, and, unless it is harvesting energy from the environment and thus soaring in thermals or upwash on hills, the bird inevitably drops in altitude if it maintains forward flight speed. As a bird flaps its wings, the incurrent air on any spanwise location on the wing is the sum of the translational velocity of the bird, the tangential velocity of the location on the wing, and the velocity induced by the bird’s wing into the air as it produces lift (Figure 3A). Thrust is generated by producing

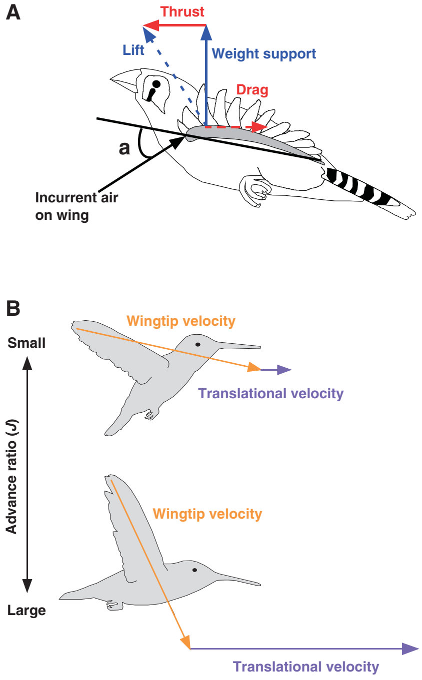

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Figure 3. Flapping wings produce lift for weight support and thrust.
A bird produces lift using its wings, and this lift simultaneously provides weight support and thrust when the bird is flapping (A). In contrast, a typical airplane provides weight support using wings and thrust using propellers or jets. The aerodynamics of flapping wings varies as a function of advance ratio (*J*), which is the ratio of forward translational velocity of the bird to the velocity of the wingtips (B). Shown in (B) are outlines representing a hummingbird flying forward at 2 m s^{-1} (*J* = 0.3) and 12 m s^{-1} (*J* = 1.3). Flapping flight approaches the aerodynamics of a helicopter as *J* decreases to zero in hovering. Unsteady (time-varying) aerodynamics characterize bird flight at small *J*. In contrast, flapping wings function more similarly to a fixed-wing aircraft as *J* increases to the numerically undefined case of gliding (tip velocity = 0 m s^{-1}), and quasi-steady models of aerodynamics in these instances are useful for describing wing function. A gliding bird supports weight but does not provide thrust, so the bird descends (loses potential energy) to maintain a steady horizontal flight velocity.

a forward-oriented lift vector, which is defined perpendicular to the incurrent air velocity.

The ratio of forward flight velocity to wing tip velocity is called advance ratio (*J*), and has important effects on wing aerodynamics (Figure 3B). Weight support dominates power costs during hovering and slow flight when *J* is small, and thrust exponentially increases in significance as flight speed increases (at greater values of *J*). These two trends give rise to a U-shaped curve of the power required for flight as a function of flight speed (Biewener, this issue). At small *J*, birds use large wingbeat amplitudes and high angles of attack, circulation on the wing is large, and velocities induced into the wake are also large (Figures 1B and 2). As flight speed, and thus *J*, increases, a greater mass of air already moving past the wings requires relatively less acceleration to support the weight of the bird, so circulation on the wings, wingbeat amplitude, angle of attack, and induced velocities decrease. However, form and friction drag on the body and wings, otherwise known as 'parasite' and 'profile' drag, respectively, increase such that the flapping motions must increase thrust (Figure 3A).

Most bird species progressively flex their wings during upstroke of forward flight as their speed increases. This reflects the progressively increasing ease of weight support and increasing cost of drag on the wings. Ultimately, a bird's top speed will be set by its ability to flap its wings fast enough to produce thrust (Figure 3) to match drag on its wings and body. Because tangential velocity of a wing with a given angular velocity is a linear function of span, small birds inevitably cannot fly as fast as large birds. This pattern may be partially offset by the scaling of wingbeat frequency which declines as body mass and wing length increase.

