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10 Morphological and Behavioral Correlates of Flapping Flight

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Active flight, characterized in birds by wing flapping, requires greater power output than swimming, walking or running (Schmidt-Nielsen, 1972; Harrison & Roberts, 2000). The power required for flight varies as a function of flight speed approximately according to a U-shaped curve, with more power required for hovering and fast flight than for flight at intermediate speeds (Pennycuick, 1975; Rayner, 1985; Tobalske *et al.*, 2003; Askew & Ellerby, 2007; Tobalske, 2007). Metabolic rates during flight are up to 30 times greater than basal metabolic rate (Nudds & Bryant, 2000). We begin this chapter by exploring the anatomy of the muscles that generate this power output and the skeletal elements that provide support for these muscles. In separate sections we then examine how the functional morphology of the flight apparatus affects flight performance. In each case, we observe that wing morphology and body size are key elements governing flight performance. We begin with the ontogeny of flight ability in precocial birds and use this model system to describe a novel, testable model for the origin of flight. We then turn to a style of flight that requires high power output: vertical escape after take-off. Next, we examine intermittent flight styles that offer energetic savings relative to continuous flapping. We move to maneuvering, an area that clearly needs new data and a modern synthesis since much of what is predicted about the ability to maneuver is based upon fixed-wing aerodynamics, pertinent only to gliding, and the highly flexible, morphing bird wing is scarcely ever fixed in shape, even during glides. Finally, we turn to hovering, the ultimate exertion of control during flight.

FUNCTIONAL MORPHOLOGY OF THE WING

There are a variety of features of the wings of birds that are associated with the production of high power output. The primary flight muscles include the major downstroke muscle, the pectoralis, and the major upstroke muscle, the supracoracoideus (Figure 10.1). Empirical studies of the function of these muscles using *in vivo* electromyography, sonomicrometry, and bone strain measurements as well as *in vitro* ergometry all indicate that these two muscles are generally designed to produce relatively high force per unit cross-sectional area (stress) while undergoing a relatively large length change (strain) during contraction (Dial *et al.*, 1997; Biewener *et al.*, 1998; Hedrick *et al.*, 2003; Tobalske *et al.*, 2003; Askew & Ellerby, 2007; Figure 10.2). While the pectoralis is comprised exclusively of fast-twitch fibers in most flying birds, some soaring birds have a deep anterior

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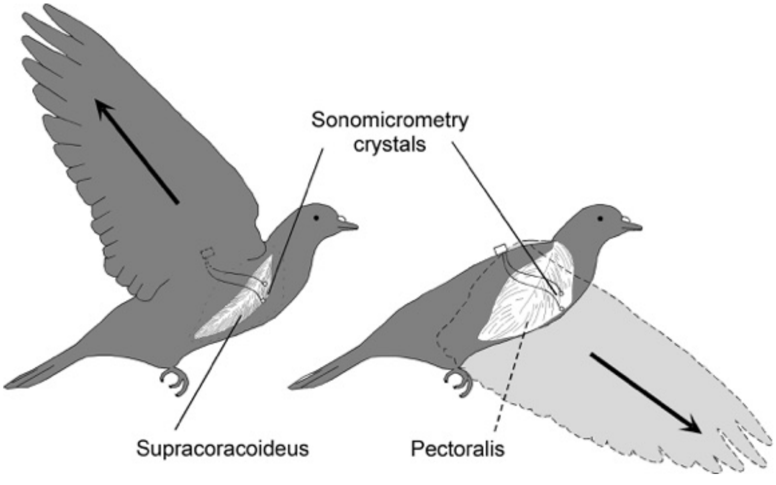

Fig. 10.1 The primary flight muscles in bird flight are the supracoracoideus (SUPRA) and pectoralis (PECT). These muscles function to decelerate and accelerate the wing, and these functions have been revealed *in vivo* using sonomicrometry transducers to measure changes in muscle length, and electromyography to measure neuromuscular activation. (From Tobalske & Biewener, 2008.)

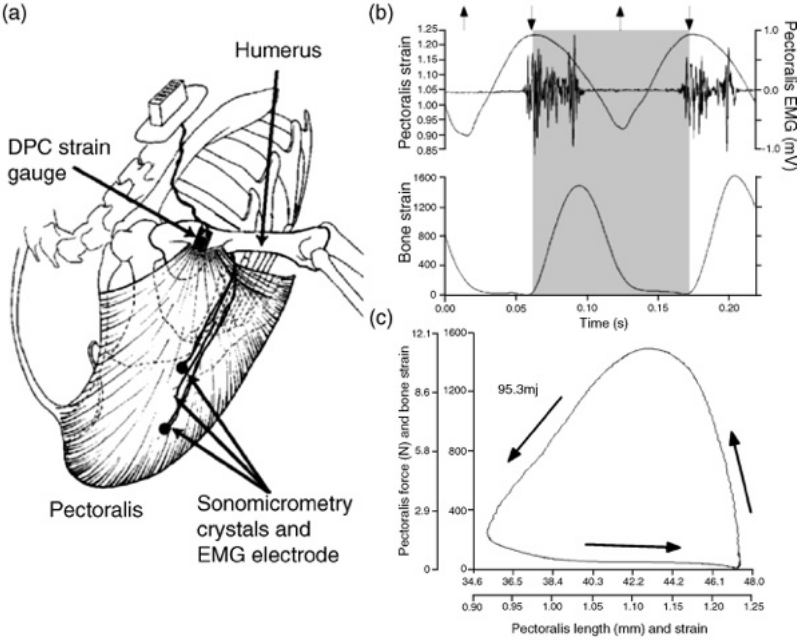

Fig. 10.2 In flying birds, the primary flight muscles appear to be designed to maximize the output work and power rather than isometric force. (A) This conclusion has emerged from *in vivo* measures of mechanical work that are obtained using sonomicrometry, electromyography, and strain-gauge measurements on the deltopectoral crest (DPC) of the humerus. These data reveal length change, neuromuscular activation, and force development in the muscle (B). Plotting muscle force as a function of muscle length produces a work loop (C); the area inside the work loop is the net work-output by the muscle (From Hedrick *et al.*, 2003; Tobalske *et al.*, 2003.)

portion of their pectoralis that consists of slow fibers and is thought to be a specialization for maintaining economical isometric contractions (Rosser & George, 1986a,b; Rosser *et al.* 1994; Meyers & Stakebake, 2005).

During flapping, the pectoralis muscle decelerates the wing at the end of upstroke and reaccelerates it at the beginning of downstroke (Dial, 1992a). The peak force observed in the muscle occurs at the middle of downstroke (Figure 10.2a), and the muscle typically changes between 20 and 42% of its resting length during contraction (Figure 10.2b). The large stress and strain in the muscle are evident in work loops obtained from *in vivo* measurements (Figure 10.2c). The area inside the work loop is a measure of work output by the muscle, and the rate of accomplishing this work, a function of wingbeat frequency, is the power output by the muscle.

Similar length change (muscle strain) and even higher force per unit area (muscle stress) are exhibited by the primary upstroke muscle, the supracoracoideus (Figure 10.1). This muscle decelerates the wing at the end of downstroke and reaccelerates it at the beginning of upstroke. A key function of the supracoracoideus is to accomplish long-axis rotation (supination) of the wing during the transition between downstroke and upstroke (Poore *et al.* 1997; Tobalske & Biewener, 2008). The supracoracoideus features a long tendon that inserts dorsally on the proximal humerus via a foramen triosseum that is bordered by the coracoids, furcula, and scapula (Baumel *et al.*, 1993). The tendon elastically stores and releases energy put into by the supracoracoideus, and this process may contribute up to 60% of the net work of the muscle (Tobalske & Biewener, 2008). The furcula may also function to elastically store and release energy (Jenkins *et al.*, 1988).

