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Primer

Biomechanics of avian flight

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Throughout recorded human history, birds have fascinated and inspired humans to dream of flying. The Greek myth of Daedalus and his son Icarus, who flew too close to the sun and fell to his death, first written by Diodorus (60–30 B.C.E.) and later poetically revised by Ovid (8 C.E.), evokes the dangers of hubris. Many indigenous peoples invoke spiritual qualities and protection ascribed to birds that were symbols of freedom and viewed as sacred messengers of the gods. As a student of bird flight, Leonardo da Vinci (1452–1519) was the first to document dynamic soaring by birds. And, subsequently, the flight of birds inspired human engineered pursuit of powered aircraft design, with the Wright Brothers being the first to design and achieve sustained flight at Kitty Hawk, NC, USA in 1903.

Bird flight performance and behavior continue to captivate large numbers of recreational and professional ornithologists. In many locales, annual bird counts are carried out to assess how avian biodiversity is being affected by climate change and human impact. Consideration of how birds have evolved to achieve key traits for flying of their feathers, wing and body form, as well as the underlying neuromuscular and skeletal machinery, provides an opportunity to 'look under the hood' to appreciate how they power their impressive acrobatic flight abilities. I will begin this primer by briefly summarizing the key morphological changes that led to the evolution of flapping flight, a remarkable evolutionary achievement that resulted in the explosive diversification and success of modern birds.

Evolution of avian flight

The capacity for powered flapping flight exhibited by modern birds arose in the theropod dinosaurs within the Paraves. Although debate continues regarding a gliding ('trees down') *versus* wing-assisted terrestrial ('ground up') origin for flapping flight, the fact that early birds evolved from small predatory bipedal ('two-legged') theropod ancestors strongly skews the evidence in favor of a terrestrial origin. Based on estimates of wing loading — the ratio of wing area to body weight — and flight muscle power capability, a variety of early fossil birds (Avialae), including the iconic *Archeopteryx*, show evidence for the potential of powered flight. Several early birds were therefore likely employing an incipient forelimb wing flight stroke that could assist in a variety of ground-running behaviors by generating aerodynamic force, in addition to the forces that their hind limbs exerted on the ground.

The high-power requirements for effective flight subsequently resulted in the conserved evolution of several key anatomical features. Among these are asymmetric, stiff flight feathers and aerodynamic wings (Figure 1A,B); a stiff, lightweight skeleton, with