Aerodynamics vary with angle of attack of the wings

At low angles of attack, flow stays attached over the wings. This is

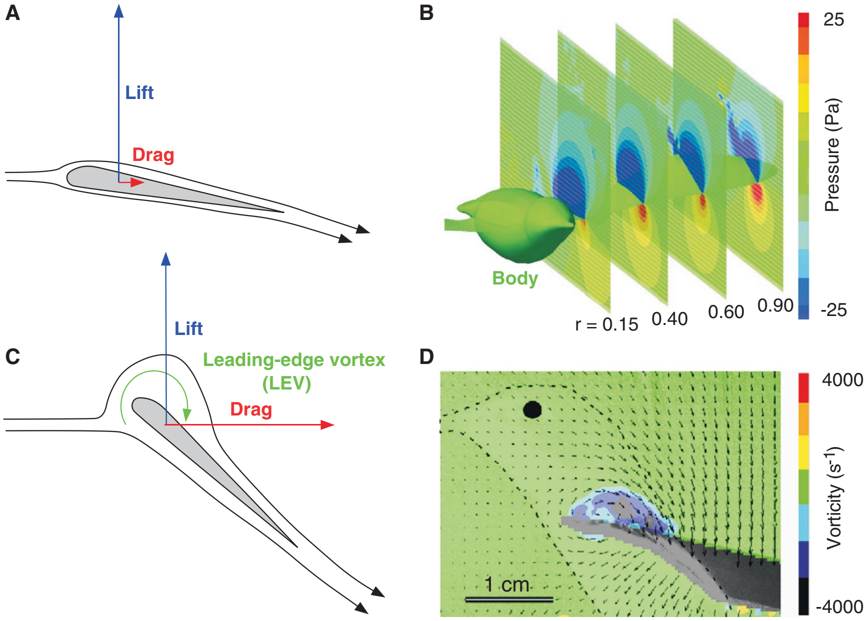

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Figure 4. Wing aerodynamics vary according to angle of attack.
At larger advance ratios (*J*) and during gliding (A), birds use their wings at relatively small angles of attack, the flow is attached to the wing, and lift dominates drag of the wing. Under these circumstances, quasi-steady models are useful for describing flow over the wing. Such simple models may be compared with more sophisticated computational fluid dynamics models (B), here showing a hummingbird modeled at mid-downstroke of cruising flight at 8 m s^{-1}. Parasagittal planes illustrate pressure (in Pascals) at relative spanwise locations (r) along the wing. During flight at small *J*, birds flap their wings at higher angles of attack (C), and a non-steady aerodynamic structure called a leading-edge vortex may form on the upper surface of the wing. This represents dynamic stall of the wing. Hummingbirds exhibit leading-edge vortices on their wings when hovering as shown in this image from particle image velocimetry (D) where the leading-edge vortex is visible as negative vorticity (s^{-1}) at the middle of downstroke. Leading edge vortices may also form on the wings during gliding flight with flat, thin wings at low angles of attack, for example, in swifts.

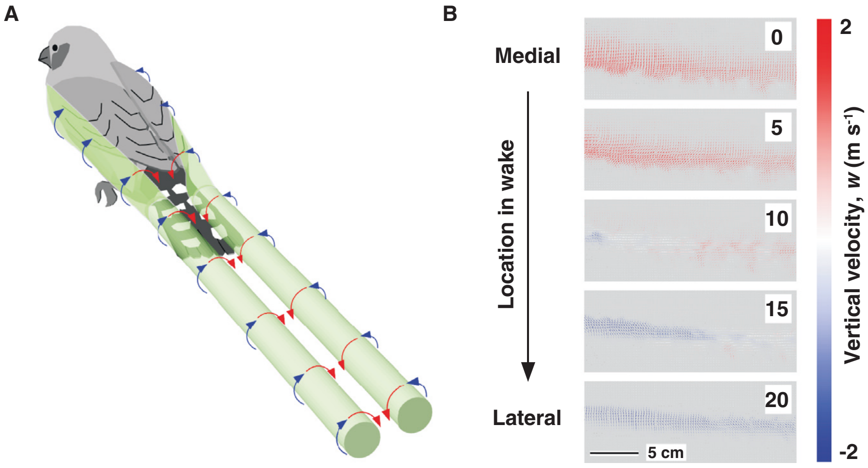

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Figure 5. Tail function during flight.
The function of the tail during bird flight is less understood compared with the wings, which is ironic given the complexity of wing motion during flapping flight. Intermittent flight provides an opportunity to study the tail when the wings are not flapping. Many species of small birds up to the size of large woodpeckers use intermittent flight consisting of flapping phases interspersed with flexed-wing bounds (A), and the body and tail produce lift that supports 10–15% of body weight during bounds. Lift by the tail induces downward velocity in the wake as revealed using particle image velocimetry (B) with samples indicated along a transect from the midline of the tail (mm). The tail also functions as a 'splitter' plate that helps recover static pressure in the caudal region and thereby reduce parasite drag on the body. New research reveals that the downwash from the tail improves span efficiency during gliding.

typical of flight at greater advance ratios (*J*), such as in forward cruising flight and during gliding (Figure 4A,B). Gliding is the only case where bird aerodynamics may be described as steady (non-varying) over time, but aerodynamics of forward flapping flight at higher *J* may be reasonably approximated using steady or quasi-steady models.

