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Hummingbird flight

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(Article begins on next page)

of a vernalized plant would flower before the onset of winter. Resetting the vernalized state means that each generation of plants is able to respond appropriately to the changing seasons.

Many different species of plants show a vernalization response — do they all use the same mechanism to control this response? No, the vernalization response has clearly evolved independently in monocots like wheat and barley and in dicots like *Arabidopsis*, canola and other Brassicas. While the physiological properties of the vernalization response are similar between the two plant kingdoms, the molecular details differ. As we've seen, in *Arabidopsis, FLC*, a repressor of flowering, is the target of epigenetic regulation. In cereals, the expression of a related gene, *VERNALIZATION 1,* a promoter of flowering, is also under epigenetic control. In both cases, the epigenetic control is provided by the activity of Polycomb group proteins.

What about tulips — they need to be cold treated to make them flower, don't they? Just to confuse you, the response in tulips is somewhat different from the classical vernalization response that I've described. Rather than initiating floral development in tulips, the cold allows the inflorescence stem to grow. Growth of the stem raises the flower bud, which is formed during the warm summer days, above the ground so that you can see the flower.

Where can I find out more?

Angel, A., Song, J., Dean, C., and Howard, M. (2011). A polycomb-based switch underlying quantitative epigenetic memory. Nature *476*, 105–108.

Balk, P.A., and Douwe de Boer, A. (1999). Rapid stalk elongation in tulip (*Tulipa gesneriana* L. cv. Apeldoorn) and the combined action of cold-induced invertase and the water-channel protein γTIP. Planta *209*, 346–354.

Finnegan, E.J., and Dennis, E.S. (2007). Vernalization-induced trimethylation of Histone H3 lysine 27 at *FLC* is not maintained in mitotically quiescent cells. Curr. Biol. *17*, 1978–1983.

Schmitz, R.J., and Amasino, R.M. (2007). Vernalization: A model for investigating epigenetics and eukaryotic gene regulation in plants. Bioch. Biophys. Acta *1769*, 269–275.

Trevaskis, B., Hemming, M.N., Dennis, E.S., and Peacock, W.J. (2007). The molecular basis for vernalization-induce flowering in cereals. Trends Plant Sci.*12*, 362–367.

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Primer

Hummingbird flight

Douglas Warrick[1], Tyson Hedrick[2], María José Fernández[3], Bret Tobalske[4], and Andrew Biewener[5]

Hummingbirds are very distinctive in their form and behavior, the evolution of which is tightly connected to the evolution of their primary source of energy — floral nectar. About forty million years ago, the practical use of this dense fuel, available only in widely-dispersed, insect-sized aliquots — it was originally intended for insect pollinators — presented a severe test to the avian bauplan. This selective pressure forced broad changes in form and function, affecting anatomical structures ranging from the feeding apparatus to the locomotor system. We describe here how these pressures shaped a bird that flies like a bird into one that flies like a fly.

In terms of cost per unit distance, flight is easily the most efficient form of movement over terrestrial landscapes — making foraging at these dispersed, diminutive larders worthwhile. Assuming that flying while removing nectar is better than landing, the locomotor system must continue to operate efficiently while the bird is at the flower; moreover, it must be precisely modulated to allow a safe approach and steady feeding. How does a hummingbird meet these requirements?

Theoretically, efficiency in hovering flight is a tall order. Data from analyses of aerodynamic models and from empirical studies of the mechanical power and metabolic cost of flight at different speeds in birds all agree that hovering flight is much more expensive than intermediate speed forward flight (Figure 1). Most birds avoid the expense of low speed flight by spending little time flying at those speeds; indeed, many large avian species lack the mass-specific power to fly at slow speeds, requiring gravity or wind to provide them with sufficient energy to get airborne. Because of this adverse scaling of the

