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Review

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Evolution of avian flight: muscles and constraints on performance

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Competing hypotheses about evolutionary origins of flight are the 'fundamental wing-stroke' and 'directed aerial descent' hypotheses. Support for the fundamental wing-stroke hypothesis is that extant birds use flapping of their wings to climb even before they are able to fly; there are no reported examples of incrementally increasing use of wing movements in gliding transitioning to flapping. An open question is whether locomotor styles must evolve initially for efficiency or if they might instead arrive due to efficacy. The proximal muscles of the avian wing output work and power for flight, and new research is exploring functions of the distal muscles in relation to dynamic changes in wing shape. It will be useful to test the relative contributions of the muscles of the forearm compared with inertial and aerodynamic loading of the wing upon dynamic morphing. Body size has dramatic effects upon flight performance. New research has revealed that mass-specific muscle power declines with increasing body mass among species. This explains the constraints associated with being large. Hummingbirds are the only species that can sustain hovering. Their ability to generate force, work and power appears to be limited by time for activation and deactivation within their wingbeats of high frequency. Most small birds use flap-bounding flight, and this flight style may offer an energetic advantage over continuous flapping during fast flight or during flight into a headwind. The use of flap-bounding during slow flight remains enigmatic. Flap-bounding birds do not appear to be constrained to use their primary flight muscles in a fixed manner. To improve understanding of the functional significance of flap-bounding, the energetic costs and the relative use of alternative styles by a given species in nature merit study.

This article is part of the themed issue 'Moving in a moving medium: new perspectives on flight'.

1. Overview

Muscles are obviously key to the capacity of birds for flight, and the goal of this review is to explore current hypotheses of the ways muscles permit and constrain this capacity. Insight into the phylogeny of birds is improving rapidly, and this offers great promise for improving understanding of how evolution transformed ancestral theropod forms [1] into the derived, volant bird species we observe today. Genomic study [2–4] and the extraordinary rate of new discovery of fossil dinosaurs [5–10] have provided rich phylogenetic hypotheses from which we can begin to test patterns of historical transformation [11]. Concurrently, modern empirical and modelling techniques in comparative biomechanics offer new ways of testing hypotheses that link form and function. These include *in vivo* and *in situ* measures of the contractile behaviour of muscle [12–14]; high-speed, three-dimensional videography that can reveal details of wing motion [15,16]; X-ray videography of skeletal kinematics [16,17]; particle image velocimetry and computational fluid dynamics to reveal aerodynamics [18–20]. Research into the biomechanics of avian flight, to some extent, moved away from an ecomorphological and comparative to a phylogenetic emphasis during the past 20 years, in part because of excitement

(and funding opportunities) linked to the bioinspired design of autonomous flying robots [21,22]. Thus, detailed information on muscle contractile behaviour in relation to flight performance is often available only for selected model species such as the pigeon (*Columba livia*), only in rare cases within clades of closely related species [23,24], and formal synthesis of new insights into the phylogeny of birds with the form and function of their muscular systems is not presently feasible. New comparative studies will be essential for providing such a synthesis. In the meantime, the results of broad macroevolutionary processes are manifest in the general relationships between flight performance and body size in living birds; indeed, for the case of maximal power output, within-phylogeny studies provide useful new insight [24,25]. Thus, after summarizing exciting new thinking about flapping or gliding evolutionary origins of avian flight, I briefly describe key aspects of musculoskeletal design relative to wing morphing in extant birds and then use as an organizing theme the profound effects of body size upon muscle form and function.

2. Evolutionary origins of avian flight

Whether avian flight evolved beginning with gliding or flapping in an ancestor continues to fascinate and provoke passionate debate. Using wingbeats to support weight and generate thrust requires enormous work and power output from the primary flight muscles [12,13,26,27] whereas gliding, with isometric contractions, requires a smaller mass of muscle to support body weight [28,29]. The massive energetic investment in paired pectoralis and supracoracoideus muscles used to power flight in extant birds [30,31], coupled with a prominent, ossified keel that does not appear in early fossil forms [1,32], make it initially appear obvious that flapping must be more derived than gliding. Historically, the argument over which kinematic event was most likely to provide an incremental first step in the origin of bird flight, something that could be favoured by directional selection for increased performance, was framed as a dichotomy between an arboreal hypothesis in which ancestors climbed up and then glided down (e.g. [33,34]) or a cursorial hypothesis in which they used flapping to enhance running capacity and ultimately take-off from the ground to move upward (e.g. [35,36]). One alternative hypothesis for the use of flapping as a precursor to powered flight is the pouncing-predator hypothesis in which swooping motions of the wings of a predatory proaves could be used to catch prey [37].