During slower forward flight, at low *J*, the wings are used at higher angles of attack and various time-varying 'unsteady' aerodynamics characterize wing function (Figure 4C,D). The wings of hummingbirds produce rotational circulation at the end of each half stroke. Doves produce a pulse of thrust at the upstroke–downstroke transition during slow flight when they use a 'tip-reversal' and 'clap-and-fling' upstroke.

In a remarkable example of convergent evolution, leading-edge vortices are formed on thin, rotating wings at small advance ratio (*J*) and are understood to enhance aerodynamic force production (both lift and drag) to facilitate slow flight. Leading-edge vortices have been observed in hovering insects, bats and hummingbirds (Figure 4C,D) as well as rotating, descending samaras (seeds from trees). Leading-edge vortices are a form of dynamic (time-varying) stall that are permitted by rotation of the wing as well as, in animals, time-varying changes in angle of attack and reversal of wing trajectory.

The wings of swifts also produce leading-edge vortices during gliding, and model wings emulating flapping motion in cruising geese also suggest leading-edge vortices are formed on the wings. Testing for ubiquity of leading-edge vortices in birds awaits further comparative study.

Wake recapture, harvesting energy in the shed wake (Figure 2), has been measured in models of insects operating at low *J*, but only leading-edge vortices (Figure 4C,D) and rotational circulation have thus far been observed in hummingbirds. Birds operate at Reynolds Numbers (Re) that are generally larger than those for insects. Re is a dimensionless ratio of inertial to viscous forces. The larger Re of birds may preclude wake recapture because self-convection of the wake (Figure 2) is likely greater than at lower Re.

Tail function in flight

Tails are less studied than wings in birds. Their morphing is perhaps less dramatic, but the avian tail represents a fascinating evolutionary trajectory from long-tailed theropod ancestors. The trend is to distribute body mass proximally in extant birds in a manner that is more extreme than the parallel trajectory of decreasing distal mass of the wings. Birds have fused distal skeletal elements of the wing and partially automate wing morphing via linkage systems (Biewener, this issue), but, in the tail, the pygostyle and muscles that control morphing are entirely proximal.

Intermittent flight is widespread in birds, consisting of flapping phases interspersed with flexed-wing bounds or extended-wing glides. Flap-bounding provides an opportunity to study tail function independently of wing flapping (Figure 5). Evidence from flap-bounding birds indicates that the tail (and body) provides lift that supports 10–15% of body weight. The tail organizes flow in a manner that has been modeled using delta-wing theory. Vortices are shed into the wake from the points of maximal span of the tail, lift is oriented upward and induced velocity is oriented downward (Figure 5).

This pattern is surprising compared with that of the tail in a typical airplane where horizontal stabilizers produce lift that is oriented downwards, meaning they function to counteract any downward pitching of the airplane. The center of mass of a stable aircraft is located anteriorly to the center of lift of the wings. The location of the center of mass of birds relative to the center of lift produced by the wings is largely unmeasured, but the upward orientation of lift from the tail of flap-bounding birds provides compelling evidence that birds are intrinsically less stable than aircraft, with dynamic stability effectively managed by their highly-derived central nervous and musculoskeletal systems (Biewener, this issue).

