
Commentary

Biomechanics of bird flight

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Accepted 11 July 2007

Summary

Power output is a unifying theme for bird flight and considerable progress has been accomplished recently in measuring muscular, metabolic and aerodynamic power in birds. The primary flight muscles of birds, the pectoralis and supracoracoideus, are designed for work and power output, with large stress (force per unit cross-sectional area) and strain (relative length change) per contraction. U-shaped curves describe how mechanical power output varies with flight speed, but the specific shapes and characteristic speeds of these curves differ according to morphology and flight style. New measures of induced, profile and parasite power should help to update existing mathematical models of flight. In turn, these improved models may serve to test behavioral and ecological processes. Unlike terrestrial locomotion that is generally characterized by discrete gaits, changes in wing kinematics and aerodynamics across flight speeds are gradual. Take-off flight performance scales with body size, but fully revealing the mechanisms responsible for this pattern

awaits new study. Intermittent flight appears to reduce the power cost for flight, as some species flap–glide at slow speeds and flap–bound at fast speeds. It is vital to test the metabolic costs of intermittent flight to understand why some birds use intermittent bounds during slow flight. Maneuvering and stability are critical for flying birds, and design for maneuvering may impinge upon other aspects of flight performance. The tail contributes to lift and drag; it is also integral to maneuvering and stability. Recent studies have revealed that maneuvers are typically initiated during downstroke and involve bilateral asymmetry of force production in the pectoralis. Future study of maneuvering and stability should measure inertial and aerodynamic forces. It is critical for continued progress into the biomechanics of bird flight that experimental designs are developed in an ecological and evolutionary context.

Key words: wing, kinematic, muscle, work, power, wake, take-off, intermittent, maneuver, stability.

Introduction

Power (work per unit time) is a dominant theme when exploring flapping flight in birds because the power required for flight is greater than for other forms of animal locomotion (Schmidt-Nielsen, 1972). Muscle mass-specific mechanical power output varies from 60–150 W kg⁻¹ during cruising flight (Tobalske et al., 2003; Askew and Ellerby, 2007) to 400 W kg⁻¹ during take-off (Askew and Marsh, 2001; Askew et al., 2001), and metabolic rates during flight are up to 30 times basal metabolic rate (Nudds and Bryant, 2000). As a consequence of high power demands, most studies of bird flight assume that the internal and external wing design in flying birds has been, and continues to be, shaped by natural selection for efficiency in flight, with efficiency defined as mechanical power output from the muscles divided by metabolic power input to the muscles. This assumption, like any hypothesized to be associated with selective pressures, should be explicitly tested more often than is the case (Gould and Lewontin, 1979). Nonetheless, from this starting premise, considerable progress has been made into understanding how power output varies with flight speed, mode

(level, take-off and ascending, descending), wingbeat kinematics, and flight style (intermittent, maneuvering). Recent research furthering this progress is the focus of this review. As a variety of new technologies have made it more feasible than ever before to measure variables bearing upon flight performance, this is an exciting time to be engaged in studies of the mechanics of bird flight.

Power is measured at three different levels pertinent to flapping flight. The first level is metabolic power input (P_{met}) to the muscles, directly of interest to a flying, foraging bird, and generally a realm of study for respiratory, thermal and chemical physiologists. P_{met} is the rate the bird expends chemical energy to supply the flight muscles, and it may be measured using double-labeled water (Nudds and Bryant, 2000; Ward et al., 2004; Engel et al., 2006), labeled bicarbonate (Hambly et al., 2002), oxygen consumption and carbon dioxide production (Ward et al., 2001; Ward et al., 2004; Bundle et al., 2007). P_{met} equals the sum of mechanical power output from the muscles (P_{mus}) and the rate of heat loss from the muscles. Thus, P_{met} may also be modeled using measures of heat transfer (Ward et al., 2004).

At the next level, still inside the animal, P_{mus} acts upon the skeleton and feathers. Except for thermal losses in connective tissue, which are presently unknown:

$$P_{\text{mus}} = P_{\text{iner}} + P_{\text{aero}}, \quad (1)$$

where P_{iner} is inertial power required to oscillate the wing and P_{aero} is the aerodynamic power required for flight. Biomechanists measure P_{mus} *in vivo* using surgically implanted strain-gauges and sonomicrometry crystals (Dial and Biewener, 1993; Tobalske et al., 2003; Hedrick et al., 2003) (Fig. 1A) and *in vitro* using isolated muscle fibers and ergometers (Askew and Marsh, 1997; Askew and Marsh, 2001; Askew and Ellerby, 2007). Electromyography (Dial, 1992a) is used to measure neuromuscular control of P_{mus} , and wing kinematics from high-speed film or video are used to estimate P_{iner} (Hedrick et al., 2004).

External to the animal, P_{aero} is the third level of power output of interest:

$$P_{\text{aero}} = P_{\text{ind}} + P_{\text{pro}} + P_{\text{par}} + \Delta(E_p + E_k)/t, \quad (2)$$

where P_{ind} is induced power, the cost of lift production, P_{pro} is profile power, used for overcoming drag on the wings, P_{par} is parasite power, used for overcoming drag on the body, E_p is potential energy, E_k is kinetic energy, and t is time. Kinematic measurements, coupled with mathematical theory (Pennycuik, 1975; Rayner, 1979a; Rayner, 1979b; Ellington, 1984), provide estimates of each of the components of P_{aero} , while empirical measurements involve the use of techniques including accelerometry (Pennycuik et al., 2000; Hedrick et al., 2004), pressure transduction (Usherwood et al., 2003; Usherwood et al., 2005), force balances (Csicsáky, 1977; Pennycuik et al., 1988; Lentink et al., 2007) and digital particle image velocimetry (DPIV) (Spedding et al., 2003; Warrick et al., 2005).

To introduce the biomechanics of bird flight, I will first summarize current understanding about the functional morphology of the avian wing with implications for P_{mus} . Then, I will evaluate how P_{aero} varies with flight speed and explore some of the wingbeat kinematics, flight modes and styles that covary with P_{aero} . Other variables besides work and power are of great importance to the biology of flying birds, including the ability to maneuver (Warrick et al., 2002) as well as be stable (Thomas and Taylor, 2001; Taylor and Thomas, 2002; Taylor and Thomas, 2003). Compared with the amount of empirical data describing steady hovering and forward flight, less is known about the biomechanics of maneuvering and stability, and these subjects represent a new frontier of study. Thus, I will include a synopsis of current data from maneuvering flight before concluding with reflections on promising avenues for future research.