A novel hypothesis favouring a flapping origin that has risen to the forefront of the debate in recent years involves wing-assisted incline running (WAIR) in which a bird uses flapping motions of its wings to develop incrementally useful amounts of force that assist its effort to climb substrates to gain access to refugia, for example, to escape from predators ([38–40]; figure 1). This behaviour has been studied extensively in ontogenetic series up to adults in several species of Galliform birds [32,38–43] and in adult pigeons (*C. livia*; [26]). Additionally, wing-assisted swimming and branching behaviour are described for developing ducks (Anseriformes) and owls (Strigiformes; [44]). Once in an elevated location, extant birds use flapping and not gliding to control their descent; observation of this pattern led to the ‘fundamental wing-stroke’ hypothesis that flapping is plesiomorphic for birds [42]. The central argument is that the developing wing can provide

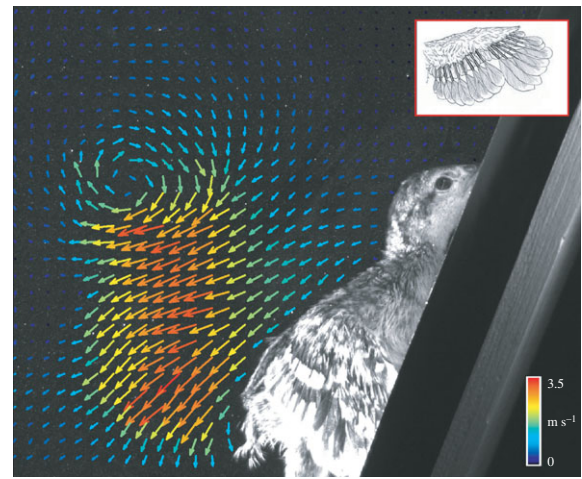


Figure 1. A cross-section of a shed vortex in the wake of a baby chukar (*Alectoris chukar*), 6 d.p.h., as measured using particle image velocimetry as the bird engaged in wing-assisted incline running [40].

useful, incrementally increasing forces for locomotion even before the birds can fly. Notably, this is also when they do not have fully ossified skeletons [32].

In direct competition with this idea, recent research into the gliding and steering capacity of insects and other non-avian taxa including amphibians [45–47] leads to a ‘directed aerial descent’ hypothesis in which static stability associated with wing and tail postures in parachuting and gliding [48,49] requires less from the neuromuscular and skeletal system, and therefore reveals that gliding is more parsimonious as the ancestral precursor to bird flight [50].

Different fossil evidence is invoked to support the fundamental wing-stroke hypothesis [32] or the directed aerial descent hypothesis [5,46,50]. Analysed in the context of a flapping origin, the locomotor capacity of fossil forms has been bracketed or estimated using fossilized details of wing anatomy and body size, extant data on limb kinematics in flying birds and running lizards, and empirical measures of aerodynamic force production by the partially developed wings of juvenile birds [51]. According to this line of reasoning, the incremental acquisition of locomotor capacity within ontogenetic series of birds is a useful extant system that can provide insight into evolutionary trajectories precisely because the incremental changes during ontogeny each result in improved functional capacity [32,44]. Proponents argue that an extant model system is more parsimonious as an explanation for incremental evolutionary steps. In line with this argument, there are no reports of extant bird species (or species of other vertebrates) that are known to incrementally adopt a sequence of gliding, low-amplitude flapping and fully formed flapping, which is the sequential trajectory indicated by the directed aerial descent hypothesis. Clearly, though, caution is warranted as the musculoskeletal system of modern birds is highly derived compared with their ancestors. In support of directed aerial descent, incremental improvements in the capacity for stability and manoeuvring are apparent when minor postural changes are made during gliding as measured in physical models designed upon the anatomy of a fossilized four-winged theropod [50]. A possible explanation for the lack of extant intermediate styles of wing motion is that they may not represent peaks in an adaptive landscape *sensu* Wright [52]. This possibility merits testing in ways that integrate palaeontology, phylogenetics and biomechanics [32,50,51].

Table 1. Nomenclatures.

F	frequency of vortex shedding (Hz)
d	diameter of trailing edge of rotor blade (m)
A	vertical amplitude of wing-tip excursion (m)
J	advance ratio (dimensionless)
St_{cruise}	Strouhal number during cruising flight (dimensionless)
St_{rotor}	Strouhal number for a rotor or propeller during hovering or low advance ratio (dimensionless)
U	translational velocity of the body (m s^{-1})
U_{blade}	tangential velocity of a given blade element along the length of a rotor or propeller