New research has revealed that the tail assists the wings in distributing downwash in a manner than improves span efficiency. The distribution of induced velocity is more uniform along the entire span than it presumably would be if a

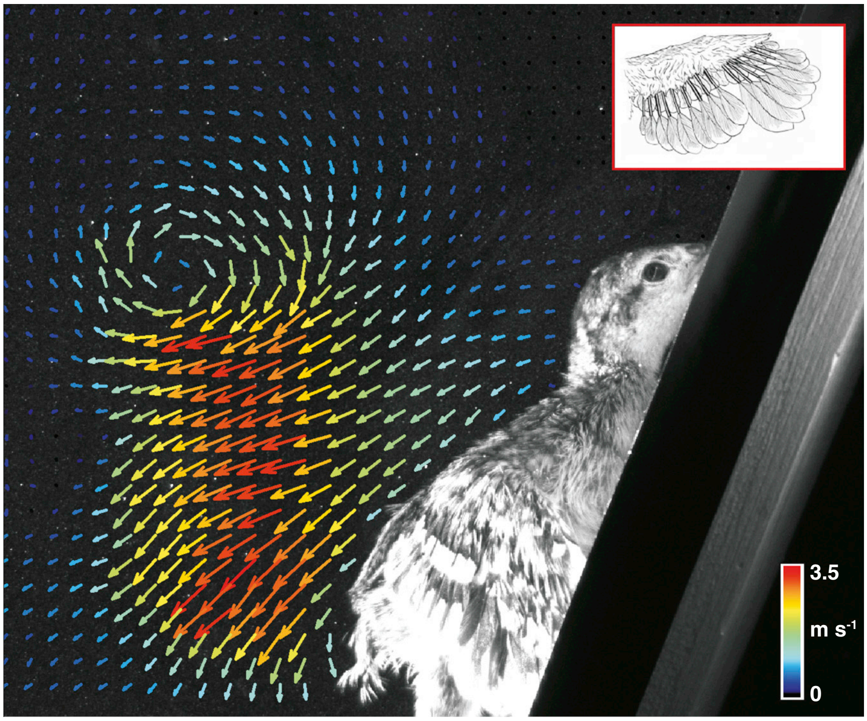

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Figure 6. Wing-assisted incline running in a baby chukar.
The wake due to downstroke during wing-assisted incline running in a baby chukar, ~6 days post-hatching as it uses its wings to help its legs climb an incline. The inset illustrates the morphology of the partially-developed wing of this precocial species. The feather barbs have not fully emerged from their sheaths. A baby chukar at this stage of development is not yet capable of flight, yet it can produce useful lift for climbing. Escape from predation using the wings is likely an important ecological function during the juvenile period of avian development when selection pressure is high. Wing-assisted incline running in juvenile birds, incapable of powered flight, provides a novel hypothesis for the biomechanics and aerodynamics of the evolutionary origin of flight.

bird lacked a tail. As feathers readily regrow, a potentially useful test of this hypothesis would include removal or clipping of tail feathers. However, resultant changes in mass distribution, moments about the center of mass, and instabilities due to the removal of a source of drag all might inadvertently affect the bird's use of its wings.

Other studies reveal that the tail reduces the vertical width of the wake. This is evidence that the tail is functioning as a 'splitter' for recovery of static pressure on the caudal side of the bird. Lacking a tail, the expectation is that a bird would exhibit greater parasite drag.

Future directions

Flow sensing in birds is poorly understood, yet recent work involving kinematic and neuromuscular responses to turbulence indicate birds effectively adjust to variation in flow patterns in their environment. Flow patterns in nature are more complex than in laboratory tests to date, so exploring sensing and control as well as studying responses to turbulence in nature are worthwhile avenues of study.

Much research in recent decades has been motivated in part by efforts to develop bioinspired, miniature autonomous vehicles (flapping robots that mimic insects, birds or bats). In many cases, we have information on aerodynamics from specific kinematic events in only one or a few bird species. To more fully reveal the biological significance of variation in avian wing kinematics, morphing of wing and tail surfaces, it will be useful to pursue comparative studies that will ultimately help trace historical pathways of evolutionary change.

The acquisition of flight during ontogeny also merits new research. The development of flight capacity has important implications for the life history and ecology of birds, yet most studies of avian flight are performed using adults. The juvenile phase in birds is often a time of intense natural selection where locomotion is relatively uncoordinated, skeletal components are not fully ossified, flight feathers are shorter and more porous than in adults, and power output from flight muscles is less. Studies have shown that young birds can use their wings to produce lift to help climb slopes well before they are able to support their weight in the air (Figure 6). This is known as wing-assisted incline running. Wing-assisted incline running is broadly exhibited among bird species and among age classes within species, but the frequency of its use in natural settings is unstudied. The ontogeny model, producing force using a partially-developed wing, provides an intriguing extant model for the evolutionary origin of flight in birds.

DECLARATION OF INTERESTS

The author declares no competing interests.

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