It may be that the pectoralis is the minimum muscle required for level flapping flight in birds, as experiments have shown that birds can fly without use of their supracoracoideus (Sokoloff *et al.*, 2001) or the distal muscles of the forearm and wrist (Dial, 1992b). However, future study should seek to clarify the relative contribution of other muscles of the wing to power output. Consider, for example, the scapulohumeralis caudalis. This is the third largest muscle of the wing, it inserts ventrally on the humerus, and the timing of its activation suggests that it is involved in wing pronation and depression at the start of downstroke (Dial, 1992a). Based upon patterns of neural recruitment, the intensity of electromyography signals, it is thought that the distal muscles of the wing are primarily used to alter wing shape to permit a bird to engage in different modes of flight or maneuver. A four-bar linkage system made up of the humerus, radius, ulna, and proximal metacarpus is hypothesized to automatically flex and extend the distal wing when proximal muscles such as the pectoralis are activated (Dial, 1992b).

Skeletal elements provide surface areas for the origins and insertions of the wing muscles, and, acting as levers, they transmit muscle forces to the air. Key features of the skeleton that support powered flight include the proportionally massive keel of the sternum, the enlarged deltopectoral crest (DPC) of the humerus, and the strut-like, stout coracoids (Figures 10.2a and Figures 10.3). The keel provides the origin for the pectoralis and supracoracoideus, and the deltopectoral crest provides the insertion for the pectoralis.

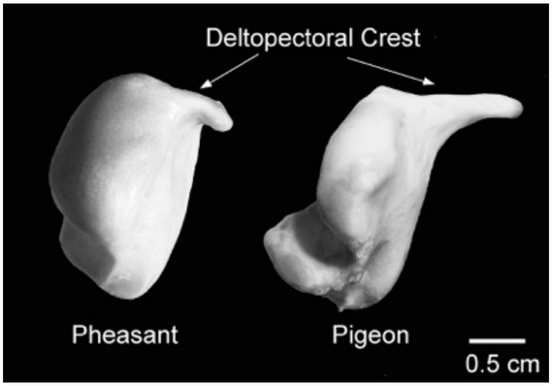

Fig. 10.3 The ventral side of the deltopectoral crest of the humerus (seen in medial view) is the insertion site for the primary downstroke muscle, the pectoralis. There is considerable diversity of shape in the deltopectoral crest as is evident in this comparison of bones from a ring-necked pheasant (*Phasianus colchicus*) and a rock dove (*Columba livia*). (From Tobalske & Dial, 2000.)

Proportionally large areas for muscle attachment presumably lessen the risk of detachment by holding tendon stress (force per unit area) below the point of failure, although this safety factor has not been studied explicitly for the pectoral girdle of birds. Among species, there is considerable diversity in DPC size and shape (Figure 10.3). Since this is the point of force transmission from the pectoralis to the rest of the wing, with clear implications for the majority of the lift produced by the wing, the functional significance of the diversity in DPC shape deserves study. The coracoids are oriented and shaped to resist compression of the thorax during contraction of the pectoralis and supracoracoideus (Pennycuick, 1968; Baier *et al.*, 2007). The furcula shows variation in form that is consistent with different uses of the wing, and flapping fliers exhibit less variation in shape compared with, for example, soaring birds or subaqueous flappers (Hui, 2002). As the furcula can contribute to elastic energy storage (Jenkins *et al.*, 1988), comparative mechanical analysis of the furcula is also warranted.

ONTOGENY AS A MODEL FOR THE EVOLUTION OF FLAPPING FLIGHT

Few subjects in science ignite such polarizing discussions as the origin and evolution of avian powered flight. Until recently, the vast literature on the subject remained firmly entrenched within two camps referred to as the ground-up (cursorial) and tree-down (arboreal) proponents (for review see Witmer, 2002). Cursorial hypotheses contend that the ancestors of birds ran bipedally using their long and slender theropod hind limbs, while their clawed and feathered forelimbs functioned to grab prey. Flapping the forelimbs in order to generate aerodynamic power and sustain powered flight came later. An extant model for this behavior is not apparent. The arboreal hypothesis suggests proto-birds quadrupedally climbed trees or other elevated structures to gain potential energy and then glided downwards (as observed in extant flying squirrels, e.g. *Glaucomys*; Bishop, 2006). The putative sequence of steps between gliding and powered flight is not fully resolved. Dudley *et al.* (2007) maintain that small motions of the appendages permit an animal to control the direction of descent during a glide, thus offering a precursor to flapping. Likewise, small-amplitude flapping motions may contribute to stability in flying squirrels (Bishop, 2006). Significantly, though, no extant gliders have been observed to actively flap their webbed appendages or fins (e.g. flying fish, Exocoetidae, Davenport, 1994) in an effort to produce thrust and extend their glide distance. An alternative, hypothesis-based approach to the origin of avian flight, explored by Garner *et al.* (1999) gave rise to a "pouncing predator" model, which satisfies several major phylogenetic assumptions. Nonetheless, an extant analog of the pouncing predatory model has also not been identified, so it is not presently possible to empirically test the functional morphology – mechanics and physiology – of the model.

Where can we find extant analogs to the origin of powered flight in birds? Where else can one find an incipient avian wing but on a baby bird? Before juvenile birds can fly, they readily use their wings in a form of escape behavior known as wing-assisted incline running (WAIR) that consists of flapping the wings during climbing (Dial, 2003; Dial *et al.*, 2006). This escape behavior may be used by ground-dwelling species such as the Galliformes when they have access to a sloped terrain (cliff, boulder, tree, etc.), and is common among nestlings of a diverse array of bird species (Dial *et al.*, 2008b). If partially developed wings in precocial birds are reasonably analogous to the incipient wings that the presumed ancestors of modern birds possessed, then the ontogeny of WAIR in extant species offers a novel, testable biomechanical model for the origin of powered flight in birds (Bundle & Dial, 2003; Dial, 2003; Dial *et al.*, 2006). This model assumes development in external wing morphology is representative of transitional adaptive stages (Bock, 1965) that led to the complex structure of the extant avian wing. An obvious limitation of the model is uncertainty in how extant avian neuromuscular control and contractile behavior as well as external wing motions compare with ancestral forms.

During ontogeny in chukar partridge (*Alectoris chukar*), feathers are structurally symmetrical (i.e. equal feather surface on either side of rachis) from day 6 through to day 14 (Figure 10.4). Potentially analogous feather symmetry is apparent in theropod fossils hypothesized to represent ancestors of extant birds (Quiang *et al.*, 1998; Xu *et al.*, 1999). In chukars, wing surface area increases in a near-linear fashion with age during the first 30 days and is asymptotic by day 45. The growth in body mass is such that wing loading (weight per unit surface area of the combined wings) remains relatively constant throughout their normal growth phase, with the lowest wing-loading values recorded during the first 30 days of development.

In adult chukar, there is no significant variation in the patterns of wing motion used during WAIR, descending, and level flight (Dial *et al.*, 2008b; Figure 10.5). Likewise, developing birds move their incipient wings, and, later, their fully developed wings, through a stereotypic kinematic pathway so that they may flap–run over obstacles, control descending flight and ultimately perform level flapping flight (Figure 10.5). As the same basic wing motion can allow an adult bird to accomplish disparate modes of locomotion, and baby birds use this basic pattern of wing motion before they can fly, Dial *et al.* (2008b) proposed an "ontogenetic–transitional wing hypothesis" that the transitional stages leading to the evolution of avian flight correspond both behaviorally and morphologically to the transitional stages observed in ontogenetic forms.