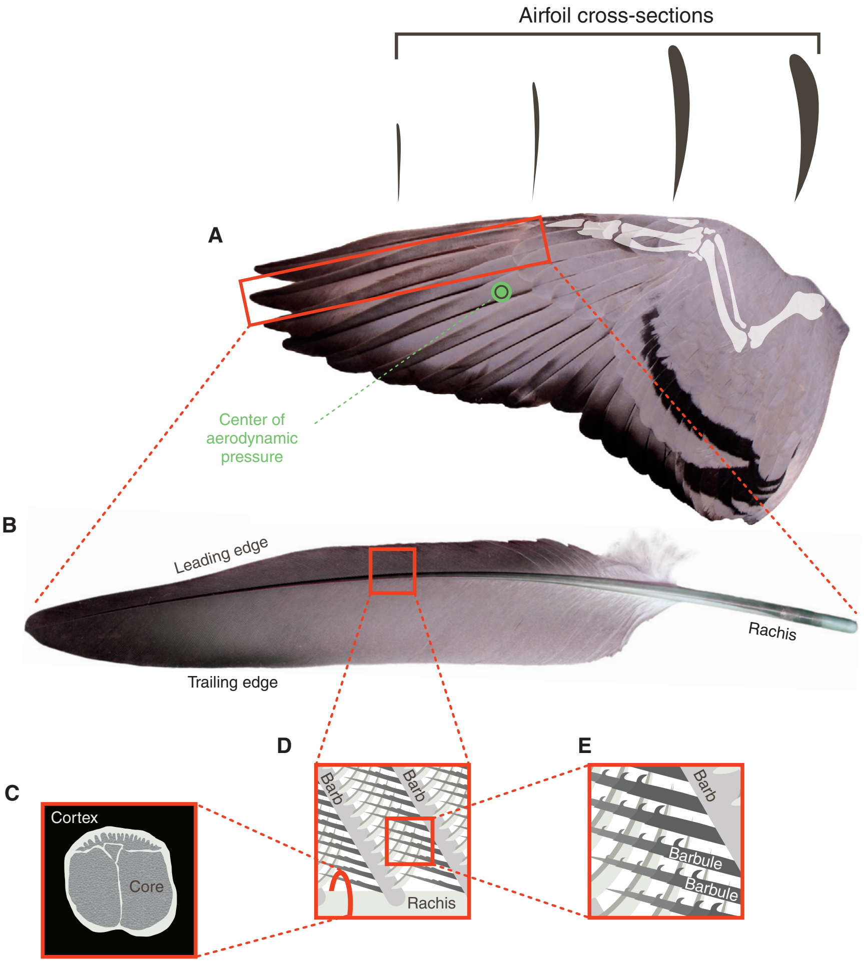

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Figure 1. Avian wing adaptations for flight.
The forelimb wings of birds converged on an aerodynamically efficient design for generating lift and thrust to support their weight and overcome drag. (A) This involved a radical reduction in distal forelimb bones that support large primary flight feathers of the hand wing, providing an efficient (high lift versus drag) airfoil chordwise cross-sectional shape, and modification of forelimb joints to stabilize the wing in elevation and depression while allowing for flexible adjustments of the wing planform shape to facilitate flight maneuvering. (B) The primary and secondary flight feathers evolved an asymmetric aerodynamic shape (narrow leading edge versus trailing edge vane) supported by a stiff light-weight rachis, with (C) a dense keratinized cortex reinforced by an inner open-cell core. Interlocking keratinized (D) barbs and (E) barbules branching off the feather shaft underlie the feather's lightweight aerodynamic design and readily reorganize their structural integrity in response to preening. Artwork kindly produced by Philip Fahn-Lai.

air-filled bones (Figure 2A) linked to respiratory air sacs, substantially reduced distal wing bone elements, and forelimb joints facilitating elevation–depression movements of the wing as a whole while allowing for changes in wing planform shape; substantial enlargement of the power-generating flight muscles (pectoralis and supracoracoideus) with a concomitant expansion of the sternum by means of an extensive ventral keel (Figure 2B); and modification of the avian shoulder joint with passive structural support provided by means of robust coracoids, a furcula ('wishbone') and joint ligaments to resist and transmit the aerodynamic forces generated by the wings to the bird's trunk. Let us first examine the aerodynamic and biomechanical properties of flight feathers.