An interesting criticism of ontogenetic deployment of a fundamental wing stroke representing an evolutionary origin for flight is that vigorous, high-amplitude flapping at slow forward speeds is aerodynamically inefficient and thus could not have been favoured by directional selection [53]. This is based on the analysis of mechanisms of oscillating flow that are described by the Strouhal number (table 1); here, described for cruising flight (St_{cruise})

$$St_{\text{cruise}} = \frac{fA}{U}, \quad (2.1)$$

where f = the frequency of vortex shedding (Hz), A = wingbeat amplitude (m) and U = translational velocity of the whole body. For a diverse array of flying and swimming animals engaged in cruising locomotion, patterns of wing or hydrofoil oscillation conform to $St_{\text{cruise}} \sim 0.2$ [54]. Moving limbs to maintain $St_{\text{cruise}} \sim 0.2$ is interpreted to optimize propulsive efficiency, the ratio of aerodynamic power output to mechanical power input [55]. If one vortex is shed per downstroke, St_{cruise} is the ratio of wing-tip velocity to body velocity. Invoking St_{cruise} in relation to historical transformations leads to the conclusion that an evolutionary trajectory must have been from low-amplitude, low-frequency wing movement when an animal is moving slowly towards higher-amplitude, higher-frequency flapping when moving faster [53]. Thus, this analysis is consistent with the predictions of the incremental changes in the trajectory of wing kinematics in the directed aerial descent hypothesis [46,50].

There are two potential shortcomings of invoking St_{cruise} as a model for flapping motion during slow-speed locomotion, however. The first is an open question about whether evolutionary innovation could arise first for efficacy, getting a task accomplished, instead of efficiency, propulsive efficiency in this case, or, even more broadly, mechanical output relative to metabolic input. The other possible shortcoming is more detailed. The relationship between St_{cruise} and vortex production assumes a pitching and heaving airfoil or hydrofoil that is translating linearly forward (i.e. in the direction of propulsion; [55]). Consistent with the idea of lift-based propulsion, the wake of birds engaged in WAIR and using a 'fundamental wing stroke' indicates a single, dominant vortex is shed per downstroke ([40]; figure 1). However, during hovering or slow-forward motion of an animal's body, the aerodynamics of its wings engaged in large-amplitude flapping in many ways more closely resembles those of a propeller or rotor [56,57] for which an alternative,

wing-centred formulation of St_{rotor} is instead appropriate (e.g. [58]).

$$St_{\text{rotor}} = \frac{fd}{U_{\text{blade}}}, \quad (2.2)$$

where d = the diameter of the trailing edge of the rotor blade and U_{blade} = the tangential velocity of the blade. Equation (2.2) describes vortex formation by blade elements along the length of a rotor and, of course, helicopters and propellers are designed for efficiency given their intended use in thrust production. The wings of an animal under conditions of relatively slow forward progress as in WAIR are operating at high angles of attack where distinctions between lift and drag become arbitrary and it is sometimes more useful to discuss net pressure distribution [56,59]. Stated more simply, at slow forward speeds, the flapping wings of birds are behaving like a mixture of an airfoil and a paddle. Thus, although St_{cruise} is understood to be a constraint upon the use of wings in cruising [54], it is not solely the appropriate constraint to impose upon an evolutionary model of flapping in an animal translating forward at slow speeds such as those characteristic of WAIR.

Even if locomotor strategies such as WAIR are ultimately discounted as valid models of the origin of avian flight, they appear to be important components of the development of locomotor capacity during ontogeny in living birds [38,41,43,44] and in the behavioural repertoire of adult birds [26,43]. They may be critical for survival and contribute to the evolution of alternative life-history strategies given the intense predation pressure upon the nestlings of some species [60]. In some circumstances, WAIR may be a readily employed mode of climbing in adults because of adverse scaling of available power for flight [43], or because the species evolved on cliffs [26]. Almost all of our insight about these styles of locomotion comes from laboratory studies, so new field studies in a comparative context are critical for improving understanding of the ecological relevance, testing the ubiquity, of these styles of locomotion that integrate the use of the hindlimb and forelimb modules [61].

3. Muscle function proximal to distal in the wing

Volant birds exhibit massive, paired pectoralis and supracoracoideus muscles that originate from their keel and comprise up to 25% of the mass of the body [30]. Present understanding is that the pectoralis via downstroke provide the majority of the work and power necessary for flapping flight [12,31] even in hummingbirds, where the upstroke contribution during hovering and slow flight is 25–30% of the total lift production [19,20,62,63]. The fibre composition of the pectoralis is remarkably uniform among most species, including only fast-twitch fibres with relatively limited variation in myosin isoforms [64,65]. Exceptions to this pattern are certain soaring birds that exhibit deep accessory bellies composed of slow-twitch fibres [66,67]. However, not all soaring species have this accessory [68,69]. The supracoracoideus accomplishes upstroke, including long-axis rotation of the humerus [70], and it, along with other shoulder muscles and the acrocoracohumeral ligament [17] stabilizes the shoulder. It has a long tendon of insertion that, in the pigeon, stores and releases elastic energy on a par with the inertial work required for wing turnaround at the downstroke–upstroke transition [31].