To reveal the aerodynamics of incipient wings during WAIR, Tobalske & Dial (2007) used particle image velocimetry (PIV) and measured flow dynamics in the wake of these animals as they engaged in WAIR and ascending flight (Tobalske & Dial 2007; Figure 10.6). The ontogeny of lift production was evaluated using three age classes:

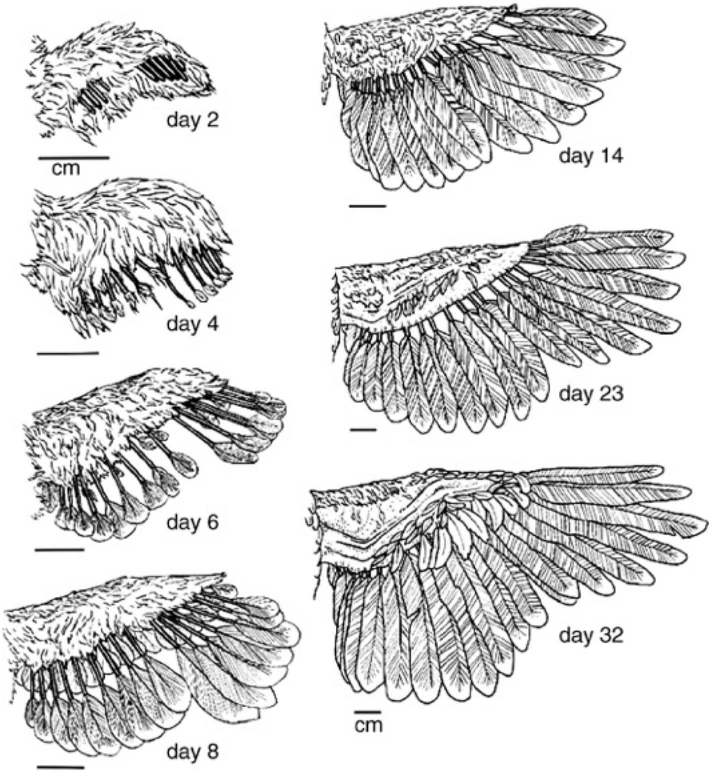

Fig. 10.4 Wing and feather development for the chukar partridge (*Alectoris chukar*) during ontogeny. By day 8, flapping the wings provides aerodynamic force that enhances the ascending and descending performance of the chicks. (From Dial *et al.*, 2006.)

Fig. 10.5 Locomotor development during ontogeny in the chukar partridge (*Alectoris chukar*) from hatching to adulthood. The sequence of transitional stages during development in an extant species may be relevant to understanding the origin and evolution of extinct forms. Stroke curves represent the trajectory of the wing during wing-assisted incline running (WAIR) (grey) and flight (black). Vectors indicate average lift during WAIR (grey) and the estimated lift (black) during slow level flight and descent. (From Dial *et al.*, 2008b.)

baby birds incapable of flight (5–8 days post-hatching) and volant juveniles (25–28 days) and adults (45+ days). All three age classes of birds, including baby birds with partially emerged, symmetrical wing feathers (Figure 10.6), generate circulation with their wings and share a wake structure that consists of discrete vortex rings shed once per downstroke. Unlike during flight when the wings produce lift to support body weight and match drag, during WAIR, lift from the wings

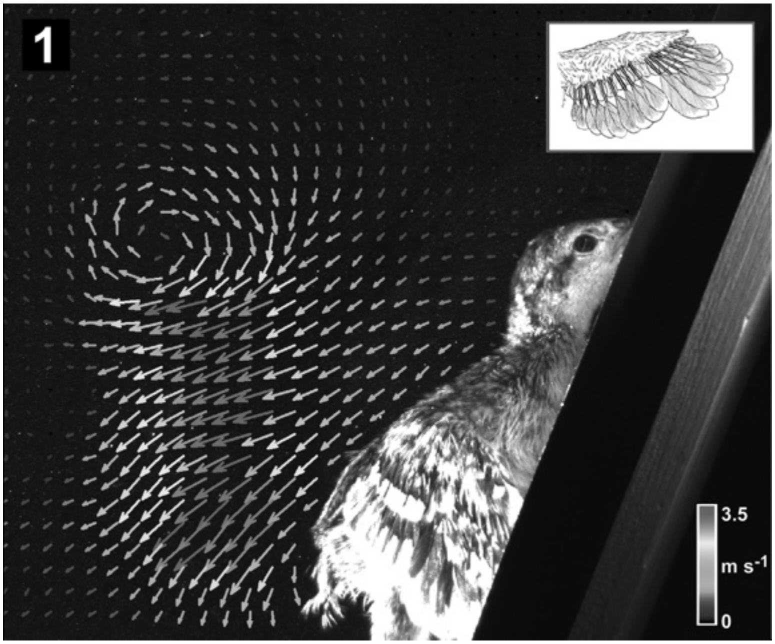

Fig. 10.6 Airflow in the wake of a flightless chukar partridge (*Alectoris chuk*ar) chick engaged in wing-assisted incline running. Velocity in the flow field was revealed using particle imagery velocimetry (PIV); the wake reveals evidence of lift production in a manner similar to juvenile and adult birds that are capable of flight. At day 8 of development, the chick has symmetrical remiges (inset, upper right). (Adapted from Tobalske & Dial, 2007.) [This figure appears in color as Plate 10.6.]

accelerates the body toward the surface of the substrate being climbed, thereby increasing friction and aiding the feet in gaining purchase. These data show that partially developed wings, not yet capable of flight, can produce useful lift during WAIR.

These aerodynamic experiments show that factors besides external wing morphology may be functioning as primary constraints upon the onset of flight ability during development (Tobalske & Dial, 2007). Potential variables that should be tested include neuromuscular control and power output of the muscles moving the wings. Nonetheless, the aerodynamics of WAIR in baby chukar provides new insight into how an ancestral incipient wing that was not capable of supporting flight may have been an exaptation (Gould & Vrba, 1982) originally used solely for WAIR.

TAKE-OFF AND ESCAPE FLIGHT

When flying to escape a predator, or voluntarily initiating flight from the ground, take-off and the gain in potential energy that occurs during flight demand more power than most other forms of flight (Pennycuick, 1975; Rayner, 1979a,b, 1985; Ellington, 1991). Although some of the mechanical power from the flight muscles is used to overcome profile (pressure and skin-friction) drag on the wings, the majority of power output during take-off and vertical flight is used to induce a massive downward velocity to the air. Induced power is the product of this induced velocity multiplied by body mass and any net vertical or horizontal acceleration (including gravity) (Askew *et al.*, 2001). More broadly, flight speeds at take-off are relatively slow, and induced power output is modeled as being greatest at low speed, decreasing exponentially with increasing air velocity over the wing.

Since few birds are capable sustaining flight at zero velocity (see *Hovering*, below), and acceleration requires even more muscle power than hovering, take-off imposes induced-power demands beyond the capabilities of most avian wings. Birds therefore depend on their legs to provide assistance. The contribution of the legs to the velocity of the bird at the end of take-off, defined as the end of the first downstroke after the feet have left the ground varies from 59% (rufous hummingbird, *Selasphorus rufus*; Tobalske *et al.*, 2004) to 90% (blue-breasted quail, *Coturnix chinensis*; Earls, 2000). Peak jumping forces can be as low as 1–3 times body mass during voluntary take-off (Heppner & Anderson, 1985; Bonser & Rayner, 1996) and reach about 4–5 times body weight in escape flight in the passerines (Passeriformes; Earls, 2000; Jackson, unpublished data) and 7.8 times body weight in blue-breasted quail (Earls, 2000).

The legs are only in contact with the ground for a fraction of a second, so the wings must eventually take over, and short wings are better suited for rapid take-off. Power output is a function of work per wingbeat (Figure 10.2b) divided by the duration of the wingbeat. Thus, everything else being equal, the higher the wingbeat frequency, the more induced power a bird can produce, and the quicker it can accelerate vertically. Within a group of similarly shaped birds (Tobalske & Dial, 2000), wingbeat frequency during take-off decreases with increasing body mass (m), approximately proportional to the cube-root of mass ($m^{-1.3}$). Comparing species of different wing shapes but similar mass, however, it appears that wingbeat frequency is inversely related to wing length (Pennycuick, 1996). Consider, for example, a species such as an albatross (Diomedeidae) with long and pointed (high aspect ratio) wings. Although the wing shape is thought to be extremely efficient for gliding, the birds have a difficult time getting off the ground, and usually have to run into prevailing winds before taking off (Pennycuick, 1975). Comparatively, a gallinaceous bird of similar mass such as the wild turkey (*Meleagris gallpavo*), which has short and rounded wings, is ideally suited for high-acceleration take-off (Tobalske & Dial, 2000; Askew *et al.*, 2001).