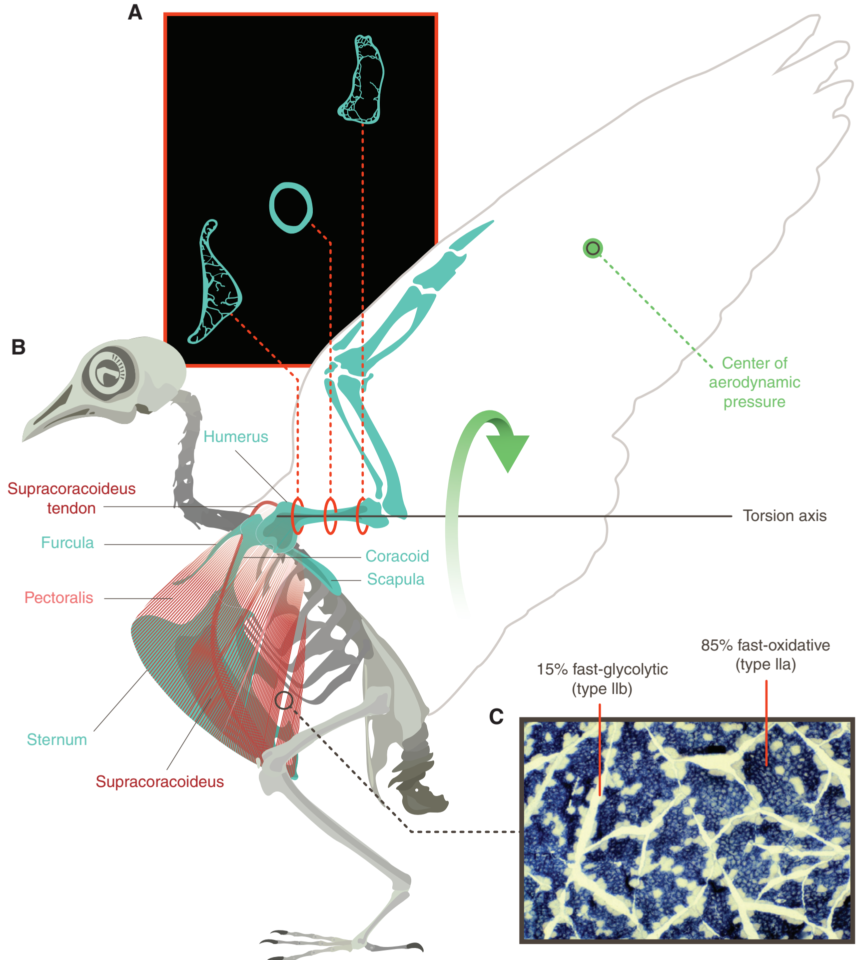

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Figure 2. Avian musculoskeletal adaptations for flight.
(A) The forelimb, shoulder and trunk skeleton of birds underwent several substantial evolutionary modifications to facilitate an effective flapping wing stroke powered by large flight muscles: the main downstroke pectoralis muscle (light red), and the main upstroke supracoracoideus muscle (darker red). The ventral keel of the sternum is enlarged, allowing for increased size of the pectoralis and the underlying supracoracoideus, which acts via its tendon and by means of a skeletal pulley at the shoulder to elevate the wing. The shoulder joint is supported by robust coracoids that articulate with the scapula above and sternum below, along with joint ligaments and anteriorly by the furcula (wishbone). The skeleton is lightweight by (B) many of the wing bones being air-filled and with the loss of a bony tail and teeth. The center of aerodynamic lift acts at the hand wing anterior to the humeral axis, causing substantial torsional loading which is effectively resisted by the bone's large polar moment of inertia achieved by its expanded, hollow circular cross-sectional shape. (C) The pennate pectoralis is largely comprised of fast-twitch oxidative (type IIa) fibers that allow for rapid shortening and sustained flight. Fast-glycolytic (type IIb) fibers are recruited for non-sustainable burst flight activity. Artwork kindly produced by Philip Fahn-Lai.

Aerodynamic and biomechanical design of feathers

Feathers, which evolved from modified keratinized scales, were present within non-avian archosaurs well before flight evolved, and likely served thermoregulatory, body protection and communication display roles. With the advent of powered flight, pennaceous flight feathers (particularly the primaries located in the distal hand wing) evolved an asymmetric shape (narrow leading-edge vane *versus* a broader trailing-edge vane, Figure 1B). Branching from the main feather shaft, or rachis, sets of keratinized barbs and self-reorganizing and interlocking barbules (Figure 1C–E) create an efficient aerodynamic design, increasing the lift versus drag force ratio of the feathers and the wing as a whole. The presence of overlapping primary and secondary flight feathers not only achieves a lightweight, efficient airfoil design for generating lift, but also allows for flexible changes in wing shape ('morphing'), effected by wing joint movements that are controlled by small arm muscles to adjust the wing's lift versus drag properties in relation to its angle of attack (defined as the angle of the wing's surface to the incident airflow), key to maneuvering and flight stabilization in response to airflow disturbances.

The central feather shaft provides a lightweight and stiff structural support for the feather vanes. Flexural stiffness is achieved through the material stiffness (elastic modulus) of keratin in combination with the cross-sectional shape of the shaft that gives it a high second moment and polar moment of area — shape expansion features that are key to a beam's resistance to bending and torsion; similar to the thin-walled tubular frame of a bicycle that makes the bicycle frame stiff but light, compared to if the bike frame were constructed from solid rods. The flexural stiffness of the feather shaft maintains the feather's effective airfoil shape and orientation during the wing stroke, while contributing a lightweight design. A high flexural stiffness is favored relative to the risk of damage due to bending or buckling failure, with the rachis' rectangular cross-sectional shape also increasing