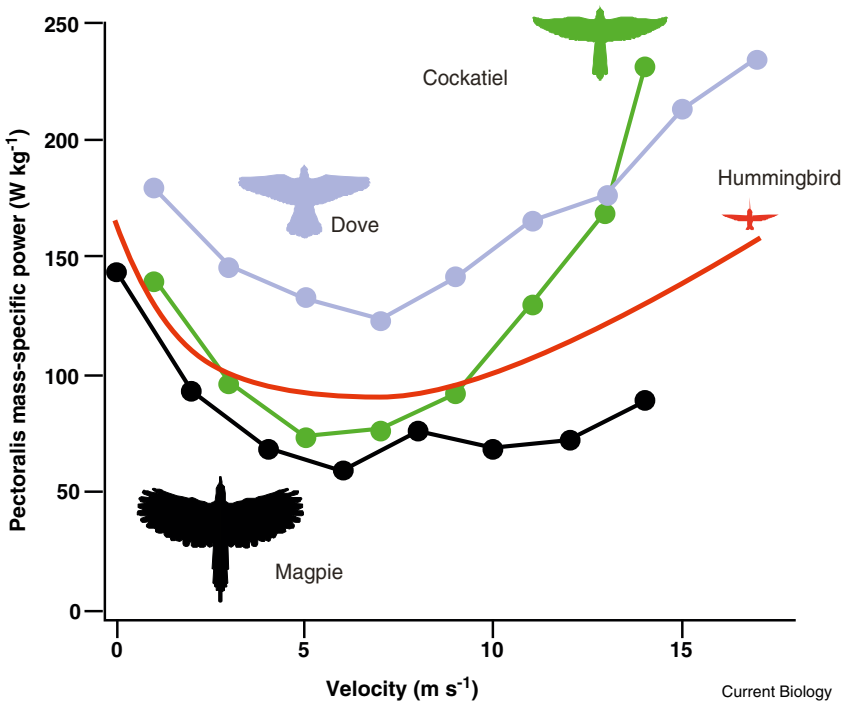

Figure 1. The mechanic power produced by birds in flight.
While the mass-specific power produced by their flight muscles is similar to that of other birds at a flight speed of zero, only hummingbirds (red curve) can produce that power aerobically, and thereby sustain hovering indefinitely. Modified from Clark and Dudley (2010) and Tobalske *et al*. (2003).

mass-specific power available for flight and the high power required for hovering flight, sustained, aerobically driven hovering is a more attainable goal for small birds. Therefore, in combination with the limited absolute quantities of food produced by flowers, selection for small size was probably integral to hummingbird evolution from the outset.

But being small isn't enough. For most birds in slow or hovering flight, the recovery stroke (henceforth, upstroke) of the wings is of little or no use for weight support. For such a bird trying to maintain altitude, the downstroke must produce roughly double the weight support during the downstroke, resulting in alternating ascents and free-falls within each wingbeat cycle. Although an average vertical position could be achieved, the rapid displacements would not allow the precision needed to maintain position at a flower and extract nectar. Moreover, the cessation of useful aerodynamic force during upstroke would also result in intermittent loss of positional control in the other two dimensions, presenting an additional challenge for a bird needing to track motions of flowers driven by the wind.