During take-off and vertical flight, birds must use muscle power to do work to raise their center of mass against gravity and to accelerate. The amount of mechanical power produced by the muscles in relation to body-mass (i.e. mass-specific power) therefore largely determines the actual flight performance. Extant flying birds range in mass from a 2 g bee hummingbird (*Mellisuga helenae*) to a 14 kg mute swan (*Cygnus olor*; Dunning, 1993). While it is readily observed that a swan is not capable of hovering at a flower or even taking-off vertically like a hummingbird, the underlying mechanism, the mass-specific power available for flight relative to the amount required, is not fully understood. Bird species in general scale isometrically (Greenewalt, 1962), meaning that muscle masses are the same proportion of body mass, and wing-lengths are the same proportion of body length. Scaling theory would, therefore, predict that available mass-specific power should scale proportional to wingbeat frequency ($m^{-1/3}$; Hill, 1950; Pennycuick, 1975; Ellington, 1991). According to this line of reasoning, since large species tend to have lower wingbeat frequencies, their muscles produce less mass-specific power, which translates into lower take-off performance compared to smaller species. This could account for the observed trend of decreasing take-off performance with increasing size in birds if the mass-specific power required for flight is independent of body mass (Figure 10.7; Tobalske & Dial, 2000; Dial *et al.*, 2008a). On the other hand, aerodynamic modeling suggests that the mass-specific power output during take-off actually increases with body mass (Askew *et al.*, 2001). Consistent with the notion that mass-specific power is not limiting flight performance in larger birds, proportional load-lifting ability increases with increasing body mass (Marden, 1994) and larger hummingbirds exhibit greater ability to climb with added load or support their weight in reduced-density air compared with smaller hummingbirds (Chai & Millard, 1997; Altshuler *et al.*, 2004). For hummingbirds, nonisometric scaling of muscle morphology or physiology may compensate for the impact of body mass (Chai & Millard, 1997). While variation in relative muscle mass, muscle morphology, and fiber physiology, and wing shape and size all could explain some of the variation in take-off performance, body-mass is likely a fundamental determinant of burst flight performance during take-off.

Some bird species experience significant fluctuations in body mass due to migratory fat loading or egg production. Since their body mass increases but muscle mass and wing size typically do not,

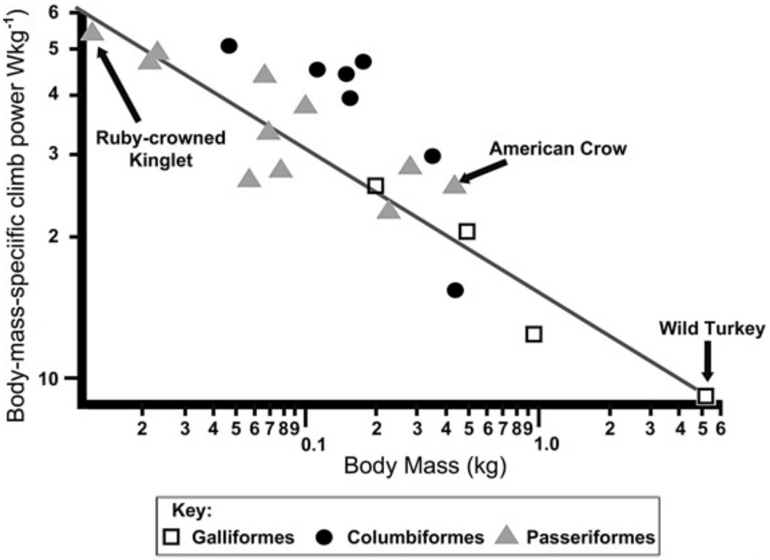

Fig. 10.7 Vertical escape-flight performance in three orders of birds spanning three orders of magnitude of body mass: Galliformes (squares), Columbiformes (circles), and Passeriformes (triangles). Whole-body (external) mass-specific power output is proportional to mass raised to the −0.3 power ($m^{-0.3}$). (From Dial *et al.*, 2008a.)

individuals of these species may experience reduced take-off performance (Hedenström & Alerstam, 1992; Witter *et al.*, 1994; Kullberg *et al.*, 1998). The trade-off between fat-loading to decrease risk of starvation vs. foraging minimally to maintain take-off and predator-escape performance is a rich area of study. However, not all species demonstrate reduced take-off performance with fat-loading, some reduce acceleration or velocity, while others reduce only the angle of ascent. The factors that drive the variation in strategy, and the ecological and evolutionary implications of this trade-off, are mostly unknown.

INTERMITTENT FLIGHT

The vast majority of small and medium sized birds use one of two forms of intermittent flight during which they regularly interrupt flapping phases to hold their wings either in a flexed-wing "bound" posture, during which the wings are held tightly against the body, or in an extended-wing "glide" (Rayner, 1985; Tobalske, 2001; Figure 10.8). Some species, such as the budgerigar (*Melopsittacus undulatus*) use bounds, glides, and partial-bounds during which the wings are partially extended (Tobalske & Dial, 1994). These flight styles are characterized by undulating flight paths as the birds gain altitude using flapping and lose altitude during the fixed-wing pauses (Figure 10.8). The flight style of the black-billed magpie (*Pica*

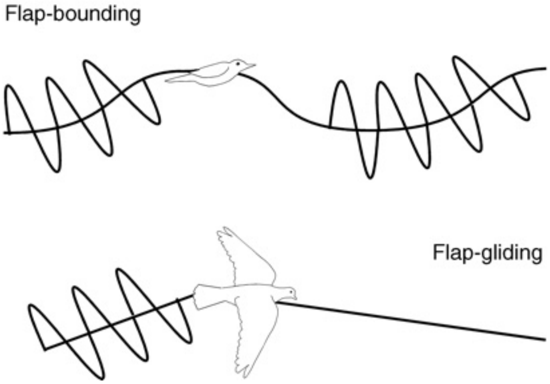

Fig. 10.8 Intermittent flight features regular, brief pauses in between flapping phases. A bound occurs if the bird flexes its wings against its body and a glide occurs when the birds holds its wings extended. Some species exhibit intermediate wing postures (partial bounds or glides).

hudsonia) is a novel form of intermittent flight, which consists of regular variation in wingbeat frequency and amplitude during flapping phases as well as intermittent bounds and glides (Tobalske *et al.*, 1997). Flap-bounding is readily observed during foraging and migratory flights in many small passerines (Passeriformes; Danielson, 1988) and woodpeckers (*Picidae*; Tobalske, 1996). Flap-gliding flight is exhibited during flight in a diverse array of birds including swallows (Hirundinidae; Bruderer *et al.* 2001), swifts (Apodidae), accipiters (Accipitridae), wood pigeons (*Columba palumbus*), and northern harriers (*Circus cyaneus*).

Intermittent flight appears to be a strategy for saving energy by reducing the average power required for flight in comparison with that required for continuously flapping. Mathematical models developed from aerodynamic theory indicate that flap-bounding can be an attractive strategy when flying relatively fast (Rayner, 1985; Ward-Smith, 1984a), while flap-gliding may offer greater advantages at slower speeds (Ward-Smith, 1984b; Rayner, 1985). The production of lift by the body and tail may help extend the range of aerodynamically attractive speeds for flap-bounding to include maximum range speed, the speed predicted to be optimal for sustained cruising flight (Rayner, 1985; Tobalske *et al.*, 1999). Measurements of body acceleration and wake dynamics in live birds as well as force measurements on prepared specimens all indicate that birds can support 10–15% of their body weight even with their wings fully flexed in a bound posture (Csicsáky, 1977; Tobalske *et al.*, 1999, 2009). The contribution of "turn-out" phases during which the wings are extended after a bound may allow flap-bounding to offer an advantage over a broad range of speeds (DeJong, 1983). Likewise, variation in flight speed and thrust can result in predicted energetic advantages for both flap-bounding and flap-gliding over a wide range of speeds (Rayner *et al.*, 2001). Kinematics reveal that variation in flight speed is typical of intermittent flight (Tobalske, 1995; Tobalske *et al.*, 1999), and correlations between body motion and muscle activity suggest that thrust likely varies as well (Tobalske & Dial, 1994; Tobalske, 1995; Tobalske *et al.*, 2005; Askew & Ellerby, 2007).

