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A bird? A plane? No, it's a bat: an introduction to the biomechanics of bat flight

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9.1 Introduction

Bats are unique among mammals for their ability to fly. A substantial body of research has focused on understanding how they do so, and in 1990, Norberg's landmark volume provided an up-to-date understanding of diverse aspects of bat flight (Norberg, 1990). Building on work accomplished before 1990, our understanding of bat flight has changed significantly in the last two decades, and warrants an updated review. For example, many hypotheses about how bats fly were based either on aircraft aerodynamics or on studies of birds. In some respects, these predictions did fit bats well. However, recent advances in the study of bat flight have also revealed important differences between winged mammals and other fliers. Although we have, of course, always known that a bat is neither a bird nor a plane, the significance of the differences among bats and all other flyers are only now becoming clear.

In this chapter, we provide an overview of the morphology of bats from the perspective of their unique capacity for powered flight. Throughout the chapter, we provide references to classic literature concerning animal flight and the bat flight apparatus, and direct readers to sources of additional information where possible. We focus on relatively newer work that over the last 20 years has begun to change the ways in which we understand how bats carry out their remarkable flight behavior, and that has altered the way we understand the structural underpinnings of bat flight.

This chapter is organized to provide a review of several topics relevant to bat flight, and we hope that readers will understand each section better for having read them all. First, we explain the basic principles of aerodynamics necessary to understand bat flight. These include Reynolds number, lift and drag forces,

Evolutionary History of Bats: Fossils, Molecules and Morphology, ed. G. F. Gunnell and N. B. Simmons. Published by Cambridge University Press.

unsteady effects and Strouhal number. Next, we review the morphological characters of bats relevant to flight, which include the compliant skin and bones of the wings, the overall geometry of the wings and their bones, the distribution of sensory hairs across the wings and the physiology of the musculature that drives the wings. Finally, we review whole-bat flight performance, from forward flight to hovering flight, maneuvering and landing. We believe that it is only through study of all these disparate topics – fluid mechanics, anatomy and behavior – that one can have a truly integrative understanding of bat flight.

9.2 Aerodynamic principles of flight

The aerodynamics of flapping flight is a complex subject, and we will not attempt to convey a detailed summary of the aerodynamic underpinnings of the flapping flight of bats here. For more detailed discussions, we refer the reader to excellent sources on general aerodynamics (e.g., Anderson, 2005) or animal flight (Norberg, 1990; Azuma, 2006). Our much more limited objective is to introduce the reader to fundamental concepts in aerodynamics that are necessary to appreciate the flight performance of bats.

To understand how an animal flies, one must first identify the requirements of flight. In simple terms, a bat must move the air with its wings in such a way as to produce aerodynamic force. The component of the aerodynamic force that moves the bat forward is thrust, and the component that keeps the bat from falling and moves it vertically is lift. These are opposed by drag and gravity, respectively. In comparison with bats, airplanes are simple: engines provide constant thrust, and the resulting movement of air over fixed wings also constantly produces lift. Bat flight aerodynamics are more complicated because neither thrust nor lift are constant; both are produced in a cyclic manner because the wings are flapping.

One fundamental concept necessary to understanding flapping flight is the Reynolds number, a non-dimensional number that characterizes the relative magnitude of inertial and viscous forces, and hence the overall character of a fluid flow around or within a solid object (see also Purcell, 1977; Vogel, 1981 for more on the Reynolds number in biological systems). The Reynolds number, *Re*, is defined as:

$$Re = \frac{\rho U c}{\mu} \tag{9.1}$$

where U is flight speed, c is a typical length scale, usually the average wing chord, ρ is the fluid density, approximately 1.21 kg m^{-3} for air at standard atmospheric conditions and μ is the fluid viscosity, approximately 1.7×10^{-5} kg m^{-1} s^{-1} for air at room temperature. The way a fluid moves over a wing is entirely dependent on Reynolds number, so it is impossible to understand how bats fly without considering it.