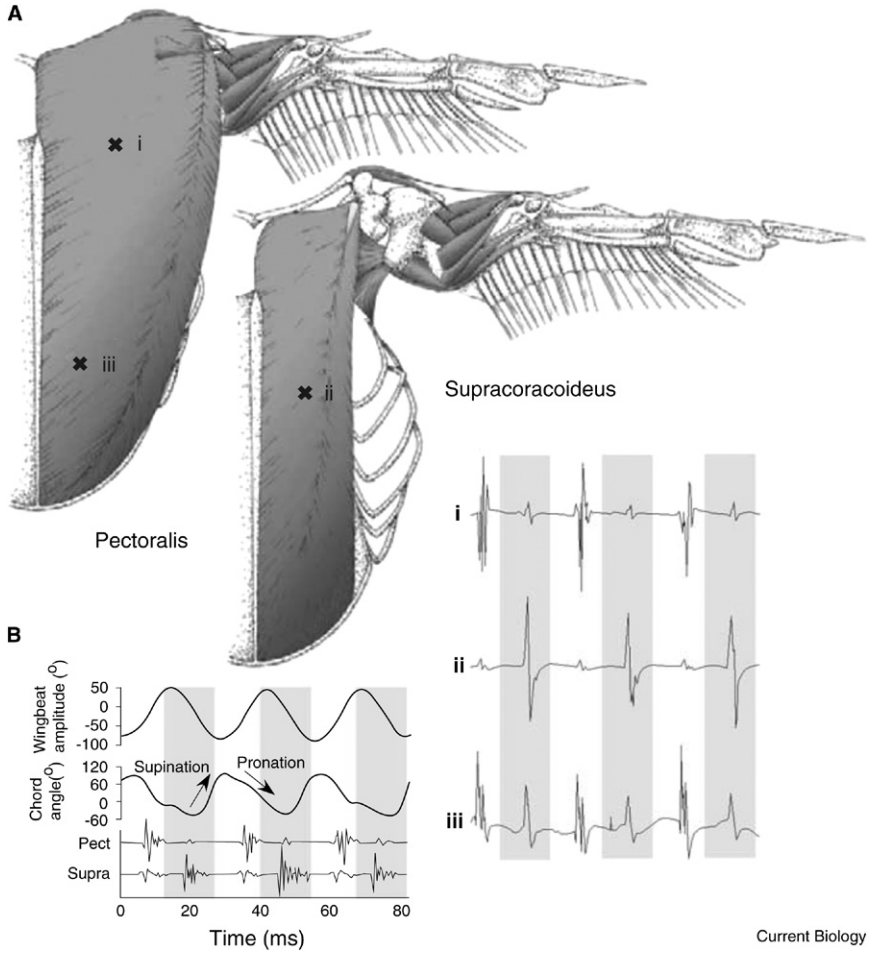

Figure 2. Flight muscle activity in hummingbirds.
Muscle activity in hummingbirds during hovering; shaded areas represent kinematic downstroke in both A (Anna's hummingbirds) and B (Rufous hummingbirds). (A) Ventral view of the flight muscles, with regional (i–iii) variation in muscle activity. (B) Timing of muscle activity with wing movement. (A) modified from Altshuler *et al*. (2010); (B) modified from Tobalske *et al*. (2010).

Muscle mechanics

The muscles responsible for the movement of the avian wing through the downstroke and upstroke are, respectively, the pectoralis and supracoracoideus. In most birds with aerodynamically limited upstrokes, the supracoracoideus is typically 1/5th the size of the pectoralis. Tasked with more than just upstroke recovery, the supracoracoideus of hummingbirds is about half the size of the pectoralis. These large flight muscles are composed exclusively of fast oxidative-glycolytic fibers (type IIa), with giant mitochondria occupying ~50% of total volume, allowing hummingbirds to sustain very high wingbeat frequencies and high aerobic power. Indeed, hummingbirds display some of the highest known mass-specific metabolic rates among vertebrates. These high ATP requirements are met by high rates of sugar and fatty acid oxidation, made possible by high enzymatic flux capacities in the flight muscles. These allow hummingbirds to switch between fuels, depending on prandial state and flight behaviour. For instance, Ruby-throated hummingbirds migrating across the Gulf of Mexico likely rely on fatty acid oxidation. Nevertheless, when glucose is oxidized compared to fatty acids, hummingbirds achieve a ~15% increase in mitochondrial P/O ratio (the relationship of ATP production to oxygen consumption), making glucose a preferable fuel for hummingbirds operating at higher ATP requirements or in oxygen scarce environments such as at high elevations.

The extreme frequency of flight muscle contraction (the smallest hummingbird, the Bee hummingbird, has a wingbeat frequency of ~80 Hz) and the aerobic nature of those muscles result in a distinctive pattern in their activity. Whereas in most birds the contraction of the pectoral muscles results in an electrical signature (electromyogram, or EMG) showing many spikes, corresponding to variations in the timing of the recruitment of motor units, hummingbird EMGs are tightly synchronized, generally displaying only a few (one to five) spikes (Figure 2A,B). In that wingbeat frequency does not change appreciably with changes in flight speed or air density, it is perhaps not surprising that neither does this spike pattern change under these conditions. However, when taxed by flying at very high speed, or hovering in low density air, the amplitude of the wingbeats increases, as do the amplitudes of the EMG spikes, suggesting an increase in the number