Activity in the major flight muscles decreases during intermittent pauses compared with during flapping phases (Meyers, 1993; Tobalske & Dial, 1994; Tobalske, 1995, 2001; Tobalske *et al.* 2005; Askew & Ellerby, 2007; Figure 10.9). During intermittent glides, the pectoralis exhibits an isometric contraction and the supracoracoideus is inactive, whereas during bounds, both muscles are inactive (Tobalske, 2001). Sonomicrometry reveals that the pectoralis does not change length during intermittent pauses (Tobalske *et al.*, 2005; Askew & Ellerby, 2007).

There are prominent effects of body size and wing shape upon the performance of intermittent flight. Small birds with rounded, low-aspect ratio wings such as the zebra finch (*Taeniopygia guttata*; 13 g; aspect ratio, $AR = 4.2$) appear to only use intermittent bounds (Tobalske *et al.*, 1999, 2005). In contrast, species of about the same body mass but with more pointed, high-aspect-ratio wings such as the barn swallow (*Hirundo rustica*; 20 g; $AR = 6.2$) and house martin (*Delichon urbica*; 17 g, $AR = 6.5$), use both bounds (or partial bounds) and glides (Bruderer *et al.*, 2001). Regardless of aspect ratio, species of intermediate mass between 34 g budgerigars ($AR = 7.1$) and 150 g black-billed magpie ($AR = 4.1$) use both forms of intermittent flight. Above 300 g, birds do not appear to be able to use intermittent bounds so, for example, the rock dove, *Columba livia* only uses gliding during pauses in wing flapping (Tobalske & Dial, 1996).

What limits the upper-size range for the ability to bound? The largest species observed to regularly bound is the pileated woodpecker (*Dryocopus pileatus*; 270 g; Tobalske, 1996, 2001). As described above for whole-body power output during take-off and vertical flight performance, there is an observed decline in the performance of bounds as body size goes up. The percentage of time spent flapping increases with increasing body mass among passerines engaged in migratory flight (Danielson, 1988) and woodpeckers engaged in foraging flight (Tobalske, 1996, 2001; Figure 10.10). The scaling is proportional to mass raised

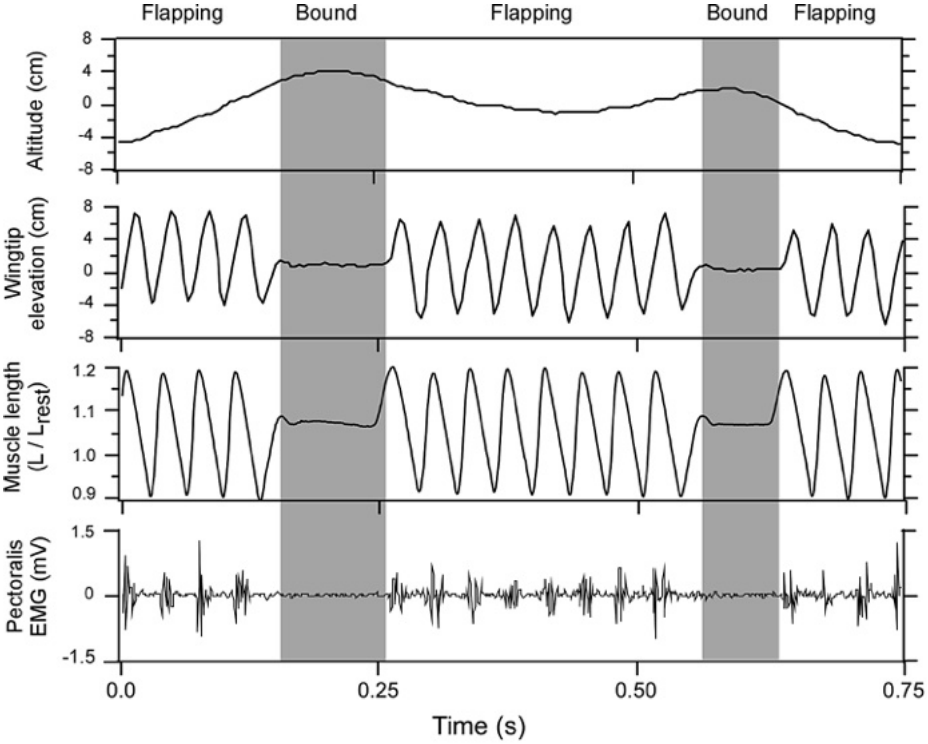

Fig. 10.9 Patterns of wing and body motion and muscle contractile behavior during flap-bounding flight in a zebra finch (*Taniopygia guttata*). The bird gains altitude during the latter half of flapping phases and loses altitude during the latter half of bounds. The pectoralis is inactive during bounds: there is no neuromuscular activity as measured using electromyography, and there is no change in muscle length as measured using sonomicrometry. (From Tobalske *et al.*, 2005.)

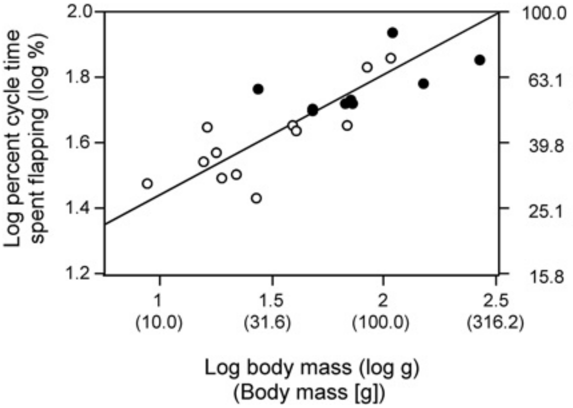

Fig. 10.10 The percentage of time spent flapping during flap-bounding flight in 12 passerine (Passeriformes, open circles) and seven woodpecker (Picidae) species varying in mass from 10 to 250 g. Percent time flapping scales proportional to body mass raised to the 0.37 power ($m^{0.37}$). (From Tobalske, 2001.)

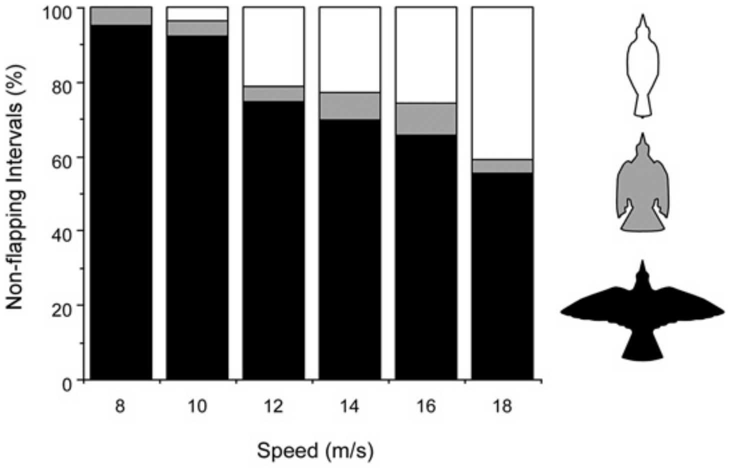

Fig. 10.11 Flight speed affects the type of wing posture assumed during intermittent pauses in some species. These data, from European starlings (*Sturnus vulgaris*), show the percentage of bounds (white), partial bounds (gray), and glides (black) among all nonflapping phases exhibited at a given speed. As speed increased, the percentage of glides decreased while the percentage of bounds increased. (From Tobalske, 1995.)

to the 0.37 power ($m^{0.37}$). A potential explanation for this is that the sustainable mass-specific power available from the flight muscles is proportional to wingbeat frequency, and, therefore, decreases as a function of increasing body mass (Hill, 1950; Pennycuick, 1975). Consistent with such a hypothesis, wingbeat frequency scales proportional to $m^{-0.37}$ in flap-bounding birds (Tobalske, 1995) Alternatively, the lift per unit power output may decrease with increasing body mass (Marden, 1994). The aerodynamic mechanisms responsible for this decrease in relative lift production need to be measured empirically.