A major characteristic of the wings of birds is that they morph extensively during flapping ([16,71,72]; figure 2)



Figure 2. Wing-tip reversal upstroke in a pigeon (*Columba livia*) engaged in slow forward flight [72]. The wing morphs constantly during the upstroke; where it is flexed, there is long-axis twist due to supination of the distal wing, and the feathers are bent. The relative contribution of the muscles to such morphing is not well understood.

and during intermittent flight including bounds and glides [73–75]. Such morphing probably has significant effects upon aerodynamic function [72,74,76], but direct tests for such effects in most cases await new research. Direct measures of strain reveal that the biceps and triceps function for elbow flexion, extension and stabilization [77]. The control of more-distal elements is less clear. One hypothesis, from the results of denervation experiments during which pigeons could maintain level flight but not accomplish take-off or landing, is that the forearm muscles are responsible for much of the morphing during circumstances where birds depart from the fundamental wing stroke [78,79]. However, anatomical study suggests an alternative wherein large-scale changes in planform, including, for example, the prominent wing-tip reversal upstroke that is exhibited by pigeons and many other species of birds that have relatively pointed wings (figure 2), can be effected by inertial loading and movement directed by the skeletal elements including the four-bar linkage in the forearm and the articulations at the wrist joint [80–82]. Hummingbirds exhibit supinated hand-wing presentation during upstroke while hovering, and movements of their skeletal elements account for only about 60% of total long-axis rotation of the wing; the remainder is due to inertial and aerodynamic loading of the feathers [16,83]. All of the distal wing muscles exhibit neuromuscular activation during steady flight, but they exhibit increased recruitment in non-steady modes such as take-off or manoeuvring [77–79,84]. It is not clear that bilateral asymmetry in activation of these muscles is necessary for manoeuvring [77,84,85]. New tests of muscular contributions to wing morphing are warranted, and this is a prominent example of where we have extremely limited comparative data.

4. Scaling of flight performance

(a) On being large

It is apparent that flight performance, the capacity of a bird to do anything other than maintain level position in the air, declines with increasing body size among birds ([23,86]; figure 3). But until recently the mechanisms responsible for this trend remained obscure [87]. A classic prediction that has shaped predictions about this issue for the past

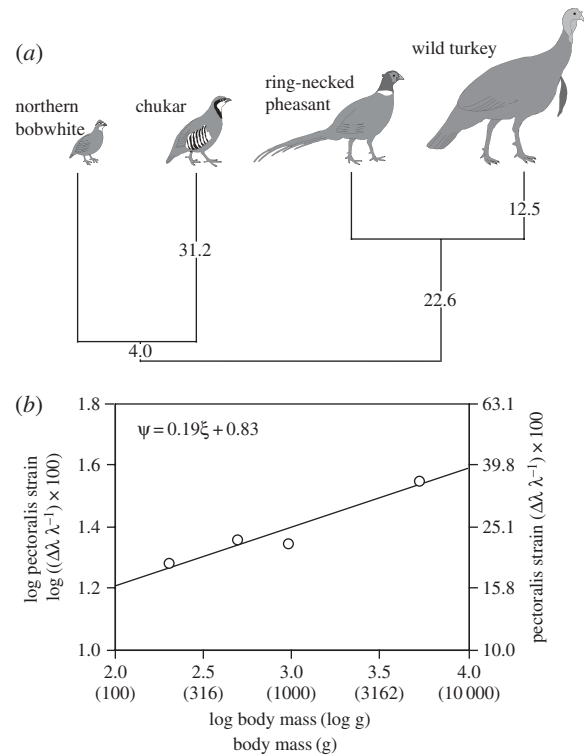


Figure 3. Scaling of pectoralis strain during escape take-off in four species in the Phasianidae (from [23]). (a) Species drawn to scale, along with hypothesized phylogenetic relationships: northern bobwhite (*Colinus virginianus*), chukar (*Alectoris chukar*), ring-necked pheasant (*Phasianus colchicus*) and wild turkey (*Meleagris gallopavo*). Branch lengths are in millions of years. (b) Reduced-major-axis regression of pectoralis strain in relation to body mass; independent contrasts regression has steeper slope: $y = 0.23x$.

75 years emerges from a starting assumption of geometric and dynamic similarity across body sizes [87,88]. If force in the muscles scales with surface area proportional to length squared (L^2), and length change scales proportional to total length (L), then work (force \times length) should scale proportional to volume ($L^2 \times L = L^3$). We may substitute mass (M) for volume to conclude that mass-specific work available from locomotor muscles scales directly proportional with mass (M^1), so mass-specific work is invariant across body sizes (M^0). According to dynamic similarity and an assumption of similar stress limits in muscle insertions [88], the time course of limb oscillation varies directly with length, so rate of oscillation scales as L^{-1} and, therefore, $M^{-1/3}$. In sum, the rate of doing work (power) therefore does not keep pace with increasing body size, and mass-specific power declines proportional to wingbeat frequency (i.e. $M^{-1/3}$).