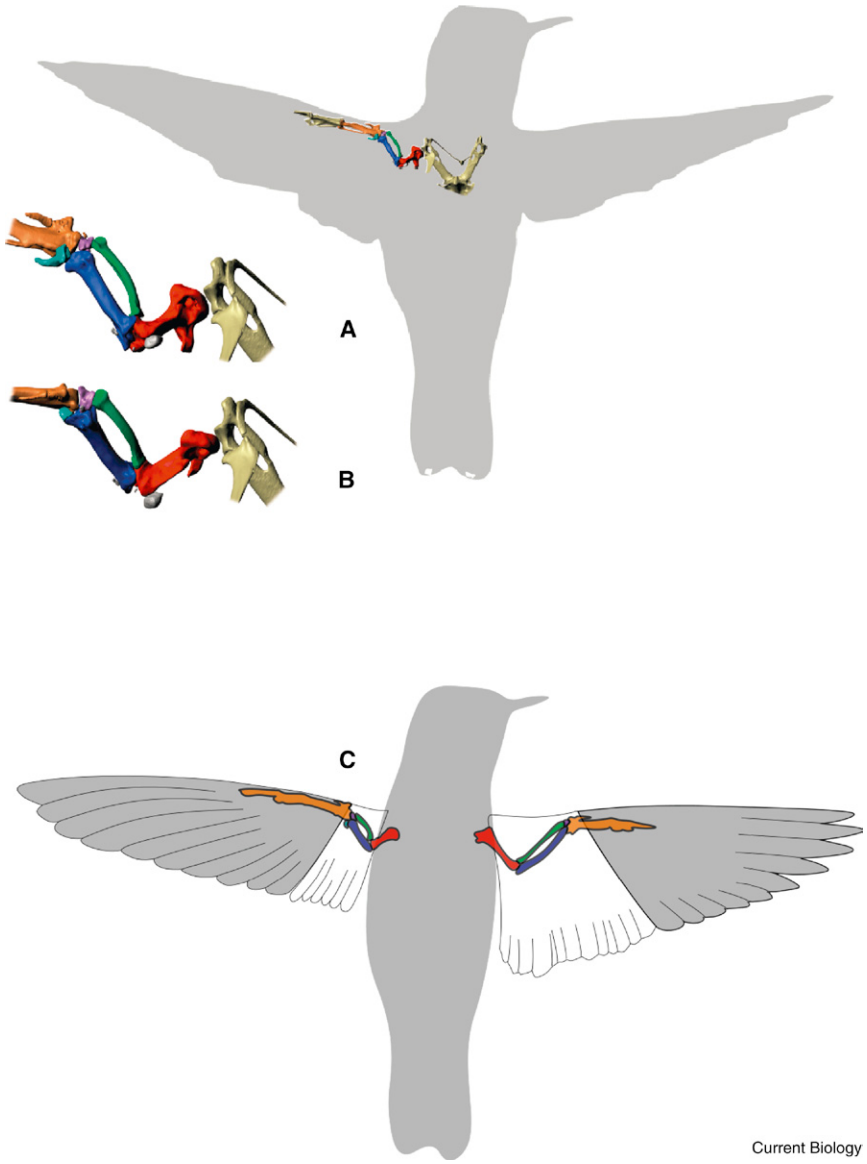

Figure 3. Hummingbird forelimb skeleton in hovering flight.
(A) Position at mid-downstroke. (B) Position at mid-upstroke. (C) Left, hummingbird wing, with handwing feather (primaries) in grey. Right, pigeon wing scaled to hummingbird wing length, illustrating the proportionately smaller handwing. Off-white, pectoral girdle; red, humerus; blue, ulna; green, radius; brown, manus. Modified from Hedrick *et al*. (2011).

of motor units recruited. Furthermore, when forced to briefly lift a heavy load, the number of spikes increases, suggesting that individual motor units and muscle fibers are being recruited multiple times in a single stroke, possibly at a frequency too high to sustain with ATP supplied by aerobic metabolism.

Musculoskeletal dynamics

Together with an enlarged supracoracoideus that provides power for upstroke, hummingbirds must also invert their wings to produce useful aerodynamic force for weight support. Recent high-speed X-ray videos of the hummingbird wing skeleton have revealed that most of the inversion of the wing is produced by supination of the forearm, which inverts the bones (and feathers) of the handwing (Figure 3A,B). In pigeons that also display a 'wingtip reversal', this inversion of the hand wing has been shown to produce aerodynamic forces that are used in both weight support and maneuvering during slow speed flight. However, this long-axis rotation of the forearm only inverts the primary flight feathers. For most birds, the handwing accounts for ~50% of total wing area. Hummingbirds, by contrast, have exceptionally long primary flight feathers, which form 75% or more of the wing area (Figure 3C). Consequently, by inverting their handwing, hummingbirds achieve a more completely reversed airfoil during upstroke. Although the neuromuscular control and musculoskeletal dynamics of the hummingbird's forearm are not completely understood, the robust bones hint at their ability to deliver this range of motion under what must be exceptionally large torsional loads.

The same X-ray video recordings revealed another key to hummingbird hovering flight linked to movements of the humerus. The humerus of hummingbirds is substantially shortened in comparison with that of other birds (except for their close relatives, the swifts). It is also held nearly perpendicular to the leading edge of the wing, and is strongly rotated about its long axis during the middle of upstroke and downstroke. In this posture, rather that supinating or pronating the wing, the torque produced by the pectoralis and supracoracoideus about the humeral long-axis substantially increases the translational velocity and excursion of the wing.

The use of this mechanism is dictated by the absolute scale of the hummingbird body. The aerodynamic force produced by the skeleton and its overlying feathers is a function of the square of the incident air velocity over them. That is, these muscles need to move the forelimb at high velocity — a difficult task when the wing is only a few centimeters long and is rotating like a tiny propeller at the shoulder. Hummingbirds achieve these limb velocities by having the pectoralis and supracoracoideus operate through the very short input lever afforded by the posteriorly-oriented humerus. While these muscles can thus produce large limb excursions and velocities without requiring of them excessive and inefficient contractile velocities, they must consequently be at a considerable mechanical disadvantage in terms of absorbing the resulting aerodynamic output forces. This may be another reason hummingbirds possess, for their body size, the largest downstroke

muscles and upstroke muscles of any bird.