Flight speed has significant effects upon intermittent flight behavior as it appears to influence the percentage of time spent flapping as well as the nonflapping postures adopted during intermittent pauses. In zebra finch, a species that only flap-bounds, there is a decrease in time spent flapping from 89% during brief hovering episodes to 55% during fast forward flight ($14\,\mathrm{m\,s^{-1}}$). In the budgerigar and European starling, species that use both intermittent bounds and glides, the percentage of time spent flapping varies according to an upwardly concave, "U-shaped" curve (Tobalske, 2001). Similarly, mean effective wingbeat frequency varies as a U-shaped curve in barn swallows and house martins (Bruderer *et al.*, 2001). Among the species that use both bounds and glides, there is a tendency to flap-glide at slow speeds and flap-bound during faster flight (Tobalske & Dial, 1994; Tobalske, 1995; Bruderer *et al.* 2001; Figure 10.11). However, recent research did not reveal the same trend to switch from the use of bounds to the use of glides as flight speed increased in rose-colored starlings (*Sturnus roseus*; Engel *et al.*, 2006).

MANEUVERING

The high velocities – and hence, kinetic energy – characteristic of flight must place a selective premium on control. Clearly, the broad utility of avian flight would not have been realized without development of effective stability and maneuvering (Thomas & Taylor, 2001; Taylor & Thomas, 2002; Warrick *et al.*, 2002).

During gliding (e.g. Pennycuick, 1971), a maneuvering bird can be described by well-understood aircraft dynamics: turns are effected by creating a bilateral force asymmetry, imparting a rolling moment about the long axis of the body to establish a bank angle, thus redirecting the lift force to provide a centripetal force. Maneuverability in this case has been defined by radius of turn (Norberg & Rayner, 1987); with a fixed-wing assumption, the radius of turn will be determined by wing loading (mass × wing area^{-1}; Pennycuick, 1971). Even given the assumption of fixed-wings, maneuverability has considerable explanatory power; variation in wingloading and maneuverability have been used to cogently describe differences in habitat use in bats (Aldridge, 1987; Norberg & Rayner, 1987), and foraging behavior and prey selection in swallows (Warrick, 1998). Further, they have the desirable feature of being among the few flight performance parameters that can be inferred when the fossil record provides reliable estimates of body mass and wing area (e.g. Pennycuick, 1988).

To create force asymmetries to produce roll, a bird can manipulate one or more lift variables: wing surface area, angle of attack, or wing speed. In fast gliding flight, a bird can merely increase the angle of attack by supinating a wing, while simultaneously pronating to decrease angle of attack on the other. The wings can be used to create moments around the other two body axes as well. By moving the wings' center of lift forward or aft of the bird's center of mass, birds create pitching rotation to change whole-body angle (Thomas & Taylor, 2001). Likewise, any asymmetry in area or angle of attack will produce not only differential lift but also differential drag, causing yawing rotations.

Agility, the ability to create angular velocities in rolling, pitching, or yawing movements, has been distinguished from maneuverability (Norberg & Rayner, 1987) as a meaningful performance criterion of its own for some ecotypes (e.g. coursing insectivorous birds such as swallows (Hirundinidae; Warrick, 1998). However, as function of the strength of forces available relative to the inertia of a body around its three rotational axes, most small birds are intrinsically agile. Viewed another way, relative to their terrestrial ancestors, birds are intrinsically unstable – perhaps a result of selection for a compact and therefore robust body able to withstand the rigors of high frequency, periodic support (Taylor & Thomas, 2002).

While the tail during low-speed flight seems to be restricted to acting as a lifting device (Gatesy & Dial, 1996; Thomas, 1996a,b; Berg & Biewener, 2008), at high speed the avian tail can function in pitch and yaw control, both to augment maneuvering performance and stabilize level flight (Thomas & Taylor, 2001). Unilaterally depressing the tail creates a laterally directed force and yawing moment (Hummel, 1992; Thomas, 1993) away from the depressed side of the tail. Functioning much like the rudder of an airplane, this force can thus be used for countering the so-called adverse yaw that is created during wing asymmetries, when the higher lift wing must also create more drag, yawing the animal in a direction opposite to its intended direction of flight (Warrick, 1998). Empirical (Hummel, 1992) and theoretical (Thomas, 1993) studies show that the forces created by the tail are small relative to those created by the wings. This may make the tail even more useful as a stabilizing device; its ineffectiveness allows coarse motor control to produce fine-scale aerodynamic force.

For a complete understanding of maneuverability in birds, a fixed-wing assumption is inadequate. But abandoning it introduces a staggering level of complexity; not surprisingly, no single functional pathway for the control of maneuvering during flapping flight has yet been identified. However, studies of the dynamics of maneuvering flight illustrate both the central role of the pectoral architecture and the importance of the intrinsic wing muscles in controlling slow, flapping flight.

Assuming an aerodynamically inactive – or simply less active – upstroke (Rayner, 1979a; Tobalske, 2000), maneuvering in slow flight will be to some degree a saltatory affair. That is, when aerodynamic force production ceases, the centripetal force ceases, and the bird will move in a straight line until the next downstroke. Nevertheless, the smallest radius turn – a radius of zero – is available only to a flapping bird: in a hover, no centripetal force is required, and the bird simply rotates around its center mass and heads off in a new direction. More generally, a bird able to maintain high incident air velocity over its wing through flapping, while the velocity of the body is low, will produce turns of small radius.

As in gliding flight, birds may modulate aerodynamic force by varying surface area and angle of attack, but, during flapping, they may also vary

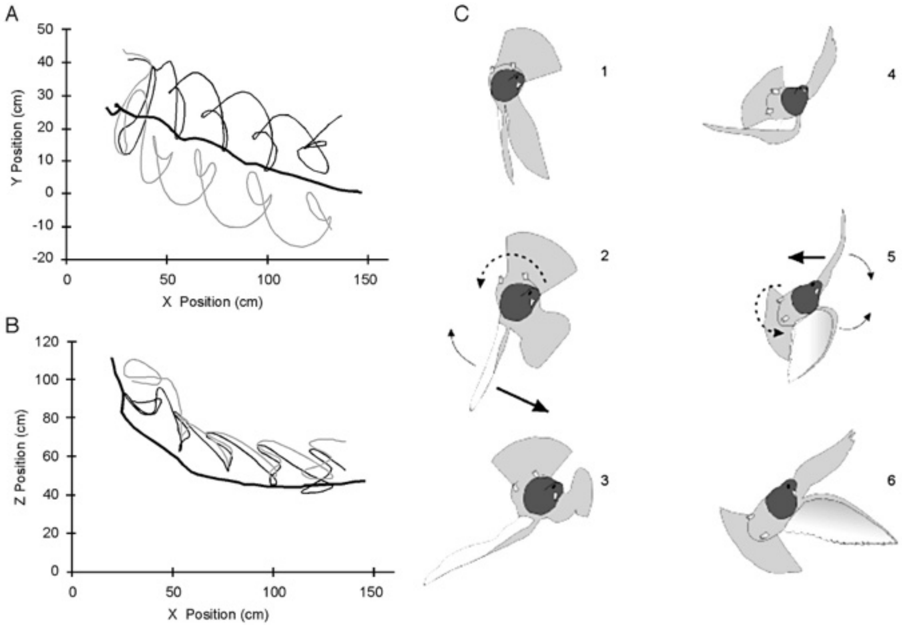

Fig. 10.12 Three dimensional kinematics (A, B) and wing and body orientation (C) of a rock dove (Columba livia) maneuvering after being held inverted and then dropped. Wingtip (right = grey; black = left) and body (bold black) kinematics of a pigeon, held inverted and dropped. With one asymmetrical wingbeat, the pigeon rights itself; with two further wingbeats (200 ms) it has arrested its descent, and flies to a perch. (D.R.Warrick, unpublished data.)