Several earlier experiments indicated an entirely different pattern for which muscle mass-specific power was invariant or increased slightly with increasing body size [89–91], although muscular mechanisms responsible for this trend were not clear and the trend was described as paradoxical [87,92]. One possibility was that fibre type in the flight muscles scaled with the proportion of more glycolytic, potentially higher-power fibres increasing with increasing body size [64,93]. Some uncertainty about the pattern now appears to be due to mixing of dependent variables. Load-lifting is an index of maximum aerodynamic force production, and a diverse array of insects and birds in static lifting [90] as well as a comprehensive comparative study of hummingbirds using dynamic loading [25] maintain that this index of

performance scales at least slightly positive with increasing body mass. However, aerodynamic force is produced using the power from the primary flight muscles, particularly the pectoralis, transmitted *via* the wing to the air as aerodynamic power, and Marden [90] suggested it may be that lift per unit power output scales negatively with size.

This did not appear as a sufficient explanation for the decline of maximum, unloaded take-off performance, however. Galliform birds exhibit a decline in whole-body, mass-specific power output (rate gain of kinetic and potential energy per unit body mass [23]), yet modelling of aerodynamic power led to the interpretation that mass-specific power output was invariant or slightly increased among species [91]. The aerodynamics in non-steady (accelerative) flight at low advance ratio (J ; the ratio of whole-body translation relative to wing-tip speed) is complicated, featuring unsteady effects that have been explored in very few species (e.g. [62,94,95]), and this introduces uncertainty in the estimates of aerodynamic power.

The paradox may be resolved, though. Using *in vivo* measures of mechanical power output during maximal escape take-off in crows and their allies (Corvidae), Jackson & Dial [24] revealed that mass-specific power output does not scale as negatively as wingbeat frequency would indicate ($M^{-1/3}$; rather, muscle strain and the shape factor of the stress-strain workloops scale positively with mass to partially offset the overall negative trend induced by wingbeat frequency, yielding mass-specific power proportional to $M^{-0.2}$. Likewise, a careful comparative study of the scaling of pectoralis mass and wing planform indicates that mass-specific power available from the flight muscles of hummingbirds scales slightly negatively with increasing mass, but not as negatively as wingbeat frequency. Hummingbirds exhibit compensatory scaling of wing dimensions and muscle mass [25,30]. Partial compensatory mechanisms are reported for positive scaling of proportions of glycolytic fibre types in the pectoralis of woodpeckers [93] and pectoralis strain in a variety of bird species ranging in size from hummingbirds to Galliform birds ([23,96]; figure 3).

In the light of this negative scaling of mass-specific power, the positive scaling of load-lifting capacity in hummingbirds is all the more impressive [25]. Performance limited by available power has significant behavioural, ecological and evolutionary implications; for example, altitude limits the capacity for force production and hence structures hummingbird assemblages along elevational gradients [25]. Maximum power from the flight muscles is the primary determinant of manoeuvring capacity during agonistic encounters [27]. As the estimates for muscle power in hummingbirds remain based upon aerodynamic models and not direct empirical measures, further experimentation is warranted. Techniques that would improve confidence in the accuracy of aerodynamic estimates of power include using flow visualization (e.g. [19,62,63]) and sophisticated computational fluid dynamic (CFD) modelling [20,83].

(b) On being small: hovering

Hummingbirds are the smallest birds, with species varying in mass from 2–12 g and a large outlier, the giant hummingbird, having a mass of 20 g [25,30]. One hypothesis meriting further study in relation to the observed positive scaling of load-lifting ability with increasing mass in hummingbirds [25] is that the smallest hummingbirds may have evolved into a morphospace where available time for muscle contraction is functioning as a constraint upon muscle force production [14,96,97]. With