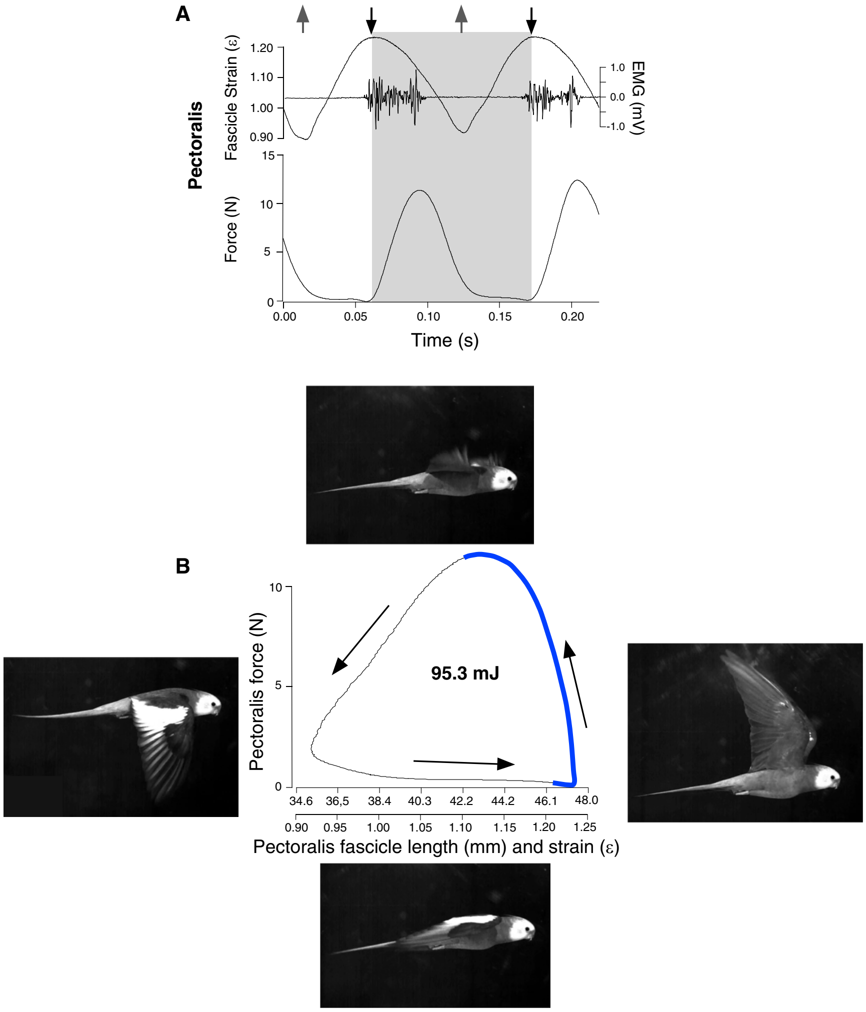

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Figure 3. Flight muscle activation, force, and length change.

(A) The pectoralis of cockatiels is activated (EMG, electromyogram) beginning with the end of upstroke to generate force during the downstroke. The muscle shortens over a large fraction of its resting length (~35%) to perform mechanical work associated with producing aerodynamic lift. It is then passively stretched during the upstroke. (B) The force versus length change of the pectoralis describes a counterclockwise 'work loop', with force rising rapidly at the start of the downstroke following activation (bold blue portion of the loop). The area within the loop represents the net work (95.3 milli-Joules in this example) performed by the muscle during its contraction cycle.

its buckling resistance. Finally, the composite design of the keratinized shaft, with a dense keratinized outer cortex that is reinforced by an open-celled inner foam core (Figure 1C), also makes the feather shaft both stiff and light. At the same time, compared with the generally rigid, fixed wings of human engineered aircraft, the ability of feathers to bend or twist (favored by the rachis' ventral groove) under changing aerodynamic loads aids in stability during flight. We now turn to the underlying musculoskeletal machinery that powers avian fapping flight.