Primary flight muscles

The pectoralis, the primary depressor and pronator of the wing, is the largest muscle of the wing (Fig. 1A), and the supracoracoideus, the primary elevator and supinator (Poore et al., 1997), is second in mass. Both muscles insert upon the humerus and decelerate and reaccelerate the wing across the transitions between upstroke and downstroke (Dial, 1992a). Because of its size, the pectoralis is perceived to be the ‘motor’ that accounts for the bulk of P_{mus} for bird flight (Dial and

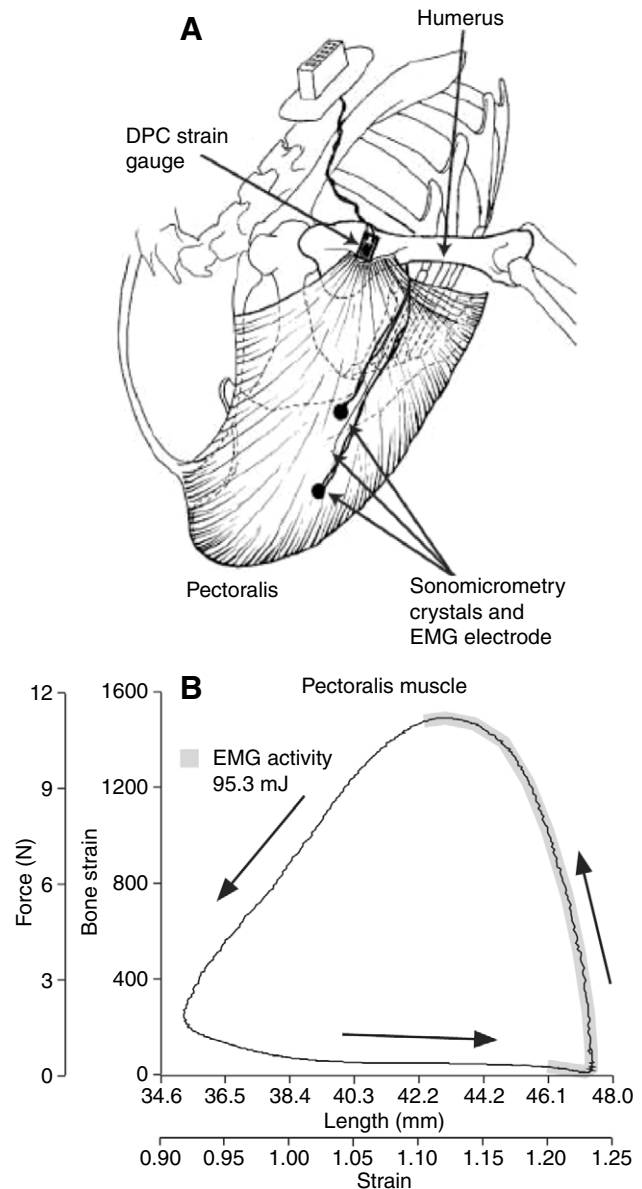


Fig. 1. *In vivo* measurements of mechanical work and power output from the pectoralis, the primary downstroke muscle of the avian wing are accomplished using surgically implanted strain gauges calibrated to measure force from bone strain on the deltopectoral crest of the humerus and using sonomicrometry crystals to measure muscle length (A). Similar methods are employed for the primary upstroke muscle, the supracoracoideus (not shown), which is located deep to the pectoralis (Tobalske and Biewener, in press). (From Hedrick et al., 2003.) (B) A ‘work loop’, the area of which represents *in vivo* mechanical work in the pectoralis of a cockatiel *Nymphicus hollandicus* during one wingbeat (adapted from Tobalske et al., 2003). Arrows indicate the progression of contractile behavior. Electromyography (EMG) activity in the pectoralis indicates that the muscle functions to decelerate the wing at the end of upstroke and accelerate the wing during the first third of downstroke.

Biewener, 1993). Birds can take-off and fly without use of their supracoracoideus (Sokoloff et al., 2001), which indicates that other flight muscles may contribute to wing elevation. Likewise, birds can fly steadily, but not take-off or land in a controlled

manner, without the use of their distal wing muscles (Dial, 1992b). Distal muscles of the wing are activated primarily during non-level modes of flight (Dial, 1992a), and bird species that regularly engage in non-steady modes of flight, including maneuvering, have proportionally bowed forearms. This outward bowing of the radius and ulna is hypothesized to be due to the need to accommodate more muscle mass with an enhanced role of distal wing muscles in these species. The forearm muscles supinate, pronate, flex and extend the distal wing (Dial, 1992b). With the exception of the supracoracoideus (Poore et al., 1997; Tobalske and Biewener, 2007), the mechanical contribution the other muscles of the wing has not yet been measured. Power output in the supracoracoideus closely matches estimated P_{iner} for upstroke (Tobalske and Biewener, in press).

In contrast with the primary muscles of the limbs of terrestrial animals that develop force nearly isometrically during walking and running, the pectoralis in flying birds is designed to produce work and power (Biewener and Roberts, 2000) (Fig. 1B). Sonomicrometry reveals that the pectoralis undergoes proportionally large length change (muscle strain), during contraction (20–40% of muscle resting length) and exhibits a contractile velocity of 4–10 muscle lengths s^{-1} among species (Biewener et al., 1998; Tobalske and Dial, 2000; Askew and Marsh, 2001; Hedrick et al., 2003; Tobalske et al., 2005). Similar levels of muscle strain and strain rate are exhibited by the supracoracoideus (Tobalske and Biewener, in press). It is important to note that the pectoralis exhibits a bipinnate architecture with regional heterogeneity in contractile behavior, which means that measurements of strain taken at any one location must be evaluated with caution (Soman et al., 2005). Using strain gauges, measurements of bone strain in the humerus adjacent to the insertion of the muscles may be calibrated to measure whole-muscle force, but there are concerns about high variance in calibrations (Tobalske et al., 2003) and some species do not have a humerus shape that is amenable to measurements (Tobalske and Dial, 2000).

Birds may use a variety of methods to modulate P_{mus} . Among flight speeds, cockatiels *Nymphicus hollandicus* primarily modulate P_{mus} by varying the proportion of motor units recruited in the pectoralis and, thereby, varying force (Hedrick et al., 2003). Likewise, pigeons *Columba livia* vary motor-unit recruitment and pectoralis force among flight modes (Dial, 1992a; Dial and Biewener, 1993). Other factors may permit modulation in P_{mus} , including the shortening fraction, trajectory, and timing of muscle activation and deactivation (Askew and Marsh, 1997; Askew and Marsh, 2001). It was formerly hypothesized that small birds were constrained by their muscle physiology to use a narrow range of contractile velocity in their pectoralis (Rayner, 1985), but sonomicrometry and electromyography reveal that they use the same mechanisms as larger birds, the timing and magnitude of neuromuscular activation as well as the contractile velocity of the muscle, for modulating P_{mus} (Tobalske et al., 2005; Tobalske and Biewener, in press; Askew and Ellerby, 2007). Many birds also regularly use non-flapping phases (brief, extended-wing glides or flexed-wing bounds) to modulate power during intermittent flight (see ‘Intermittent flight’, below).

Variation in P_{aero} with flight speed

U-shaped power curve

A variety of mathematical models may be used to estimate the effects of flight speed upon components of P_{aero} (Norberg, 1990). Models that are mostly widely employed are those of Pennycuick (Pennycuick, 1975; Pennycuick, 1989) and Rayner (Rayner, 1979a) for forward flight and, for hovering, those of Rayner (Rayner, 1979b) and Ellington (Ellington, 1984). Regardless of which model is used, the general prediction that always emerges is that P_{aero} should vary with flight speed according to a U-shaped curve, with greater P_{aero} required during hovering and fast flight and less required during flight at intermediate speeds (Norberg, 1990) (Fig. 2A). As a function of forward flight velocity, the cost of producing lift, P_{ind} , decreases, while power needed to overcome drag on the wings and body, P_{pro} and P_{par} , respectively, increases.