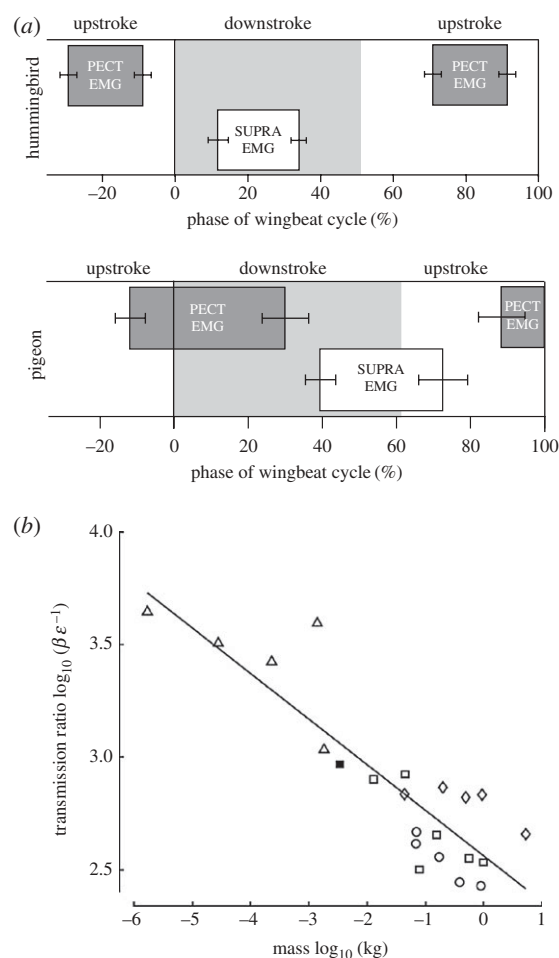


Figure 4. Muscle contractile behaviour in hummingbirds. (a) Relative timing of activation in the pectoralis (PECT) and supracoracoideus (SUPRA) of a rufous hummingbird (*Selasphorus rufus*) and a rock pigeon (*Columba livia*). Downstroke is defined using wrist motion in the hummingbird and pectoralis length in the pigeon. EMG, electromyography (from [96]). (b) Transmission ratio, the ratio of wing flapping amplitude to muscle strain varies proportional to mass^{-0.20} in a variety of insect and bird species (filled square, ruby-throated hummingbird, *Archilocus colubris*; circles, Corvidae; diamonds, Phasianidae; open squares, other birds; triangles, insects). From Hedrick *et al.* [16].

wingbeat frequencies approximately 34 Hz, the pectoralis of the Anna's hummingbird (*Calypte anna*) exhibits extremely low force-generating capacity, as does the pectoralis of slightly larger zebra finch (*Taeniopygia guttata*; [14]). Pectoralis strain is 11% in the rufous hummingbird (*Selasphorus rufus*), much less than in larger bird species where it varies up to 35% or more [36,96]. Neural recruitment of the primary flight muscles is extremely brief in relative duration to the wingbeat, the number of electromyographic spikes per contraction is much smaller than in other species, varying from one to four spikes per contraction [96–98].

Moreover, muscle activation is a half-cycle out of phase with the kinematic events that the muscles effect. The pectoralis generates force for decelerating the wing at the end of upstroke and accelerating the wing in the first half of downstroke, yet it is deactivated before the end of the kinematic upstroke. Likewise, activation of the supracoracoideus is during kinematic downstroke ([96]; figure 4). This pattern is unusual compared with larger birds (figure 4), although electromyography (EMG) duration and offset time scale with body mass in Galliformes and Corvids [23,24]. The extreme pattern in hummingbirds is due