Avian musculoskeletal organization for flight

The avian wing skeleton is lightened by having air-filled wing bones with generally thin cortices that are internally supported by small bony ('trabecular') struts at the bone's ends (Figure 2A). The reduced number and size of hand bone elements also significantly diminish the inertial cost of accelerating and decelerating the wing at high frequencies, which range from 2–4 Hz in large birds, such as hawks and eagles, to over 40 Hz in much smaller hummingbirds. The expansive ventral keel of the sternum, in combination with the furcula anteriorly, provides a large attachment area for the pectoralis, the main downstroke muscle, which inserts on the ventral surface of the deltopectoral crest of the proximal humerus. The ventral sternal keel also provides a large attachment area for the supracoracoideus, the main upstroke muscle, which lies deep to the pectoralis (Figure 2B). Although located ventrally along the bird's trunk, the supracoracoideus elevates the wing at the shoulder by means of a long tendon that passes dorsally over a specialized pulley-like triosseus canal, to insert on the dorsal proximal surface of the humerus. The sternum is supported both by thoracic ribs as well as anteriorly by the coracoids. Together with the furcula and several joint ligaments, the robust coracoids passively support the shoulder joint, serving as compressive struts to effectively transmit the large wing forces to the bird's thorax.

The avian air-filled humerus (as well as other primary wing bones) has a cross-sectional shape that is effective for resisting both the dorso-ventral bending and torsional loading (Figure 2A) that are associated with the location of the center of aerodynamic pressure acting on the wing during the downstroke that lies anterior to the humeral longitudinal axis (Figures 1A and 2B). This hollow thin-walled bone design is shared by the humerus of *Archeopteryx*, providing supportive evidence that *Archeopteryx* was capable of powered flapping flight, given its ability to resist the torsional and bending loads that an active wing stroke would impose on its humerus. Although the tissue density of avian wing bones is higher than that of terrestrial mammal limb bones, which adds weight, their greater density allows avian wing bones to have thin walls. Overall, therefore, their thin-walled design provides a reduction in weight and increases the bone's strength in bending and torsion.

Across a wide variety of avian species, the pectoralis muscles average 17% of the bird's body mass, with the supracoracoideus muscles comprising 2–4%; in combination, the two sets of flight muscles represent ~20% of a bird's body mass! By comparison, the pectoralis muscles of humans represent ~0.5% of body mass. The pectoralis muscle of most birds is composed of a large fraction (~75–95%) of type IIa or fast-twitch oxidative muscle fibers, with a smaller fraction (~5–25%) of type IIb or fast-twitch glycolytic fibers (Figure 2C). By contrast, the pectoralis of ground birds (Galliformes) including pheasants, quail, and turkeys have mainly type IIb fibers. The preponderance of fast-twitch muscle fibers reflects the high contraction rates required for flapping flight. Whereas the oxidative type IIa muscle fibers enable flight endurance, the glycolytic type IIb fibers are recruited for short bursts of accelerating flight, as during take-off or when maneuvering or ascending in steeper aerial climbs. The deep portion of the pectoralis of certain larger gliding birds, such as albatrosses, petrels, and vultures, also has a substantial fraction of type I (slow-oxidative) muscle fibers that favor more efficient, low energy cost gliding flight.