downstroke velocity. The kinematics of pigeons (Warrick & Dial 1998; Figure 10.12) and parrots (Psittaciformes; Hedrick & Biewener, 2007a; Hedrick *et al.*, 2007) show that birds use asymmetries in downstroke velocity – and to some degree in pigeons, upstroke – to create roll and yaw during slow flight. Both were shown to produce these asymmetries in the first half of downstroke, and reverse the asymmetry in the second, thus halting the rolling momentum before the upstroke. Warrick & Dial (1998) assumed that the velocity asymmetries observed were used to create aerodynamic force asymmetries, but Hedrick & Biewener (2007a,b) and Hedrick *et al.* (2007) showed that birds may also take advantage of the body rotations resulting from asymmetric wing movement. This inertial reorientation was shown to be particularly important in changing body angle within a wingbeat, and allows for an immediate, transient, and easily reversed bank angle. As these studies illustrate, the ability to produce transient bank within a wingbeat, with no net change in bank, gives the maneuvering bird an opportunity to move stepwise through its environment.

Patterns of wing motion (Warrick & Dial 1998; Hedrick & Biewener 2007a,b; Hedrick *et al.*, 2007; Figure 10.12) and measurements of the force experienced by the wings (Warrick *et al.*, 1998; Figure 10.13) show that birds frequently produce a series of asymmetries, with higher force on the outside wing, rather than simply creating a bank, holding that bank and flying symmetrically through the turn. While there has been no rigorous examination of the advantages of this maneuvering strategy, the higher success of pigeons exhibited this pattern in negotiating an obstacle course (Warrick *et al.*, 1998), and the proficiency of both these phylogenetically distant species in creating these incremental maneuvers, suggests that slow maneuvering flight is a tightly controlled

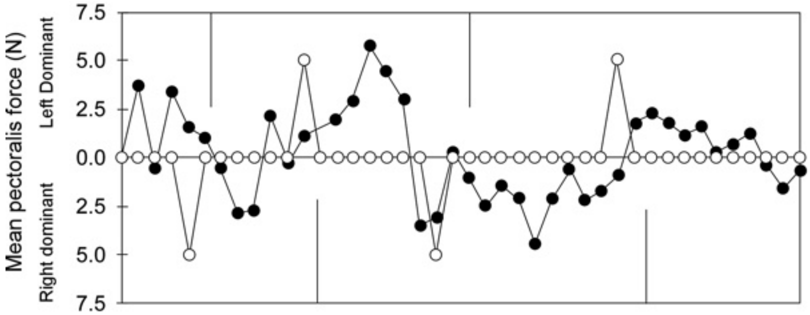

Fig. 10.13 Peak force asymmetries (black points) at mid-downstroke measured at the deltopectoral crest of a pigeon, superimposed on the obstacle course flown it was flying. The open points would be the expected asymmetry pattern if the birds simply established a bank with one force asymmetry and then flew around the barriers. The black vertical lines indicate the position of the barriers around which the birds maneuvered. (From Warrick *et al.*, 1998)

behavior. Whether reorienting through asymmetry in aerodynamic force production or inertia, these studies illustrate the intrinsic instability of birds (roll accelerations greater than 20,000° s^{-2}; Warrick & Dial, 1998; Hedrick & Biewener, 2007a,b; Hedrick *et al.*, 2007). However, a theoretical examination of stability in flapping flight suggests that symmetrical flapping itself does little to destabilize the bird (Taylor & Thomas, 2002).

While we currently lack a complete description of the muscular control of these maneuvering events, electromyogram (EMG) studies of rose-breasted cockatoos (*Eolophus roseicapillus*; Hedrick & Biewener, 2007b) and denervation studies of pigeons (Dial, 1992a) suggest that distal muscles may function to modulate the activity of the pectoralis through pronation, supination, or flexion. While Hedrick & Biewener (2007a) found no muscle activity asymmetries in these intrinsic wing muscles consistently associated with particular maneuvering kinematics, these muscles did display more asymmetry during maneuvering than during level flight, suggesting a complex synergism. In contrast, the asymmetry in recruitment of the pectoralis was consistently correlated with maneuvering kinematics. Thus it appears that, as a primary provider of both aerodynamic power and flapping wing inertia, the timing and force production of the pectoralis is critical, and may be the "key innovation" (Liem, 1973; also see Raikow, 1986) in the evolution of control of low-speed maneuvering flight.

HOVERING

As we have reinforced in this chapter, flight is an energetic affair, and control is the purpose of maneuvering; thus, no discussion of flight can be complete without exploring how birds control their kinetic energy by flying slowly. In this sense, the ultimate flight maneuver is one that requires no maneuvering at all: the hover.

True hovering – the ability to fly with incident airspeed of zero over the body of the bird is an option probably available to all small and medium-sized birds (Pennycuick, 1975; Ellington, 1991). Even if for only one or two seconds, the flexibility it provides a bird in safely moving through its environment – particularly during landing – may be profoundly important (e.g. Green & Cheng, 1998). Sustained hovering, using aerobic metabolism for indefinite time intervals (Lasiewski, 1963), is a different matter, seemingly confined to hummingbirds (Trochilidate). Hovering in still air is a particularly demanding flight style in terms of power requirements because the bird is solely responsible for inducing a large downward velocity into the air to support its weight. These induced high velocities require high power output from the flight muscles. In contrast, in forward flight, or during hovering with a headwind in birds such as kingfishers (Coraciiformes), incoming air (wind) contributes to the production of lift and the induced velocities required to support body weight are, therefore, less (Pennycuick, 1975; Rayner, 1979a,b, 1985).

The hovering ability of hummingbirds is related to their small body size (Altshuler & Dudley, 2002): most species have body masses between 2 and 8 g, and the giant hummingbird (*Patagona gigas*), unusually large for the family, is only 20 g (Dunning, 1993). Hummingbirds also exhibit a range of morphological and physiological specializations that are well suited for sustaining high power output during hovering (Altshuler & Dudley, 2002). For example, they have pectoralis and supracoracoideus muscles with relatively small-diameter fibers, high mitochondrial density, and high capillary density (Suarez *et al.*, 1991; Mathieu-Costello *et al.*, 1992). These attributes allow their muscles to sustain the highest mass-specific metabolic rates known for vertebrate skeletal muscle (Suarez *et al.*, 1991). Their primary flight muscles make up a relatively large proportion of their body mass (ca. 25%; Greenewalt, 1962; Wells, 1993). Their wing dimensions also exhibit positive allometry, meaning that wing length and area increase at a greater rate with increasing body mass than one would expect based on an assumption of geometric similarity and observed trends in other clades of birds (Greenewalt, 1962).