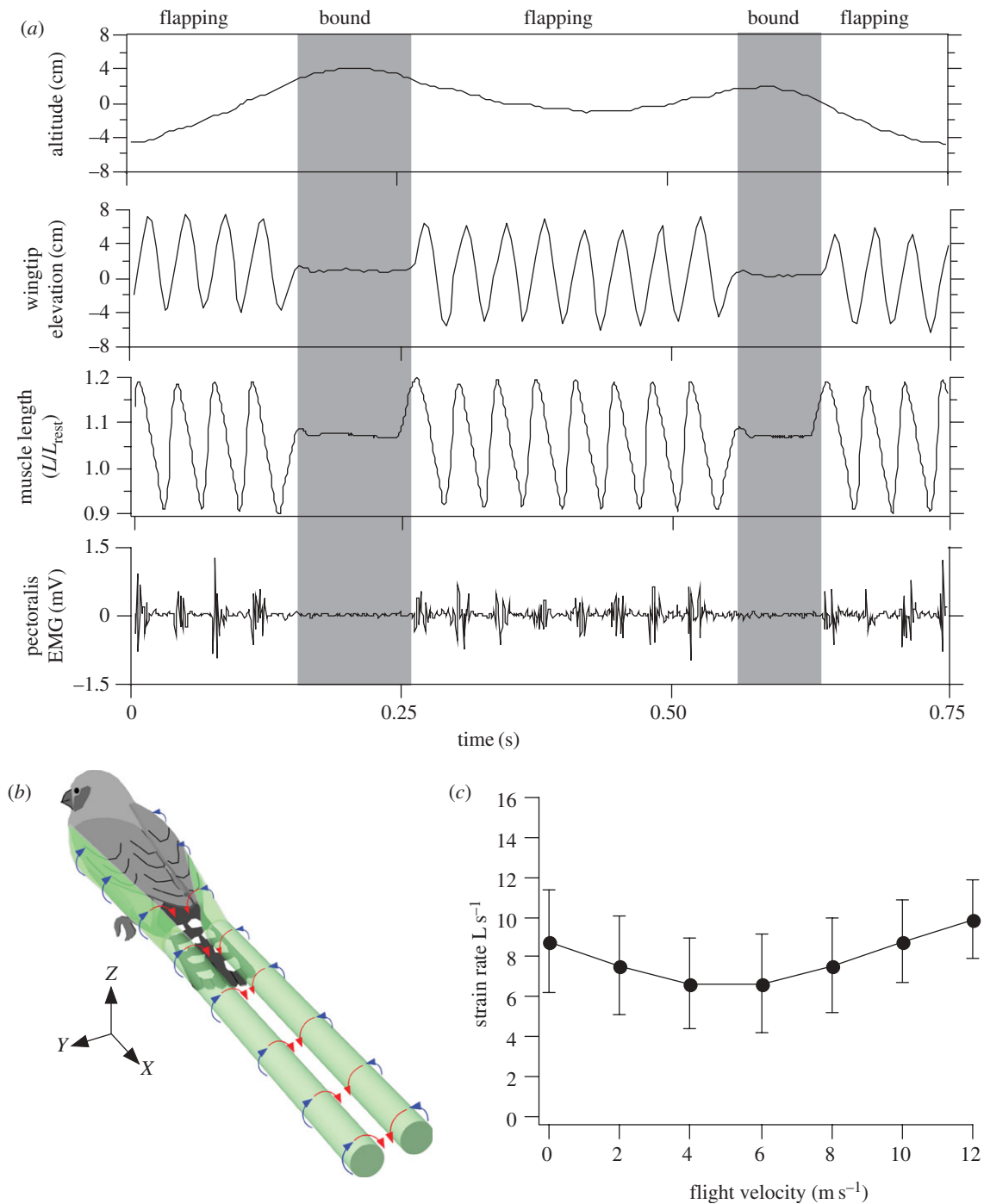


Figure 5. Kinematics, aerodynamics and muscle activity during flap-bounding flight in zebra finch (*Taeniopygia guttata*). (a) Flight in a wind tunnel at $12 m s^{-1}$ illustrating body and wing motion, muscle strain as measured using sonomicrometry, and neuromuscular activity measured using EMG. (b) During bounds airflow over the body and tail creates body lift and a pair of counter-rotating vortices are shed into the wake. (c) Contractile velocity in the pectoralis varies significantly among flight speeds (from Tobalske *et al.* [73,104]).

to the time necessary for excitation–contraction coupling which is 8 ms to peak force and 20 ms for force decay in relatively large hummingbirds [98] and may be even shorter in duration for smaller species [96].

Hummingbirds exhibit derived morphology in the skeletal elements of their wing that facilitate their capacity for hovering and generating high-mass-specific power in synchrony with constraints upon muscle activation–deactivation due to high wingbeat frequency [16,99]. Apodiformes (swifts and hummingbirds) in general have relatively short humeri compared with their other wing elements [16,100]. Hummingbirds exhibit even greater foreshortening of the humerus than swifts, with a change in orientation of the head of the humerus that permits greater adduction and an extraordinarily long deltopectoral

crest [16]. The combination of these traits causes their transmission ratio, the contractile velocity of the pectoralis relative to the velocity of the tip of their wing, to be at the interface between insects, featuring exoskeletons and other birds.

(c) On being small: flap-bounding

Most small species of birds, up to 0.3 kg in mass, use flap-bounding as their primary style of flight [93,101]. Hummingbirds sometimes engage in the behaviour [92]. Although it is rare in North American species during cruising flight, versions of the behaviour are exhibited during mating displays in hummingbird species in Central and South America (Christopher Clark, personal communication, 2009).

Flap-bounding consists of flapping phases interspersed with flexed-wing bounds during which the wings are fully adducted to the body as in perching. The primary flight muscles are not active during bounds, and the bird generates a small amount of weight support *via* body and tail lift ([102–104]; figure 5). Species may also exhibit partial bounds and glides (with wings fully extended), although, among small species, only those with relatively pointed wings of high aspect ratio modulate their non-flapping wing postures [101], while those with rounded wings appear to only use flap-bounding.

The functional significance of flap-bounding remains uncertain, which is fascinating given the widespread use of this behaviour among small birds. Modelling the power costs of flap-bounding generally indicates that this flight style can offer an energetic saving compared with continuous flapping during fast flight if, as is observed, the body and tail produce lift that is sufficient to support 10–15% of weight [103–105]. However, using kinematics of zebra finch [103], Sachs' analysis indicates that flap-bounding only offers an energetic advantage during flight into a headwind [106,107]. By contrast, it is predicted that flap-gliding offers energetic advantages over a broad range of flight speeds [105,108]. Given the high power costs for flight [109], an outstanding paradox is that birds routinely use flap-bounding during slow flight and during brief hovering episodes [103,105].