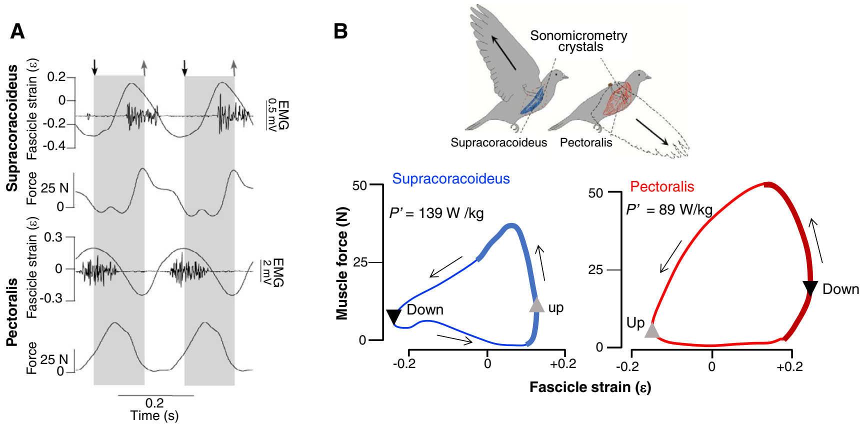

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Figure 4. Antagonistic flight muscle activation, force, and length change.
(A) The pectoralis and supracoracoideus, shown here for a pigeon during level moderate speed flight, are activated to generate force and change length out of phase with respect to each other. By contrast to the pectoralis that is activated at the end of upstroke, the supracoracoideus is activated during the second half of downstroke, functioning to overcome wing inertia and initiate wing elevation in upstroke. Like the pectoralis, the supracoracoideus also undergoes large fascicle strains. Elastic energy storage and recovery in its tendon contribute to the inertial acceleration of the wing into upstroke. (B) The timing of muscle force generation relative to fascicle length change results in a positive (counterclockwise) work loop performed by each muscle. Mass-specific power output of the supracoracoideus exceeds the pectoralis due to its much smaller size but substantial force and length change. Activation of the muscles prior to shortening enables rapid force generation to perform substantial work (pectoralis) or control the wing's inertia (supracoracoideus).

Less is known regarding the fiber type distributions of the supracoracoideus across a variety of avian species. In hummingbirds and zebra finches, however, the pectoralis and supracoracoideus muscles display similar, nearly exclusive fractions of fast-oxidative (type IIa) fibers, enabling sustained flapping flight performance and the specialization of hummingbirds to hover in place while feeding at nectar sources. Given these morphological features of the major flight muscles of birds, let us examine how the two flight muscles are activated to contract to move the wing and generate the mechanical and aerodynamic power necessary for sustained flight.

Flight muscle contractile mechanics

Measurements of the in vivo contractile strains and forces generated by the large pectoralis muscle in a variety of species show that the pectoralis undergoes large shortening strains (from +20–25% to –10–15% of resting fascicle length; ~ 35% overall) during the downstroke (Figure 3A; note that *in vivo* measurements of muscle fiber length changes are made at the level of muscle fascicles, which comprise small bundles of muscle fibers within the muscle). Electromyography (EMG) recordings show that the pectoralis is activated near the end of upstroke, so that it develops peak force while shortening during the downstroke. As a result, the muscle performs substantial mechanical work, which describes a counterclockwise 'work loop' (Figure 3B) to accelerate and move the wing. By contracting at a high frequency, the pectoralis generates a large power output (work per time, or muscle work per cycle times wingbeat frequency). The pectoralis relaxes by the end of the downstroke, enabling it to be passively stretched during the upstroke by the supracoracoideus, its primary antagonist.

Measurements of supracoracoideus motor activation (EMG), contractile fascicle strains and force generation in pigeons show that the supracoracoideus is activated late in downstroke, developing force to decelerate the wing and subsequently re-accelerate its motion in upstroke (Figure 4). Measurements of stress (force per area) in the tendon of the supracoracoideus indicate that the elastic energy stored and recovered during wing reversal into upstroke contributes ~25% of the energy to move the wing (75% being generated by work performed by the supracoracoideus muscle fibers). The pectoralis also pronates the wing in downstroke, contributing to aerodynamic thrust by changing the wing's angle of attack, whereas the supracoracoideus supinates the wing in upstroke. Thus, the pectoralis muscle functions to perform aerodynamic work. By contrast, the supracoracoideus muscle mainly functions to overcome wing inertia at the downstroke–upstroke transition of wing motion.

In comparison to larger birds, the timing of muscle activation in hummingbirds is substantially phase-advanced with respect to the wing stroke cycle, such that the pectoralis is activated during the upstroke and the supracoracoideus is activated during the downstroke. This earlier motor activation compensates for the delay in muscle force development achieved during the subsequent half cycle of wing motion due to the high contractile frequency (~40–45 Hz) of the hummingbird flight muscles associated with their ability to power sustained hovering.

Less is known regarding the details of motor recruitment, fiber type, and contractile function of the much smaller arm wing muscles. These muscles control changes in wing shape and distal wing angle of attack that are important for maneuvering, as well as being critical for the control of flight during landing. But although the small

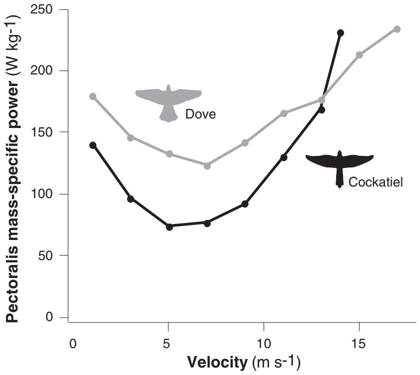

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Figure 5. Mechanical power output versus flight speed.