The U-shaped curve for P_{aero} features a characteristic minimum power speed (V_{mp}) and a maximum range speed (V_{mr} ; Fig. 2A). These characteristic speeds represent one of the most obvious ways in which the biomechanics of flight may be integrated with behavioral ecology. Often, a starting premise for ecological studies of flight is that birds should select V_{mp} for aerial foraging or searching and select V_{mr} for long-distance flight such as migration, although specific predictions change when optimal foraging factors such as rate of energy intake or prey-delivery rates are incorporated into the models (Hedenström and Ålerstam, 1995; Houston, 2006).

Consistent with the hypothesis that the pectoralis is the primary muscle supplying the mechanical power output required for flight, measures of P_{mus} *in vivo* (Tobalske et al., 2003) (Fig. 2B) and *in vitro* (Askew and Ellerby, 2007) vary as U-shaped curves in the same manner as P_{aero} . The shape of a P_{mus} curve is affected by the morphology and flight style of a given species, and this means that there is inter-specific variation in V_{mp} and V_{mr} . Some models of P_{aero} may be refined to take into account details of wing shape, wing kinematics and intermittent flight behavior (Rayner, 1979a; Rayner, 1979b; Ellington, 1984; Rayner, 1985). Thus, efforts to better understand both the biomechanics and ecology of flight will benefit from revision of these models as additional empirical evidence emerges.

Small differences in efficiency (i.e. $P_{\text{mus}}/P_{\text{met}}$) have the potential to dramatically affect the shape of the P_{met} power curve relative to that of P_{mus} and P_{aero} (Thomas and Hedenström, 1998; Rayner, 1999). Since P_{met} is the rate of energy input by a bird, the shape of the P_{met} curve, rather than that of P_{mus} or P_{aero} , is what is ultimately of importance in governing the V_{mp} and V_{mr} of interest to a bird. For many years, it appeared that the curve for P_{met} was flat at intermediate flight speeds, which suggested that efficiency is lowest in the range of preferred flight speeds (reviewed in Ellington, 1991). Recently, efforts to measure P_{met} using a variety of techniques including double-labelled water, heat transfer and gas respirometry, reveal that the curve for P_{met} is U-shaped much as that for P_{mus} and P_{aero} , with muscular efficiency in the range of 20% (Ward et al., 2001; Ward et al., 2004; Engel et al., 2006; Bundle et al., 2007) (Fig. 2C). Comparison of the curves for P_{met} and P_{mus} in cockatiels *Nymphicus hollandicus*, measured in two different

studies, suggests that efficiency is not constant across speeds and that V_{mp} and V_{mr} are both faster when measured using P_{met} compared with P_{mus} (Tobalske et al., 2003; Bundle et al., 2007) (Fig. 2). To further clarify this issue, it is vital to measure P_{met} and P_{mus} under similar experimental conditions due to potential differences in P_{aero} when a mask and respirometry cabling is added to an animal (Bundle et al., 2007).

The major difference among models of P_{aero} is the method

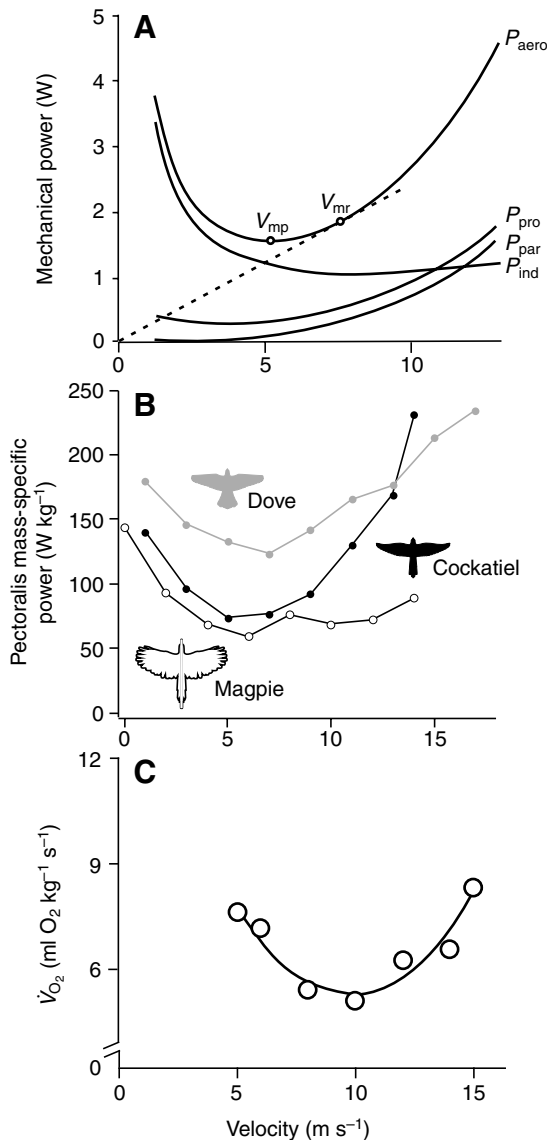


Fig. 2. U-shaped curves of power as a function of flight speed in birds. (A) Estimated mechanical power output required for flight in a European kestrel *Falco tinnunculus* (from Rayner, 1999). P_{aero} , total aerodynamic power, P_{ind} , induced power, P_{par} , parasite power and P_{pro} , profile power, V_{mp} , velocity for minimum power, V_{mr} , velocity for maximum range. (B) *In vivo* mechanical power output from wind-tunnel flight across flight speeds as measured using strain gauges, sonomicrometry and wing and body kinematics in dove *Zenaidura macroura*, cockatiel *Nymphicus hollandicus*, magpie *Pica hudsonica* (from Tobalske et al., 2003). (C) Oxygen consumption, an index of metabolic power output, measured in cockatiels over a range of flight speeds using gas respirometry (from Bundle et al., 2007).

used to estimate P_{ind} , although different approaches are also employed to estimate P_{pro} and P_{par} . In a relatively simple model that is widely used by ecologists, in part because it is available as a computer program (Pennycuik, 1975; Pennycuik, 1989), P_{ind} is estimated using a steady-state momentum-jet model. This model treats the wings as fixed-length propellers rotating and translating at a steady rate, as in a helicopter, even for the gliding flight of birds. Propellers do not fully represent the complexity of the motions and morphing ability of bird wings (Bilo, 1971; Bilo, 1972; Warrick et al., 2005; Lentink et al., 2007). In contrast, alternative models (Rayner, 1979a; Rayner, 1979b; Ellington, 1984) use vortex theory, which is capable of incorporating unsteady motion and long-axis rotation of the wings (e.g. Dickinson et al., 1999).