At low Reynolds numbers, such as those relevant for insect flight, for example ($Re < 1000$), viscous forces dominate, while at higher Reynolds numbers ($Re > 10^5$), as in the case of air moving across a fast-flying giant albatross, inertial forces dominate. Bats span a wide range of sizes and flight speeds, where Re ranges from approximately 10^3 to 10^5; this range does not overlap with that of human-engineered aircraft. Indeed, bat flight occurs in a very complex regime for aerodynamic analysis, where the onset of critical flow phenomena, such as laminar separation and the transition from laminar to turbulent flow, are extremely difficult to predict reliably (Shyy *et al.*, 1999; Torres and Müller, 2004; Song *et al.*, 2008). This, combined with the thin wing geometries typical of bats, indicates that conventional airplane aerodynamics are of limited help in interpreting bat flight aerodynamics.

When inertial forces are important, as they are at the Re of bat flight, thrust and lift arise from fluid momentum generated by motions of the wings. In flight, a bat can add downward and rearward momentum to the air, and that imparts a net force on the body that permits flight. In this case, the aerodynamic force is proportional to the flight speed, U, multiplied by the air momentum generated by the wing: ρUA, where ρ is air density and A is the wing area. We can then write the specific aerodynamic forces, lift, L, and drag, D, as:

$$L = C_L \frac{\rho U^2}{2} A \tag{9.2}$$

and

$$D = C_D \frac{\rho U^2}{2} A \tag{9.3}$$

where C_L and C_D are the coefficients of lift and drag, respectively. These coefficients are non-dimensional constants with values that typically range from 0.1 to 3.0; the exact value of these aerodynamic coefficients is determined by the shape and motion of the wing. For example, a highly streamlined wing would have a high lift coefficient and low drag coefficient; a wing that is less streamlined would have a lower lift coefficient and higher drag coefficient. One important complexity of bat flight is exemplified here; because the three-dimensional conformation of bat wings changes continuously as they flap, so the lift and drag coefficients of bat wings change continuously during the wingbeat cycle. This also, however, illustrates an avenue by which bats have the potential to actively control flight dynamics (see also below).

A *wing*, in aerodynamic terminology, is a three-dimensional lifting surface. The simplest analysis of the generation of lift comes from the examination of the local shape of an airfoil, the two-dimensional cross-sectional shape of a wing. Lift is generated when air moves over the top surface of the airfoil at higher speed than it moves over the bottom surface. The difference in airspeed between the top and bottom wing surfaces can be accomplished in several ways, such as a curvature in the airfoil surface, giving it *camber*, or an inclination of the foil relative to the oncoming air, producing a positive *angle of attack* (Figure 9.1). When we consider the shapes of bat wings in an aerodynamic context, then, any features that influence camber or angle of attack are important for performance, even without the additional effects of flapping. Examples of such features might include the length of the fifth digit and the position of the metacarpophalangeal and interphalangeal joints of this digit, the ability of the muscles of the wing to control angle of attack, or the stiffness of the wing membrane skin and its resultant state of billowing, and hence camber, when it experiences pressure differences between the wing's top and bottom surfaces.

Bats in flight, of course, do not employ fixed, static wings, but instead flap them in characteristic and complex ways. When we consider lift in relation to local flow at the wing surface, it is immediately clear that lift changes dynamically over the course of every wingbeat cycle. In general, during the downstroke, the wing has a positive angle of attack and hence generates positive lift, but during the upstroke, the effective angle of attack is lower, and may even be negative (see also below, Flight performance). This overall pattern can be modulated in a number of ways, such as by pronating and supinating the wing. Furthermore, bats do not simply flap the wing up and down, but sweep the wings through some angle other than strictly vertical, with forward or cranial motion during the downstroke and backward or caudal motion during the upstroke (Figure 9.1). The degree to which these various motions occur appears to vary with speed, for specific flight behaviors and among species, and has yet to be well described. The result of the wing posture and motion during the flapping motions of bat flight is that bat flight is characterized by a *stroke plane angle* that is not vertical (Figure 9.1). This stroke plane angle has an important influence on the relative speed and angle of attack experienced by the flapping wing: as the stroke plane angle becomes more horizontal, the speed of the wind with respect to the wing surface increases during the downstroke and decreases during the upstroke. Moreover, a wing can undergo twisting about its long axis at the same time that it undergoes flapping, and the magnitude of the twist may change along the span of the wing, and with the timing of the wingbeat cycle. This additional complexity is yet another way that the angle of attack of the wing may come to vary locally depending on the precise location within the wing, and dynamically, depending on the timing within the wingbeat cycle.