By recording the work output of the pectoralis during each wingbeat cycle and multiplying this by wingbeat frequency, the mechanical power output of the pectoralis can be measured over a range of flight speeds in a wind tunnel. Such recordings for cockatiels and for doves demonstrate a 'U'-shaped mechanical power curve that matches the aerodynamic power curve predicted by changes in induced power relative to profile and parasite powers (see the primer by Tobalske in this issue). Compared with doves, cockatiels have a more pronounced 'U'-shaped power curve with lower muscle power requirements over much of their speed range, resulting from their higher aspect ratio and more pointed wings that reduces their disc loading (area swept by the wings/body weight) and, correspondingly, their induced aerodynamic power requirement.

intrinsic wing muscles play a role in how the wing operates as an airfoil to generate aerodynamic power, they likely do not contribute much to the overall muscle mechanical power output required to support the bird's weight during flight. For example, measurements of muscle strain and activation in pigeons show that the triceps and biceps muscles stabilize and control elbow extension during downstroke and flexion during upstroke in moderate speed flight but perform little work doing so.

Muscle biomechanics and aerodynamic predictions for flight power requirements

As discussed by Tobalske in his primer on avian aerodynamics in this issue, aerodynamic theory (based on fixed-wings and steady airflow) predicts a 'U'-shaped relationship for aerodynamic power requirements as a function of forward flight speed. This is because the induced power requirement of the wings to move air downward in support of the bird's weight is high during hovering and at slow flight speeds. As a bird increases its forward flight speed, its induced power requirement decreases. With increased flight speed, however, its profile power (the drag on the wings x flight velocity) and parasite power (the drag on the body x flight velocity) both begin to increase exponentially (drag being proportional to velocity squared). The increase in profile and parasite power sets an upper limit on the maximum sustained flight speed that a bird can achieve. And, given that the total power requirement is lowest at an intermediate speed, aerodynamic theory predicts that birds can be expected to carry out most flight activities, including longer distance migration, by flying at airspeeds that either minimize their energy expenditure over time or their metabolic cost to travel a given distance. Indeed, migrating birds are believed to make use of meteorological weather patterns and air currents to reduce their flight cost.

Because the pectoralis muscles represent approximately 80% of the flight muscle mass of a bird, measurements of pectoralis mechanical power output (Figure 5) provide a direct test for how the mechanical power requirements of flight vary in relation to different flight behaviors and over a range of flight speeds. Measurements made with birds (cockatiels, *Nymphicus hollandicus*, and doves, *Streptopelia risoria*) trained to fly in a wind tunnel confirm aerodynamic predictions that the mechanical power requirements of the pectoralis are high during very slow flight, decreasing to a minimum at an intermediate flight speed, and then increasing again at faster flight speeds.

Birds show a broad suite of musculoskeletal, neural and feather adaptations that enable them to fly with remarkable agility, to navigate complex environments, and sustain robust flight performance in challenging wind conditions. By evolving the remarkable ability to fly, birds greatly expanded their geographic foraging and mating ranges, improved their ability to avoid ground-based predators, and achieved seasonal migratory routes over inhospitable regions (the Saharan desert, for example). This resulted in the successful and explosive diversification of modern birds that we know today, which number in the range of 11,000 extant species, even though the future success of many species is threatened by human impacts and climate change. Hopefully, the robust and spectacular flight abilities that birds have evolved will enable most species to adapt to changes in climate and resulting changes in the timing and locations of valued food sources.

Our understanding of bird flight biomechanics will benefit from future studies of the neuromuscular and skeletal mechanics of a broader diversity of avian species, carrying out a range of flight activities. Such studies may be integrated with field recordings of bird flight performance using remote monitoring technologies (GPS, accelerometry, and heart rate recordings) that will link the internal neuromuscular biomechanics underlying flight ability to broader ecological strategies that birds employ to navigate, migrate, and pursue prey or avoid their predators.

DECLARATION OF INTERESTS

The author declares no competing interests.

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