When a wing produces lift, there is a net circulation of air about the wing that represents a bound vortex on the wing (Rayner, 1979a; Rayner, 1979b; Ellington, 1984). The term 'bound' in this instance means attached or close to the wing, and is a definition independent of the flexed-wing bound posture used in intermittent flight. For real-world wings of finite span, the bound vortex is shed into the wake as a 'wake' vortex, and the circulation in the wake vortex is equal in magnitude but opposite in sign to that of the bound vortex. Circulation varies with translational and long-axis rotational velocity, angle of attack and camber of the wing. Lift, in turn, is proportional to circulation as well as wing span, translational velocity and air density. One simple way to think of the relationship between wake vortices and lift is that, for a given need for lift, as surface area surrounded by the wake vortices increases, the velocity that the wings induce into the wake and the cost of producing lift, P_{ind} , both decrease.

During the 1980s there was an earnest attempt to test vortex theory for flying birds using particle image velocimetry (PIV). Although the geometry of the vortices shed into the wake during slow flight matched expectations, the researchers were frustrated by measurements of momentum in the wake that were insufficient to support the weight of the bird (Spedding et al., 1984). This 'momentum deficit paradox' was resolved using modern DPIV (Spedding et al., 2003), which offers finer resolution of flow patterns in the wake. Significant new observations about wake structure will undoubtedly improve models of P_{ind} .

For example, based on wake samples in the European kestrel *Falco tinnunculus* engaged in moderate-speed forward flight (Spedding, 1987), it was formerly thought that birds varied lift primarily using wing flexion, and not by changing circulation in the bound vortex on their wings *via* changes in wing velocity, camber or angle of attack (Rayner, 1988). Instantaneous changes in circulation on the wings initiate the shedding into the wake of 'cross-stream' vortices that are parallel to long-axis of the wings. These cross-stream vortices traverse the wake, they reveal a reduction in the effective area for lift production that is swept by the wings, and this reduction in effective area is predicted to increase the cost of producing lift, P_{ind} (Rayner, 1988). Assuming a lack of significant cross-stream vortices, the kinematics of faster flight in birds such as kestrels or pigeons (*Columba livia*) emerge as an optimal pattern of wing motion (Rayner, 1999) (Fig. 3A). Modern DPIV reveals that cross-stream vortices are

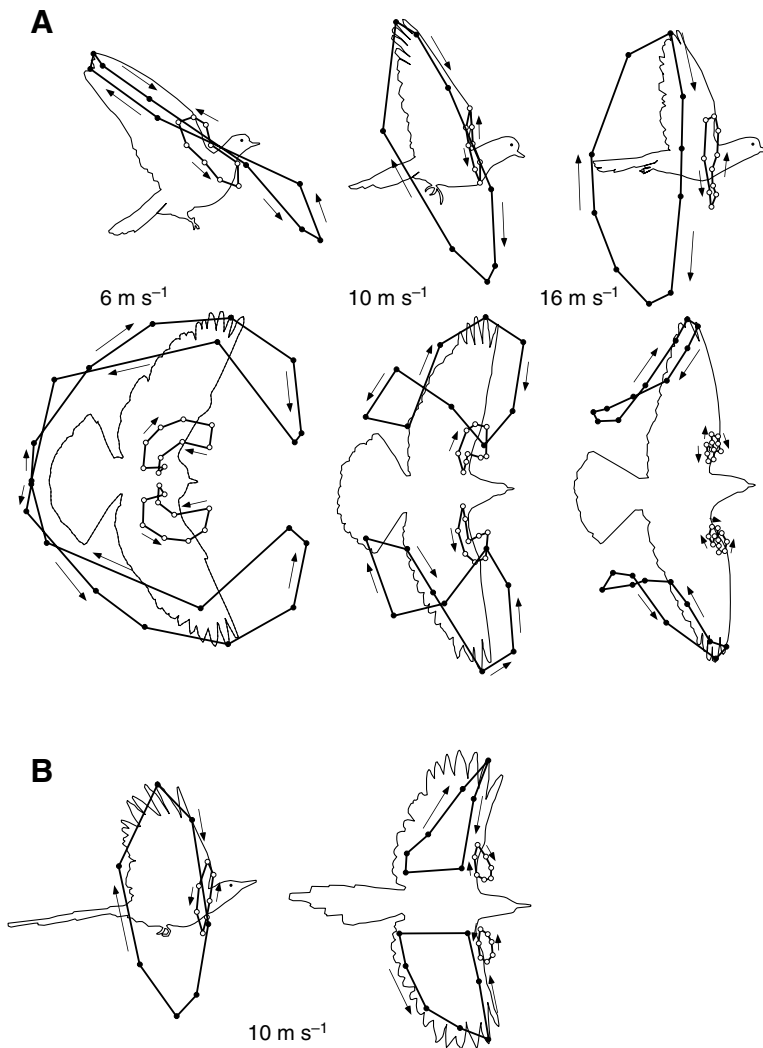


Fig. 3. Wing kinematics differ depending upon a bird's wing design and flight speed. (A) Birds with pointed, high-aspect ratio wings such as the pigeon *Columba livia* transition from tip-reversal upstrokes during slow flight to feathered upstrokes at intermediate speeds and a swept-wing upstroke during fast flight. (B) Birds with rounded, low-aspect ratio wings such as the black-billed magpie *Pica hudsonica* use a flexed upstroke at all flight speeds. Shown are wingtip (filled circles) and wrist (open circles) paths in dorsal and lateral view (from Tobalske and Dial, 1996).

typical of forward flight (Spedding et al., 2003; Hedenström et al., 2006) (Fig. 4), and this should serve to revise models of P_{ind} during fast flight.

Likewise, DPIV has recently revised our understanding of the mechanics of hovering (Warrick et al., 2005). Hummingbirds are the only birds that can sustain hovering in still air, and formerly it was thought that they supported their weight during hovering using symmetrical down and upstrokes with equal P_{ind} during each half of the wingbeat. This assumption lead to a proportionally lower estimate for P_{ind} compared with all other bird species, in which it appears that only the downstroke helps to support weight during hovering and slow flight (Rayner, 1979a). DPIV instead reveals that approximately 75% of the weight support during a wingbeat is provided by downstroke, and 25% is provided by upstroke, in hovering rufous

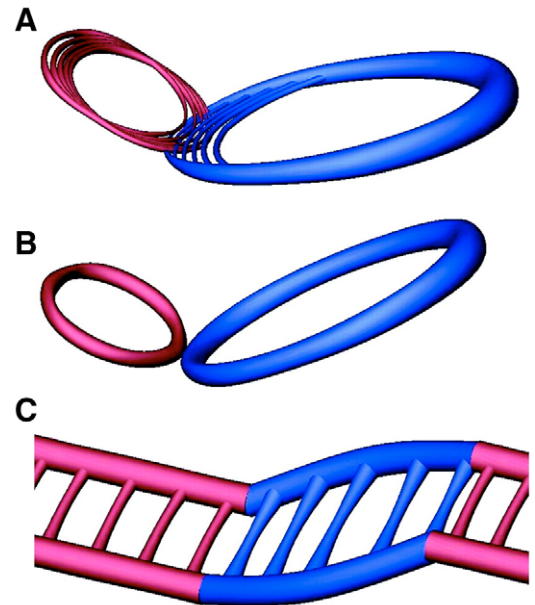


Fig. 4. Representations of vortex wakes shed from the wings of a thrush nightingale *Luscinia luscinia* at slow (A), medium (B) and fast (C) flight speeds in a wind tunnel, measured using digital particle image velocimetry [DPIV (from Spedding et al., 2003)]. Red and blue indicate the wake from upstroke and downstroke, respectively. Both phases of the wingbeat are aerodynamically active at each speed, and there are prominent cross-stream vortices apparent at the ends of half-strokes during slower flight (A,B) and throughout the wingbeat cycle during faster flight (C).

hummingbirds *Selasphorus rufus* (Warrick et al., 2005).