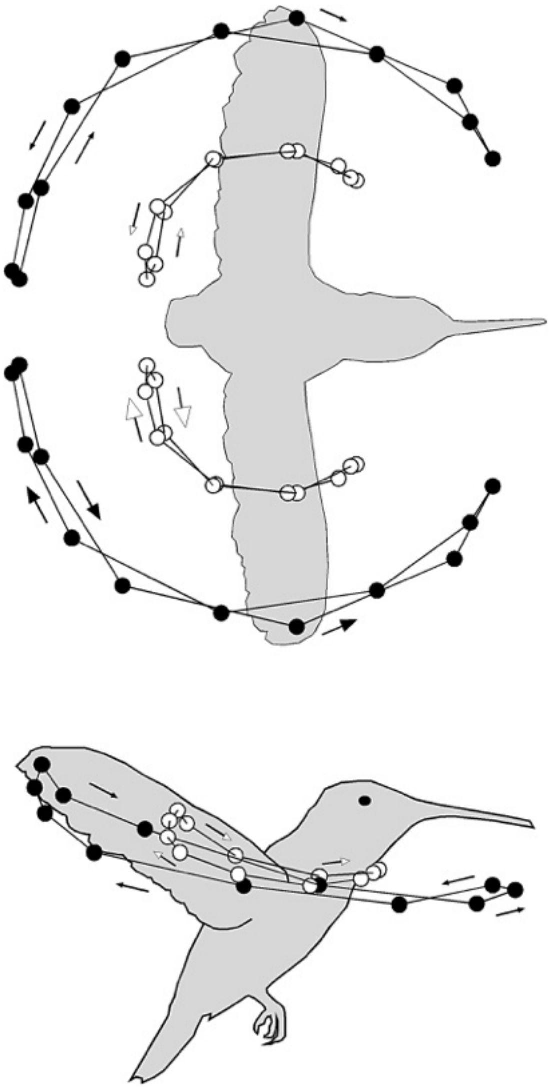

Fig. 10.14 Wing motion during hovering in a hovering rufous hummingbird (*Selasphorus rufus*). Black circles indicate position of wingtips, and white circles indicate position of wrists. Circles and arrows indicate sequential position and local direction of movement. (From Tobalske *et al.*, 2007.)

The first descriptions of the wing motions of hummingbirds illustrated a wingbeat dramatically different from all other birds (Stolpe & Zimmer, 1939; Greenewalt, 1962; Figure 10.14), which quickly set them apart, likened them to insects (Weis-Fogh, 1972; Wells, 1993), and eventually led to two aerodynamic classifications of avian hovering: symmetrical, and asymmetrical (Norberg, 1990). Aerodynamic symmetry of the two half strokes was thought to be a prerequisite for sustained, aerobic hovering, and the general similarities between hummingbird and hovering insect kinematics suggested a remarkable convergence in form and function in these long divergent (500 + Myr) taxa (Weis-Fogh, 1972). Attractive though this suggestion was, direct measurements

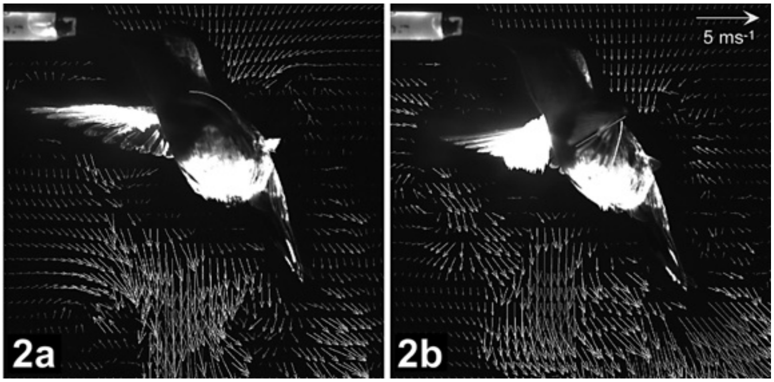

Fig. 10.15 Hummingbird wing presentation and flow field in the wake at mid-downstroke (a) and mid-upstroke (b). (a) A red line is drawn above the dorsal surface of the wing to highlight the camber of the wing. (b) During upstroke, the proximal part of the wing (red line) is not as supinated as the distal portion (yellow line). The vector scale is at top right. (From Warrick *et al.*, 2005.) [This figure appears in color as Plate 10.15.]

of airflow in the wake of hummingbirds show that the majority of weight support (75%) is provided by downstroke (Warrick *et al.*, 2005), and subtle asymmetries between downstroke and upstroke in wing velocity, area, camber, and long-axis twist (Figure 10.15) result in a two- to three-fold disparity in the lift production. Previously, it was unclear why the supracoracoideus to pectoralis mass ratio is approximately 0.5 (Wells, 1993), but relatively lower force production during upstroke helps account for this.

Although it does not produce an equal amount of force as downstroke, it is, nevertheless, upstroke that appears to be unique in hummingbirds. During upstroke, they leave their wings extended and markedly supinated. Their wingtips trace a path through the air that resembles a "figure-8" in lateral view (Figure 10.14). A dorsal view reveals that the tips and wrists trace approximately the same path during both halves of the wingbeat. In contrast, other species flex their wings to some extent during upstrokes of slow flight and hovering. Birds with rounded wings tend to adduct their entire wing during upstroke, while birds with pointed wings tend to adduct only their wrists and supinate their hand wing (Figure 10.16). There are exceptions to this general pattern. For example, Galliform birds, with rounded wings, supinate their handwing during upstroke of take-off flight (Tobalske & Dial, 2000). There is some argument that a supinated, extended handwing can produce useful lift, drag, or inertial forces, potentially representing a precursor to the hummingbird-style wingbeat, but such functions have not yet been clearly revealed (Tobalske, 2000, 2007; Tobalske & Biewener, 2008). The ability to supinate the handwing has been attributed to wrist anatomy in the mallard duck (*Anas platyrhynchos*; Vasquez, 1992); intriguingly, Vasquez (1992) observed that the relevant hummingbird wrist anatomy was different from that of the duck.

The ability to hover permits hummingbirds to exploit nectar, a concentrated source of glucose, as a food source, and recent study demonstrates that glucose oxidation in hummingbirds requires less oxygen compared with fatty-acid oxidation (Welch *et al.*, 2007). Other small nectivorous species routinely hover for brief intervals (≤ 15 s). These include two passerine groups: sunbirds (Nectariniidae; Hambly *et al.*, 2004; Köhler *et al.*, 2006) and honeyeaters Meliphagidae (Collins & Clow, 1978). Unfortunately, quantitative descriptions are lacking for wing kinematics and other details of flight styles in sunbirds and honeyeaters; such data would likely improve understanding about the relative specialization of hummingbirds and the processes that led to the independent evolution of hovering ability in what are hypothesized to be relatively distantly related clades (Sibley & Ahlquist, 1990; Livezey & Zusi, 2007).

Metabolic data for hovering sunbirds and honeyeaters reveal that hovering is more costly in terms of energy than slow or fast forward flight

Fig. 10.16 Wing-tip reversal (supination) during upstroke of slow flight in a rock dove (*Columba livia*).

(Hambly *et al.*, 2004). In contrast, data from hummingbirds suggests that there is no significant increase in metabolic power between hovering and forward flight up to speeds of $7\,\mathrm{m\,s^{-1}}$ (Berger, 1985; Ellington, 1991). This suggests that hummingbirds are uniquely efficient at hovering such that costs vary according to a "J-shaped" curve with flight speed rather than a "U-shaped" curve that may be observed when other species are flown over a wide range of speeds (Bundle *et al.*, 2007). One proposed mechanism that could account for higher efficiency in hummingbirds is elastic energy storage in the flight muscles during deceleration of the wing at the end of each half stroke (Wells, 1993)

Given their unique wingbeat patterns (Figure 10.15) and high mass-specific metabolism, what ultimately limits hovering performance in hummingbirds? This question has been explored in laboratory experiments in which air density and the partial pressure of oxygen are varied within a sealed chamber (Chai & Dudley, 1995, 1996; Altshuler *et al.* 2001; Altshuler & Dudley 2003), and also with measurements of hovering performance in the field along elevational gradients in mountains (Altshuler *et al.*, 2001, 2004; Atshuler & Dudley, 2003). These studies indicate that variation in air density is a more significant constraint than oxygen availability even though low partial pressures of oxygen can make it impossible for hummingbirds to sustain hovering (Altshuler *et al.*, 2001). As air density decreases, hummingbirds compensate by increasing wingbeat ampltitude but not wingbeat frequency, and when wingbeat amplitude reaches 180° they can no longer hover (Chai & Dudley, 1995). Populations living at higher altitudes compensate for low density by having relatively longer wings (Altshuler *et al.*, 2004). Increasing oxygen availability does not improve performance at low air densities (Altshuler *et al.*, 2001).

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