Aerodynamics

The result of these subtle but remarkable musculoskeletal adaptations is a wing-stroke cycle closely matching in form — although not quite in function — that of hovering insects. While the two half-cycles of many flying insects may achieve nearly equal amounts of lift, studies of the vortex wakes and airflow near the wings of hovering hummingbirds show that they are able to aerobically produce 25–33% of their total weight support with the upstroke, thereby minimizing their fall from floral grace (Figure 4). Remarkably, this is not much different from the weight support pigeons can generate (27%) with their tip reversal upstroke in brief periods of slow flight. While sustained slow and hovering flight is beyond the aerobic limits of pigeons, the presence of an aerodynamically active upstroke in a species that is phylogenetically distant from hummingbirds reaffirms the fundamentally avian nature of the hummingbird wing-stroke.

The absolute contribution of upstroke lift to weight support may be less important than the precise manipulation of airflow by the hummingbird wing during transitions between upstroke and downstroke. Hummingbird wings are relatively small, narrow (high aspect ratio), and extremely thin at the leading edge. As it does in insect wings, the sharp leading edge creates a leading edge flow that produces greater lift than would a laminar flow typical of large wings with rounded leading edges. In hummingbirds, the pressure differential around the sharp leading edge dominates the circulation around the wing, creating a vortex, bound to and circulating completely around the chord of the wing. This flow pattern allows the wing to rotate around its long axis inside the vortex without interrupting it — and perhaps contributing to it — during the half-stroke transitions. Thus, aerodynamic force production created by translational movements of the wing during up- and down-stroke is sustained as the wings are rotated back into position for the next up or down stroke, and only ends briefly when the translational part of that next half stroke begins. The brief (~2 ms) interruption in aerodynamic force production results in small body movements easily compensated for by motion of the hummingbird's neck, which stabilizes its head position.