Reasonable measurements of P_{pro} are largely lacking for birds engaged in flapping flight, and this highlights a clear need for new research. Models presently either assume that profile drag is constant during intermediate flight speeds (Pennycuick, 1975; Pennycuick, 1989) or apply a coefficient of drag for the wing that is obtained from fixed-wing measurements and modeled according to blade-element theory, which treats the wing as set of fixed-width strips each moving at their own velocity, due to the flight velocity of the bird as well as the angular velocity of the wing (Rayner, 1979b). Unfortunately, drag on fixed wings (Withers, 1981; Lentink et al., 2007) or during gliding in live birds (Pennycuick et al., 1992) is probably quite different from unsteady drag forces operating on the flapping wings during slow flight (Spedding, 1993; Dickinson, 1996). Promising methods for more accurate models of P_{pro} during flapping include measuring force using transducers at the base of mounted, revolving wings (Usherwood and Ellington, 2002) or robotic flapping wings (Sane and Dickinson, 2001), perhaps coupled with computational fluid dynamics (Wang et al., 2004).

Caution is always merited when interpreting the measurements from revolving wings because propeller motion does not fully emulate the complex motion of the bird wing.

Bearing this in mind, it may be that drag is higher during rotational motion of the wings compared with gliding. Maximal drag coefficients for the wings of galliform birds (Phasianidae) during rotation (Usherwood and Ellington, 2002) are approximately double the value measured for translating wings (Drovetski, 1996).

To date, dynamically scaled robotic models have only been developed for insects (Willmott et al., 1997; Sane and Dickinson, 2001), and these models have wings designed as flat plates that do not morph like bird wings (Bilo, 1971; Bilo, 1972; Warrick et al., 2005). Ideally, efforts to physically model P_{pro} will incorporate detailed 3D kinematics of the wing (Askew et al., 2001; Hedrick et al., 2002; Tobalske et al., 2007) to program robotic motion and use materials for the robotic wing that morph in a realistic manner.

As for P_{pro} , estimates of P_{par} are subject to considerable uncertainty because drag coefficients obtained from isolated bird bodies vary over 400%, from ~0.1 in varnished, footless, starling carcasses (Maybury, 2000) to ~0.4 in frozen waterfowl (Pennycuick et al., 1988). One might expect values from live birds to be lower than frozen carcasses, but a parasite drag coefficient of ~0.37 was measured from dive rates in passerines during migration (Hedenström and Liechti, 2001). Coefficients from 0.24–0.34 may be representative of live starlings in flight, and drag coefficients decrease as a function of forward flight speed (Maybury, 2000). There is some debate over the manner in which body area scales with body mass among species, and frontal projected area is necessary for a computation of coefficient of drag (Norberg, 1990). Hedenström and Rosén suggest that the frontal area of the body scales differently in passerines and non-passerines (Hedenström and Rosén, 2003), whereas Nudds and Rayner argue that scaling is similar between the two groups, and that reported differences in other studies are caused by comparing live birds with frozen specimens (Nudds and Rayner, 2006).

To further understanding of the aerodynamics of the bird body, it will be useful to take a broader view of the body to include the tail (Thomas, 1993). Treating the body as a 'parasite' upon the wings is a leftover from early aerodynamics research and is misleading, because the body is capable of producing lift even with the wings completely folded, as during intermittent bounds, which are flexed-wing pauses in between flapping phases (Csicsáky, 1977; Tobalske et al., 1999). The tail functions to reduce parasite drag (Maybury and Rayner, 2001); it contributes to the production of lift both when the wings are not present on a carcass (Maybury, 2000; Maybury et al., 2001) as well as during flight in live birds (Usherwood et al., 2005). Incorporating body lift (and, by extension, tail lift) into a model of P_{aero} reduces the estimated power required for relatively fast flight in flap-bounding birds (Rayner, 1985; Tobalske et al., 1999).

A model that is useful for describing the aerodynamics of the tail considers the tail as delta wing (Thomas, 1993). This model indicates that the tail morphology that produces the optimum lift-to-drag ratio is slightly forked when folded and triangular in shape when fanned, and that the area of the tail in front of the maximum span contributes to lift and drag, whereas the area behind the maximum span contributes only to drag. These properties of the tail serve as a foundation for testing, with

vigorously debated conclusions, whether the evolution of ornamentation, such as an elongated tail or streamers on a forked tail, represent a handicap that resulted from sexual selection or an aerodynamic benefit for activities such as maneuvering (Thomas, 1993; Møller et al., 1995; Park et al., 2000; Evans, 2004). Aspects of the model do not appear to be well supported by the use of the tail during flight in barn swallows *Hirundo rustica* (Evans et al., 2002), so new efforts are needed to modify the delta-wing model or develop alternative models.

Kinematics and upstroke aerodynamics

Unlike some forms of terrestrial locomotion in which gait selection may be identified using discrete changes in duty factor (the proportion of time a limb is in contact with the substrate, producing force) and patterns of sequential limb motion (Alexander, 1989), wing kinematics and associated aerodynamics, vary in a continuous manner with flight speed in birds.

Although downstroke kinematics are relatively invariant, upstroke kinematics differ among species and according to flight speed (Brown, 1963; Scholey, 1983; Tobalske, 2000; Park et al., 2001; Hedrick et al., 2002). Birds with wings that are relatively pointed, or of high-aspect ratio (long and thin), transition among flight speeds using tip-reversal upstrokes at slow speeds, feathered upstrokes at intermediate speeds, and swept-wing upstrokes at fast flight speeds (Fig. 3B). Birds that have rounded distal wings or wings of low aspect ratio (short and broad) tend to flex their wings regardless of flight speed. Some exceptions to this pattern exist. For example, galliform birds with rounded wings use a tip-reversal upstroke during take-off (Brown, 1963; Tobalske and Dial, 2000), and birds with rounded wings such as the black-billed magpie *Pica hudsonica* will alter upstroke postures according to acceleration and deceleration (Tobalske and Dial, 1996). Regardless of wing shape, the span ratio (mid-upstroke span divided by mid-downstroke span) generally decreases as a function of flight speed in birds, although it may increase with increasing speed in some passerines (Tobalske and Dial, 1996; Tobalske et al., 1999; Rosén et al., 2004; Tobalske et al., 2007).