A 'fixed-gear' hypothesis was a dominant attempt to explain the use of flap-bounding in circumstances where it does not make energetic sense [105]. Given uniform fibre types in the pectoralis of small birds [64,93,110] and earlier experiments that suggested a limited capacity for modulation of motor-unit recruitment in small species [98,111], the fixed-gear hypothesis predicted that birds would exhibit a narrow band of optimal contractile velocities in their pectoralis that were tuned for the output of maximum power. Rather than modulate motor-unit recruitment to vary force, or contractile velocity to vary power, the hypothesis predicts that whenever less-than-maximum power is required, small birds should use intermittent bounds. The metaphor of a multi-speed bicycle with a broken gear shifter has potent intuitive appeal—conjure the image of an unlucky *Tour de France* rider out of range of a support vehicle—yet results from the species tested thus far do not support the hypothesis.

Instead, zebra finch (*Taeniopygia guttata*) and parakeets (*Melopsittacus undulatus*), birds that use bounds during intermittent pauses, exhibit significant variation in motor-unit recruitment and contractile velocity in their pectoralis when

they fly in different modes (ascending, level, descending) or across flight speeds (0–14 m s⁻¹; [73]). Contractile velocity varies more among flight modes in the zebra finch than it does in pigeons that exceed the weight limit for being able to intermittently bound [31,73]. Significant variation in power is exhibited when observed patterns of motor-unit recruitment and contractile dynamics are programmed to *in situ* work-loop experiments using zebra finch pectoralis [13].

It is vital to note that the empirical efforts to date have not explored the metabolic cost of flap-bounding versus continuous flapping, and efficiency of conversion of chemical to mechanical energy is a central tenet of the fixed-gear hypothesis [105]. It is not straightforward to convince a given bird species to consistently alter its flight style to measure metabolic costs. However, there might be scope to explore alternative flight strategies using nestling transplant experiments. Transplanted nestling cockatoos (Psittacidae) acquire host-species flight style [112], but cockatoos and parakeets with relatively pointed wings exhibit more modulation in intermittent flight style than do species such as zebra finch [101]. Hummingbirds engaged in continuous flapping exhibit greater variation in relative amplitude of EMG activity across flight speeds compared with flap-bounding finch. Within the clade of woodpeckers, flying slowly, not body size or external wing shape, is associated with the adoption of gliding in the Lewis's Woodpecker (*Melanerpes lewis* [93]). Perhaps, in nature the fraction of flight time flap-bounding birds spend flying slowly is minimal [101]. These disparate observations underscore again that novel comparative study in a phylogenetic context may represent the best path for improving understanding of the role of flap-bounding in the biology of flying birds.

Ethics. Experiments performed by the author using live animals were approved by Institutional Animal Care and Use Committees of the University of Montana, University of Portland, and Harvard University. Animal capture, tagging and release were conducted under scientific collecting permits from the US Fish and Wildlife Service, the Oregon Department of Fish and Wildlife, and Montana Department of Fish Wildlife and Parks.

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Glossary

Advance ratio	freestream air velocity divided by wing-tip velocity, dimensionless.	Pectoralis	largest muscle of the avian wing, originates from keel of sternum and inserts on cranio-ventral aspect of deltopectoral crest of humerus, decelerates wing during latter half of upstroke and accelerates wing to provide majority of work and power for downstroke.
Bound	intermittent non-flapping phase during which the wings are adducted, held fully or partially flexed against the body and are largely aerodynamically inactive.	Strain	change in length divided by initial (usually unloaded or resting) length, dimensionless.
Computational fluid dynamics	numerical simulations of fluid flow.	Stress	force per unit area (Pa).
Directed aerial descent	steering during parachuting or gliding to guide the direction of movement.	Strouhal number	product of frequency of vortex shedding and a characteristic length of an object divided by flow velocity, dimensionless.
Dynamic similarity	moving in the same manner.	Supracoracoideus	second-largest muscle of the avian wing, deep to the pectoralis, originates from keel of sternum, inserts via foramen triosseum upon proximo-dorsal aspect of deltopectoral crest of humerus, decelerates wing during latter half of downstroke, and provides majority of work and power for upstroke.
Fast-twitch muscle fibre	muscle cell containing a myosin isoform that has the capacity to rapidly catalyse adenosine triphosphate to provide energy for contraction.	Theropod	clade of dinosaurs including coelurosaurians from which modern birds evolved.
Fundamental wing stroke	hypothesized ancestral motion of the wing during flapping that includes flexion–extension, elevation–depression, and stroke-plane orientation relative to the body.	Wing-assisted incline running (WAIR)	method of avian climbing in which aerodynamic forces from vigorously flapping wings accelerate the body of the animal upward and toward the substrate, thus contributing to weight support and improving traction for the hindlimbs.
Geometric similarity	shaped in the same manner.		
Glide	intermittent non-flapping phase during which the wings are abducted, held extended away from the body and are producing lift and drag.		
Load-lifting	experimental challenge for a flying animal consisting of take-off and ascent with added payload.		
Particle image velocimetry	method of flow visualization and analysis in which the fluid is seeded with particles and the motion of these particles is used to calculate the velocity field of the flow.		