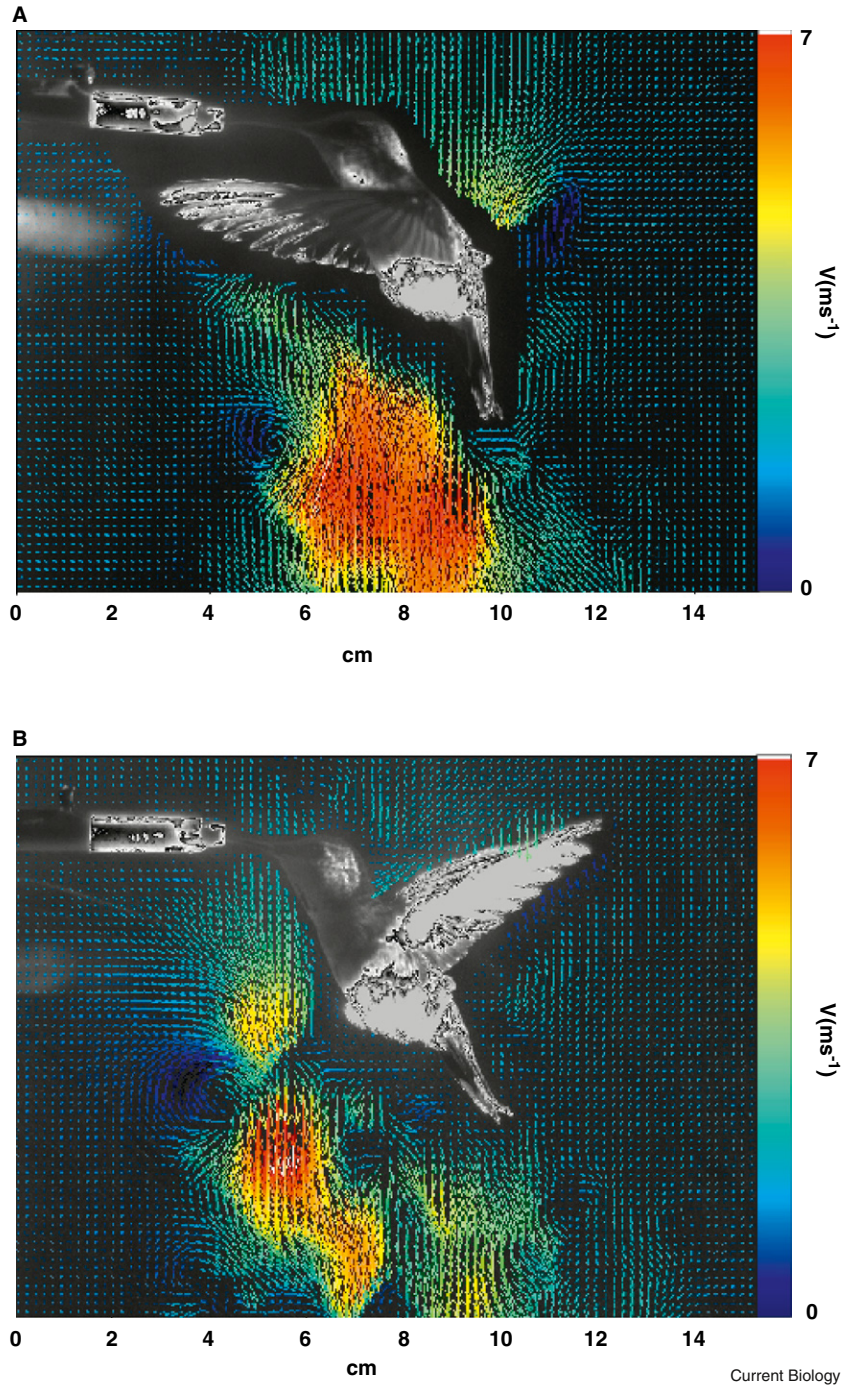

Figure 4. Hummingbird hovering aerodynamics.
Flow field (determined by particle image velocimetry) beneath a hovering hummingbird at the end of downstroke (A) and the end of upstroke (B) illustrating the relative strengths of the momentum jet (large red arrows = high velocity) at the end of each half-cycle. The momentum jet produced by the downstroke is normally two or more times that produced by the upstroke. Modified from Warrick *et al*. (2005).

Power output, maneuvering and stability

Despite the evolution of these aerodynamic and biomechanical refinements, hovering remains an expensive task for hummingbirds.

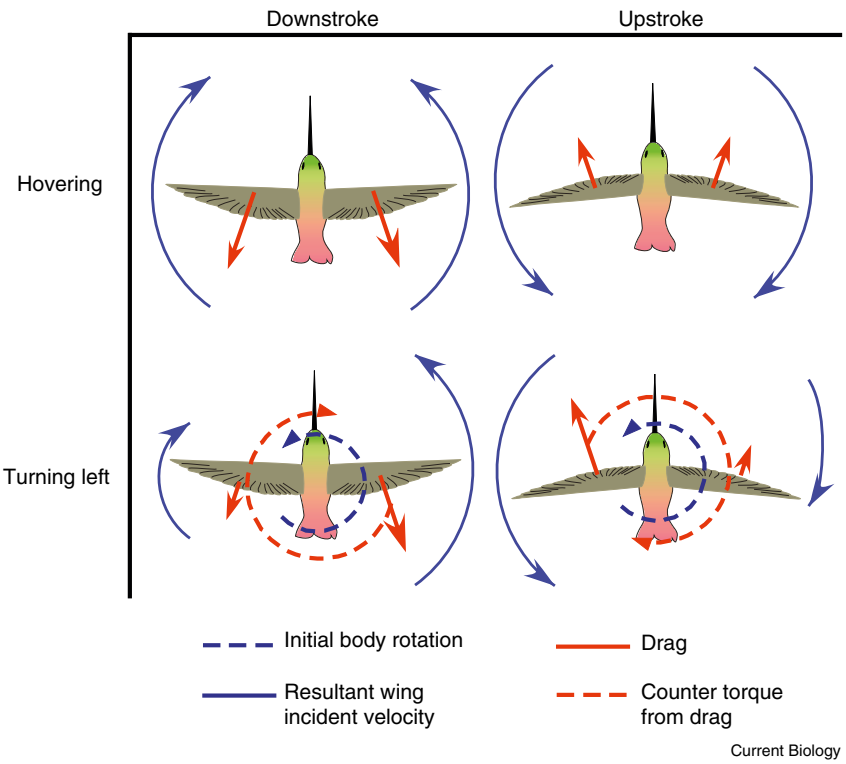

Figure 5. Hummingbird flight stability.
When perturbed into a body rotation (here, to the left), the resulting asymmetry in wing velocity and drag produces a stabilizing counter torque. Modified from Hedrick *et al*. (2011).