Formerly, it was thought that there were two wingbeat gaits in birds because early PIV experiments revealed one of two patterns. One vortex ring was shed per downstroke during slow flight (Spedding et al., 1984), and the upstroke appeared aerodynamically inactive. This was identified as a 'vortex-ring' gait (Rayner, 1988; Rayner, 1999). During faster flight (Spedding, 1987), tip-vortices were shed into the wake during the entire wingbeat, indicating a 'continuous-vortex' gait (Rayner, 1988; Rayner, 1999). Because the wake area for a continuous-vortex wake would be greater than for a vortex ring, P_{ind} was predicted to be lower for the continuous-vortex gait.

Several problems are, nevertheless, apparent with a simple two-gait scheme for classifying avian flight (Tobalske, 2000), and new data reveal that continuous, rather than discrete, variation is characteristic of wing kinematics and aerodynamics (Spedding et al., 2003; Rosén et al., 2004; Tobalske et al., 2007). Although a two-gait system is intuitively acceptable to humans, given our use of walking and running, a two-gait system does not advance our understanding of obvious differences in wing

kinematics during the presumptive vortex-ring gait of slow flight (Tobalske, 2000) (Fig. 3). All measured wing kinematics, as well as patterns of muscle activity, change in a gradual way across flight speeds (Tobalske and Dial, 1996; Tobalske, 2000; Park et al., 2001; Tobalske et al., 2007). Furthermore, DPIV measurements of wake vortices across a range of speeds (Spedding et al., 2003; Hedenström et al., 2006) reveal that upstrokes are aerodynamically active during slow flight and that upstroke function varies gradually rather than categorically (Fig. 4).

Thus, the use of modern DPIV has highlighted a need for new comparative study of the aerodynamics of bird flight. For the limited number of species studied to date using DPIV, there does not appear to be significant variation in wake geometry during forward flight (Spedding et al., 2003; Hedenström et al., 2006). Also, the magnitude of normalized circulation (a dimensionless form, equal to circulation divided by wing chord and flight velocity) in the wake is similar among species (Hedenström et al., 2006). This may indicate that wing chord and flight speed are adequate predictors of circulation upon the wing, which would be highly useful for modeling efforts (Hedrick et al., 2002), since lift is proportional to circulation. More pessimistically, it may indicate that current DPIV measurements of time-averaged wake structures lack sufficient temporal resolution to reveal important details of wing aerodynamics (Dabiri, 2005).

Instead of a gait-based system of classification, a fascinating alternative that may serve to unify comparisons of kinematics and aerodynamics among birds is that they seek to maintain their Strouhal number (frequency times amplitude, divided by forward flight speed) during cruising flight in an effort to optimize the frequency of vortex shedding (Taylor et al., 2003). A diverse array of birds, as well as flying insects and swimming fish, exhibit Strouhal numbers in the range of 0.2–0.4 during cruising locomotion. Coordinated kinematic and DPIV studies will help test how these kinematics compare with rates of vortex shedding.

Maximum effort in slow flight

One way to elicit maximal performance from a bird is to get it to fly under conditions characteristic of the left side of the U-shaped power curve for flight (Fig. 2). Efforts to measure maximal performance may involve load-lifting (Marden, 1994; Chai and Millard, 1997; Altshuler et al., 2004), hovering in air of reduced density (Chai and Dudley, 1995; Altshuler et al., 2004), allowing the animal to escape to a refuge or freedom (DeJong, 1983; Warrick, 1998; Tobalske and Dial, 2000; Earls, 2000; Askew et al., 2001), or fostering competitive interaction (Tobalske et al., 2004).

Birds are already moving with significant velocity when their feet leave the ground at the end of take-off, and the majority of their initial flight velocity is due to hindlimb thrust (Earls, 2000; Tobalske et al., 2004). Initial flight velocity increases with body size among birds (Tobalske et al., 2004) from 0.8 m s^{-1} in the rufous hummingbird (weighing 3 g) to 6 m s^{-1} in wild turkey (*Meleagris gallopavo*; 6 kg). Since they are already moving, P_{aero} required immediately after take-off is lower than it would be from a standing start at 0 m s^{-1} (Fig. 2). This may represent a significant saving in power for birds that regularly take-off

and land, so it would be worthwhile if measurements could be made in the same species for power during leg thrust (Henry et al., 2005) and P_{mus} of the wings during take-off (Dial and Biewener, 1993).

It is widely recognized that mass-specific whole-body power (W kg^{-1} ; the $\Delta(E_p + E_k)/t$ term in Eqn 2, divided by body mass), declines as body size increases among bird species (Pennycuik, 1975; DeJong, 1983; Ellington, 1991; Warrick, 1998; Tobalske and Dial, 2000). However, the mechanical explanations for this trend are not fully understood. Since whole-body power is directly relevant to escape from predation (Kullberg et al., 1998; Hedenström and Rosén, 2001), new research is needed to better understand what factors limit performance. A potential explanation is that available mass-specific power from the flight muscles declines as a function of increasing body mass (Pennycuik, 1975; Ellington, 1991). If muscle stress and strain are invariant with body mass, then mass-specific work is invariant as well, and mass-specific power should scale with wingbeat frequency, approximately with mass to the $-1/3$ power (Hill, 1950; Pennycuik, 1975; Ellington, 1991).

As expected from this line of reasoning, mass-specific whole-body power scales with wingbeat frequency in galliforms during escape flight (Tobalske and Dial, 2000). However, when wing kinematics are input to an aerodynamic model (Askew et al., 2001), it is estimated that mass-specific P_{mus} actually increases, rather than decreases, with body mass. The estimated positive scaling of P_{mus} may be due to an increase in pectoralis strain (proportional to body mass raised to the 0.26 power) (Tobalske and Dial, 2000) or pectoralis stress (proportional to body mass raised to the 0.33 power) (Askew et al., 2001). Ideally these alternatives should be tested using *in vivo* strain-gauge recording, but the humerus of galliform birds is not suited for such measurements (Tobalske and Dial, 2000). Other groups of species, such as doves [Columbidae (Dial and Biewener, 1993; Soman et al., 2005)] may prove useful for such a test. Lacking *in vivo* force data, the conclusion (Askew et al., 2001) that muscle strain scales positively with body mass during escape flight relies on the accuracy of models used for P_{aero} . As outlined above (see 'U-shaped power curve'), a variety of new methods including DPIV (Spedding et al., 2003; Warrick et al., 2005) and pressure-transducer measurements (Usherwood et al., 2003; Usherwood et al., 2005) show promise for helping to revise estimates of the cost of producing lift.

Additional evidence also indicates that flight performance in take-off or ascending flight should not necessarily be limited by a negative scaling of muscle-mass-specific power. In a broad comparison of take-off in insects and some birds, all of which had their legs immobilized, proportional load-lifting ability is reported to increase with increasing body mass (Marden, 1994). Also, larger hummingbirds exhibit greater ability to climb with added load or support their weight in reduced-density air compared with smaller hummingbirds (Chai and Millard, 1997; Altshuler et al., 2004). For hummingbirds, the positive scaling of flight performance is accounted for by departures from geometric and dynamic similarity among species. Larger hummingbirds have proportionally larger wings and use greater wingbeat amplitudes (Chai and Millard, 1997; Altshuler et al., 2004); both attributes should reduce proportional P_{ind} costs.