Hummingbirds living and feeding in less dense air at higher elevation habitats have experienced selection for increased wing size relative to their body weight in order to reduce their wing loading (weight/wing area) and the metabolic cost of hovering. But larger wings come with a price: they operate with higher inertia — both intrinsic to the wing and the added mass of the air they move — resulting in lower maximum wingbeat frequencies and lower maximum mass-specific aerodynamic power outputs. So although larger-winged hummingbirds can still hover effectively at high elevations, they have less marginal power to perform more demanding flight maneuvers such as ascent and rapid acceleration, which are important for competitive interactions. This likely affects their evasive performance, and may play an important role in intraspecific competitive interactions, which are common between highly territorial males as well as affecting their ability to capture aerial insect prey, and avoid becoming prey themselves. However, hummingbirds are able to shift their competitive ability with elevation and it has been shown that burst aerodynamic power, unlike wing loading, is significantly correlated with territorial behaviour.

So important is flight performance that there is clear evidence of sexual selection for male flight performance in many species (such as those of the 'bee' hummingbird clade). Males of several species (for example, Anna's, Allen's, Rufous) engage in ostentatious displays of mass-specific power, muscle force and maneuverability, involving repeated vertical ascents of 10–40 m, followed by rapid power descents in which birds accelerate to 25 ms^{-1} (55 mph) or more. During the recovery 'pullout', the pectoral muscles can be supporting as much as ten times the animal's body weight, each producing perhaps as much as 0.2N (0.045 lbs) of force. It is unlikely that such an honest and relevant signal of flight performance could be ignored by a female judging the genes of a suitor; nevertheless, the circumspect nature of females has driven the males of some species to add acoustic accompaniment to these displays. By precisely presenting their tail and/or wing feathers at high flight speeds, the males induce aeroelastic flutter of the feathers, producing complex, species-specific aural signals. Flutter is a condition most birds (and aerodynamic engineers) assiduously avoid, as it may impose severe stress on flight structures, potentially leading to their catastrophic failure — which may explain its use as an attention-getting sound in several hummingbird species.

It should be noted that the maneuvering skills of hummingbirds allow them access to another valuable resource: insects. Hummingbirds are not only supremely pre-adapted to gleaning insects from nearly any surface or aspect, they also capture insects on the wing — a feat made easier by their ability to expand the base of their jaws both laterally and dorso-ventrally. In that they take insects by flying their enlarged maw around the prey, rather than plucking them out of the air with tweezers, hummingbirds have converged on a technique exhibited by other aerial insectivores, for example swallows. And with this jaw suspension, it is not difficult to imagine an ancestral stem hummingbird, in constant contact with nectivorous insects, simply opting to specialize on eating these protein-rich competitors, thereby giving rise to a sister clade in the Apodiformes, the swifts. Likewise, it is not difficult to imagine the evolutionary sequence reversed, with selection for low speed insectivory on a swift-like ancestor leading to a hummingbird form pre-adapted for nectivory. The earliest Apodiformes known are early Eocene (~50 million years ago) swift-like birds, suggesting the latter scenario, with the intermediate pectoral girdle and forelimb morphology of another Apodiforme, the tree swifts (Hemiprocnidae), representing a possible ancestral state from which both hummingbirds and apodid swifts evolved. If so, the similarly robust and shortened humeri of the Trochilidae and Apodidae would represent convergence — perhaps in both a result of selection for the high transmission ratio needed to produce high limb velocities.

But spectacular maneuverability in a small animal is not surprising; indeed, more impressive is that an

animal with low inertia and relatively large surface areas presented to varying airflow conditions can maintain strict body control and a rigidly-fixed position. Yet, there is theoretical and empirical evidence that the act of flapping itself can produce passive damping effects, which make stability and control of hovering maneuvers easier than might be expected. For example, if a hovering hummingbird is perturbed by a gust of wind into a rotational movement, the induced body rotation will create a velocity asymmetry — and therefore drag — of the flapping wings that will oppose the rotation (Figure 5). Analyses of this general effect — the combination of wing and body velocities during rotation — across a range of body sizes show that this flapping counter torque slows the rotation of small animals more quickly than it does large animals, and that it provides damping in all axes (pitch, roll and yaw), as well as linear perturbations such as sideslip.

Flapping counter torque stabilizing effects require that the wings are extended. Because of this, birds that fold their wings close to their body during upstroke to reduce the energy required for the recovery stroke will be inherently less stable. Given that hummingbirds may, in addition, manipulate upstroke lift forces to their benefit, the control and stability advantages of an aerodynamically active upstroke are clear, and may be as compelling an explanation for their unique flight style as the need for efficiency while hovering.