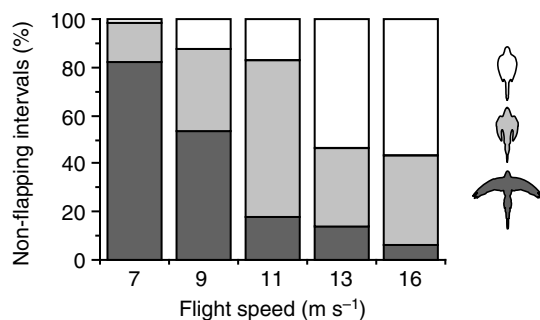


Fig. 5. Intermittent flight postures exhibited by budgerigar *Melopsittacus undulatus* as a function of flight speed in a wind tunnel. Black, glide; grey, partial bound; white, bound (from Tobalske and Dial, 1994). As flight speed increases, the proportion of non-flapping phases consisting of glides decreases, and the proportion consisting of bounds increases.

Intermittent flight

Many species of birds use intermittent flight, and the interruption of flapping phases with extended-wing glides or flexed-wing bounds has the potential to reduce P_{aero} (Rayner, 1985; Rayner et al., 2001; Tobalske, 2001). Compared with continuous flapping, flap–gliding is estimated to require less P_{aero} , at most flight speeds and in particular during slow flight, and flap–bounding is estimated to save P_{aero} in fast flight, more rapid than V_{mr} (Rayner, 1985). Generally consistent with the assumption that intermittent flight is useful for reducing P_{aero} required for flight, a variety of bird species use intermittent glides at slow speeds and switch to intermittent bounds or partial bounds at faster speeds (Tobalske, 2001; Bruderer et al., 2001) (Fig. 5). The pectoralis and supracoracoideus are inactive during bounds, and exhibit isometric contractions with reduced levels of muscle activation during glides (Tobalske, 2001; Tobalske et al., 2005).

There are profound effects of body size upon the use of intermittent flight. Species that use both flap–gliding and flap–bounding either have a body mass less than 300 g or have pointed wings of relatively high aspect ratio (Tobalske, 1996; Tobalske, 2001; Bruderer et al., 2001). Species larger than 300 g, for example pigeons, use intermittent glides but do not exhibit bounds. The scaling in passerines (Passeriformes) and woodpeckers (Piciformes) reveals that the percentage of time spent flapping increases with body mass (Tobalske, 1996; Tobalske, 2001). These patterns may be explained by an adverse scaling of sustainable mass-specific power in the flight muscles as body size increases, but this hypothesis must be tested exactly as outlined above (see ‘Maximum effort in slow flight’)

Although they can glide, small birds, less than 30 g, with rounded, low-aspect ratio wings, appear to almost exclusively use bounds during intermittent flight (Tobalske et al., 1999; Tobalske et al., 2005; Askew and Ellerby, 2007). This behavior is puzzling in light of the estimated higher P_{aero} for flap–bounding during slow flight compared with continuous flapping (Rayner, 1985; Rayner et al., 2001). Testing the underlying variables responsible for this behavior should prove challenging but, nevertheless, worthwhile, as flap–bounding is extremely common in the most diverse birds, the passerines.

An important hypothesis is that intermittent bounds are the sole mechanism available to small birds to enable them to modulate power output (Rayner, 1985), but the zebra finch *Taeniopygia guttata* (13 g) appears to be able to modulate contractile behavior in its muscles in the same manner as larger birds (Tobalske et al., 2005; Askew and Ellerby, 2007). An argument that such modulation may nevertheless be inefficient requires measurement of P_{met} during continuous flight and flap–bounding. Likewise, any argument about the functional significance of flap–bounding would be strengthened if P_{aero} was measured empirically rather than estimated from modeling and if P_{mus} could be measured *in vivo*. Unfortunately, the added weight and drag associated with masks and tubing used in gas respirometry causes small birds to stop using intermittent pauses (Bundle et al., 2007), and their bones are too small to permit strain-gauge recordings. For investigating the energetics of flap–bounding, it is feasible to use techniques other than gas respirometry for measuring metabolic rate including double-labelled water (Nudds and Bryant, 2000; Ward et al., 2001; Engel et al., 2006) or labeled bicarbonate (Hambly et al., 2002). Efficiency was estimated at 11% using labeled bicarbonate during slow flight in zebra finch *Taeniopygia guttata* (Hambly et al., 2002), and this is intriguing because this estimate is lower than a ~20% estimate for efficiency during fast flight in starlings that was obtained using double-labelled water (Ward et al., 2001). It may be possible to measure thermal efficiency of contractions in isolated muscle preparations (Barclay, 1996).

Another hypothesis is that, regardless of efficiency, variation in flap–bounding flight patterns could be constrained by neural control of limb motion. This control could be in the form of a central pattern generator such as has already been reported for the flapping motion and respiration of birds (Funk et al., 1992). Aspects of flap–bounding do not appear consistent with this hypothesis, however, as the duration of bounds and the number of wingbeats between bounds vary significantly with flight speed (Tobalske et al., 1999).

Maneuvering and stability

The ability to maneuver (Warrick et al., 2002) and the converse, controlling position to be stable in the air (Thomas and Taylor, 2001; Taylor and Thomas, 2002; Taylor and Thomas, 2003), are of great importance to flying animals. Highly maneuverable animals may respond more quickly to perturbations, thus they are expected to be better able to maintain their path during flight in turbulent conditions (Thomas and Taylor, 2001). Certainly the ability to maneuver has implications for aerial foraging (Warrick, 1998; Lentink et al., 2007). Wing morphology that is specialized for maneuvering may compromise other forms of performance such as acceleration ability during take-off (Warrick, 1998), so new research is needed to better understand how maneuvering ability may be related to escape performance.

Flapping motions may affect both maneuvering and stability. Downstroke is predicted to be a stabilizing influence about the longitudinal axis, whereas a lift-producing upstroke may be used to lower stability and thereby enhance maneuverability (Taylor and Thomas, 2002). Depending upon their posture, the

wings alone may provide longitudinal stability during gliding (Taylor and Thomas, 2002; Thomas and Taylor, 2001).

Lift and drag from the tail may also enhance stability, and the contribution of the tail is affected by morphology and posture (Hummel, 1992; Thomas and Taylor, 2001). For example, greater drag associated with a long tail contributes to longitudinal stability (Hummel, 1992), whereas pitching the tail with the trailing edge down will decrease stability (Thomas and Taylor, 2001). Kinematics from aerial insectivores indicates that the tail is used to vary total lift in concert with the wings rather than as an independent mechanism for controlling body pitch (Warrick, 1998), and this hypothesis merits new comparative study.

Because the intrinsic three-dimensionality of maneuvering presents special challenges for study, relatively few data are available at present, and a general pattern does not yet emerge for describing the mechanics with which birds accomplish maneuvers. One pattern that is shared by pigeons and two species of parrots (Psittaciformes) during slow flight is that the birds initiate rolls during downstroke (Warrick and Dial, 1998; Hedrick and Biewener, 2007a; Hedrick and Biewener, 2007b). Pigeons effect their turns using subtle, bilateral force asymmetries in their pectoralis that are maintained throughout a turn (Warrick et al., 1998). Electromyographic patterns suggest that asymmetries in pectoralis force are also used in cockatiels during turns, but the side that exhibits greater

activation switches midway through a turn (Hedrick and Biewener, 2007a). In contrast with these two species, in rose-breasted cockatoos *Eolophus roseicapillus*, electromyography indicates that bilateral asymmetries of force in distal wing muscles are more important for turning than minor asymmetries in the pectoralis (Hedrick and Biewener, 2007a; Hedrick and Biewener, 2007b).

In pigeons, roll is initiated in early downstroke with a higher velocity on the outer wing, and this roll is arrested with higher velocity on the inner wing during late downstroke or during the subsequent upstroke (Warrick and Dial, 1998) (Fig. 6). Cockatiels use asymmetric wingbeat amplitudes whereas cockatoos exhibit less significant asymmetry in amplitude, and they integrate this minor asymmetry with asymmetry in feathering angle (the angle wing chord relative to midline of the body) (Hedrick and Biewener, 2007a). Aerodynamic models suggest that velocity, amplitude and feathering-angle asymmetries cause lift asymmetries (Warrick and Dial, 1998; Hedrick and Biewener, 2007a). However, asymmetry in wing inertia may also contribute significantly (Hedrick and Biewener, 2007a; Hedrick and Biewener, 2007b; Hedrick et al., 2007). For example, in cockatoos, within-wingbeat rolling is accomplished primarily using asymmetries in wing inertia. Thus, future research would do well to measure wing inertia along with aerodynamic forces (Hedrick et al., 2007).

One conclusion that is clear from this recent work is that flapping dynamics must be incorporated into existing models of maneuvering (Taylor and Thomas, 2002; Warrick et al., 2002). Given a lack of kinematics, early attempts to model the comparative maneuvering ability of birds have treated these activities as fixed-wing events (Norberg, 1990). Moreover, even fixed-wing maneuvering predictions may need revision, given the recent observation that the distal portions of the wings of common swifts *Apus apus* may exhibit leading-edge vorticity when in a glide posture (Videler et al., 2004). Leading-edge vorticity on physical models of swift wings is of sufficient magnitude to increase lift, hence torque for maneuvering, above that predicted using blade-element wing theory. It has been hypothesized that the magnitude of this lift may help explain tight-turning maneuvers during high-speed gliding in swifts (Videler et al., 2004), but experiments with wings of varying posture indicates that it is drag reduction, rather than enhanced lift, that is the primary benefit derived from the swept-wing posture during high-speed glides (Lentink et al., 2007).

There are empirical measures of stability during flight in tethered insects (Taylor and Thomas, 2003), but no data are yet available from flying birds. Results from desert locusts *Schistocerca gregaria* indicate that they can correct for perturbations within one wingbeat. It is hypothesized that a key element to this ability to quickly react to disturbance is the tuning of their neuromuscular control to an observed pitching oscillation that occurs near the rate of the wingbeat. In the case of the locust, the pitching oscillation is at one half the rate of the wingbeat frequency. If the neuromuscular control of stability is tuned at this frequency of oscillation, the timing of neuromuscular control should scale among similarly shaped insects proportional to square root of the length of the insect (Taylor and Thomas, 2003). The tuning of the neural system for control in birds is predicted to be less constrained by a need to

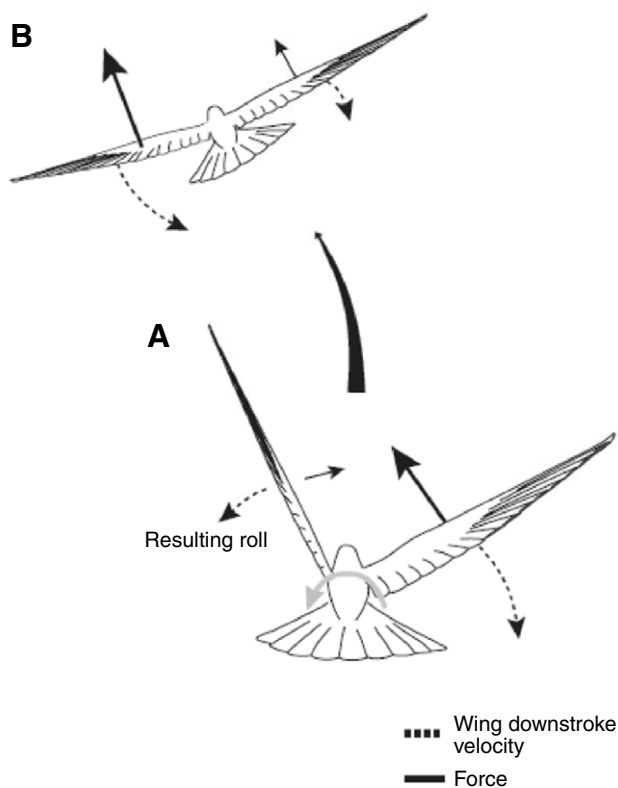


Fig. 6. Representation of a left turn during slow flight in a pigeon *Columba livia*, as seen in caudal view (from Warrick and Dial, 1998). (A) Roll is initiated using greater velocity on the outside (right) wing during the first part of downstroke. (B) Roll is arrested using greater velocity on the inside (left) wing during the latter half of downstroke.

approximate the timing of the wingbeat because the tail of birds can also control stability (Taylor and Thomas, 2003).

Reflections on future research

As recent technological developments have opened new opportunities to test hypotheses about function in bird flight, the key to enhancing development in this area of science is twofold. First, it is vital to update existing mathematical theory pertaining to bird flight by incorporating new empirical observations, and then enter into a healthy process of iteration in which empirical measures are used to test new theory and models are used to inform new experiments.

Secondly, it is imperative that biomechanical studies be integrated in an ecological, evolutionary context. A recent example of how this may be accomplished is a comparative study of flight performance in hummingbirds (Altshuler et al., 2004) that helps explain morphology, flight performance and ecological distribution in a broad array of species. Scanning the literature, there is a general trend for biomechanical studies to explore mechanisms in one representative species without explicit tests of how these mechanisms relate to the behavior and ecology of species in nature. A reductionist approach to designing experiments is a necessary first step, of course, but if it becomes a defining characteristic, it will lead to a plethora of studies that spin only in their own small domain and fail to demonstrate how flight mechanics fit into the larger reality of the biology of birds. Studying closely related species may help to reveal patterns that would be otherwise be obscured in a two-species approach (Tobalske, 1996), and a phylogenetic approach to experimental design is always mandatory for supporting an argument of adaptive significance for a trait (Garland and Adolph, 1994).

List of symbols

DPIV	digital particle image velocimetry
E_k	kinetic energy
E_p	potential energy
P_{aero}	aerodynamic power
P_{ind}	induced power
P_{iner}	inertial power associated with wing movement
P_{met}	metabolic power
P_{mus}	mechanical power output of flight muscles
P_{par}	parasite power
P_{pro}	profile power
t	time
V_{mp}	minimum power velocity
V_{mr}	maximum range velocity

I thank two anonymous referees for their helpful comments on an earlier draft of the manuscript. Supported by NSF Grant IOB-0615648.

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