Whether the primary selective pressure was for steadier feeding at a nectar source or the increased efficiency provided by an aerodynamically active upstroke, the result is a diverse clade of birds, with an order of magnitude range in body size - at 20 g, the largest hummingbird, *Patagona gigas*, exceeds the mass of many small, non-nectivorous birds — able to emulate the utility of the insects flower nectar sources originally evolved to attract. As evidence of this emulation, since the early Oligocene, when the first modern hummingbirds appeared, the Trochilidae have diversified into 300+ species, and have co-evolved along with their nectar-provider plants into hummingbird-specific, and even species-specific mutualistic relationships, just as have their insect predecessors.

The convergence on form and function in insects and hummingbirds is a striking testament to the rigors of low speed flight and the ability of natural selection to respond to achieve comparable features of flight performance linked to nectivory, despite vastly different invertebrate and vertebrate body plans.

Further reading

Altshuler, D.L. (2006). Flight performance and competitive displacement of hummingbirds across elevational gradients. Am. Nat. *167*, 216–229.

Altshuler, D.L., Dudley, R., and McGuire, J.A. (2004). Resolution of a paradox: Hummingbird flight at high elevation does not come without a cost. Proc. Natl. Acad. Sci. USA *101*, 17731–17736.

Clark, C.J., Elias, D.O., and Prum, R.O. (2011). Aeroelastic flutter produces hummingbird feather songs. Science *333*, 1430–1433.

Clark, C.J., and Dudley, R. (2010). Hovering and forward flight energetics in Anna's and Allen's hummingbirds. Phys. Biochem. Zool. *83*, 654–662.

Hedrick, T.L., Cheng, B., and Deng, X. (2009). Wingbeat time and the scaling of passive rotational damping in flapping flight. Science *324*, 252–255.

Hedrick, T.L., Tobalske, B.W., Ros, I.G., Warrick, D.R., and Biewener, A.A., (2011). Morphological and kinematic basis of the hummingbird flight stroke: scaling of flight muscle transmission ratio. Proc. R. Soc. Lond. B *279*, 1986–1992.

Ros, I.G., Bassman, L.C., Badger, M.A., Pierson, A.N., and Biewener, A.A. (2011). Pigeons steer like helicopters and generate down and upstroke lift during low speed turns. Proc. Natl. Acad. Sci. USA *108*, 19990–19995.

Tobalske, B.W., Warrick, D.R., Clark, C.J., Powers, D.R., Hedrick, T.L., Hyder, G.A., and Biewener, A.A. (2007). Three-dimensional kinematics of hummingbird flight. J. Exp. Biol. *210*, 2368–2382.

Tobalske, B.W., Hedrick, T.L., Dial, K.P., and Biewener, A.A. (2003). Comparative power curves in bird flight. Nature *421*, 363–366.

Tobalske, B.W., Biewener, A.A., Warrick, D.R., Hedrick, T.L., and Powers, D.L. (2010). Effects of flight speed upon muscle activity in hummingbirds. J. Exp. Biol. *213*, 2515–2523.

Warrick, D.R., Tobalske, B.W., and Powers, D.L. (2005). Aerodynamics of the hovering hummingbird. Nature *435*,1094–1097.

Weis-Fogh, T. (1972). Energetics of hovering flight in hummingbirds and in Drosophila. J. Exp. Biol. *56*, 79–104.

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Nonconscious fear is quickly acquired but swiftly forgotten

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The ability to learn which stimuli in the environment pose a threat is critical for adaptive functioning. Visual stimuli that are associated with threat when they are consciously perceived can evoke physiological [1] and neural [2] responses consistent with fear arousal even when they are later suppressed from awareness. It remains unclear, however, whether a specific *new* fear association can be acquired for stimuli that are never consciously seen [3], and whether such acquisition develops differently from conscious learning. It has recently been suggested [4] that, rather than simply affording a degraded version of conscious experience, processing of emotional stimuli without awareness may differ qualitatively from conscious perception, evoking different patterns of neural activity across the brain or differences in the time-course of behavioral and physiological responses. Here, we investigated nonconscious fear acquisition and how it may differ from conscious learning using classical fear conditioning, and found that conscious and unconscious fear acquisition both occur, but evolve differently over time.

We presented observers with monocular conditioned stimuli (CSs, a male and female fearful face) that could be suppressed from awareness for long durations (4 seconds) by salient dynamic stimulation of the other eye (continuous flash suppression, CFS; Figure 1A). One image (CS+) co-terminated with a mild shock to the wrist on 50% of its presentations; the other (CS–) was never paired with shock. (We define fear in this context as an anticipatory physiological response to a stimulus that predicts an aversive outcome. This is measured by phasic increases in skin conductance responses