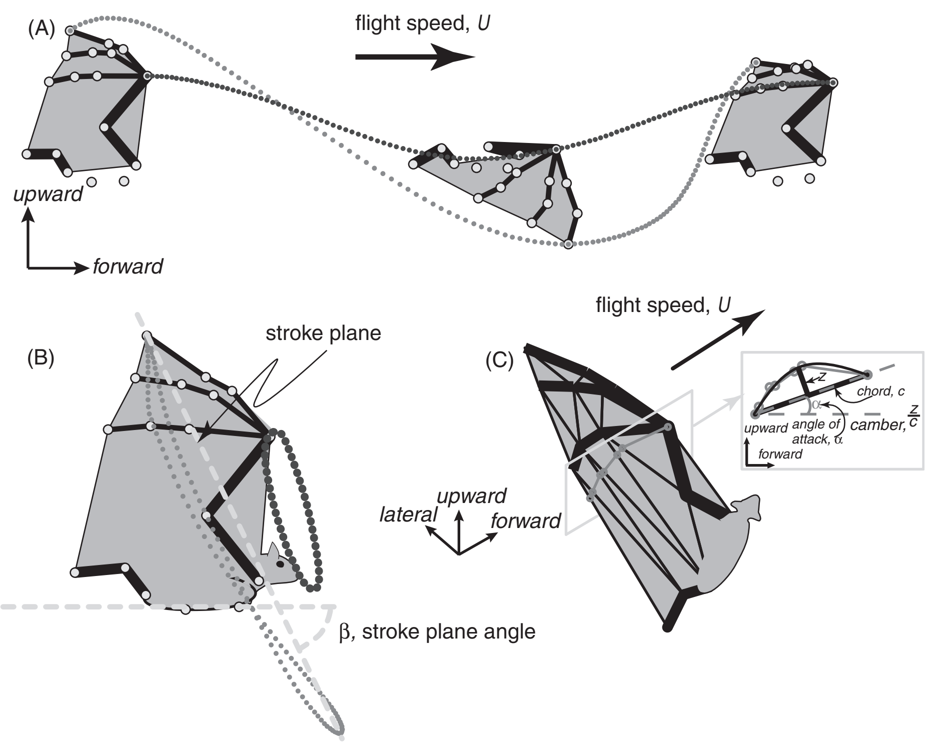

Figure 9.1 Schematic of bat in flight illustrating aerodynamic terms and concepts. (A) Lateral view of a bat wing moving through a wingbeat cycle, tracing out the motion of wingtip and carpus in frame of reference of external world. (B) In the frame of reference of the bat's body, motion of landmarks on the bat's wing can be seen as cyclical, tracing out a trajectory similar to a flattened, tilted ellipse. The movement of the wingtip defines, from its uppermost to lowermost positions, a stroke plane, which can be defined by β, the stroke plane angle, the angle between the line connecting these two points and the horizontal plane. (C) To define angle of attack, α, and camber, consider a parasagittal section though the wing, as outlined, and then shown on the right of schematic. The wing chord is the line connecting the frontmost, or leading, edge and rearmost, or trailing, edges of the wing in parasagittal section of interest. In flight, bat wings are typically curved in an upwardly convex fashion; the circles indicate the locations where an imaginary parasagittal cutting plane intersects the wing skin, and the lines connect those points, estimating the length of the wing in the cutting plane. Camber is then computed as the maximum height of the wing in the plane divided by the wing chord. See also color plate section.

9.2.1 Wake flows and trailing vortices

Although it is the wing motion that is directly responsible for the generation of lift and thrust, we can gain considerable insight into the mechanisms of aerodynamic force production by looking at fluid motion in the wake

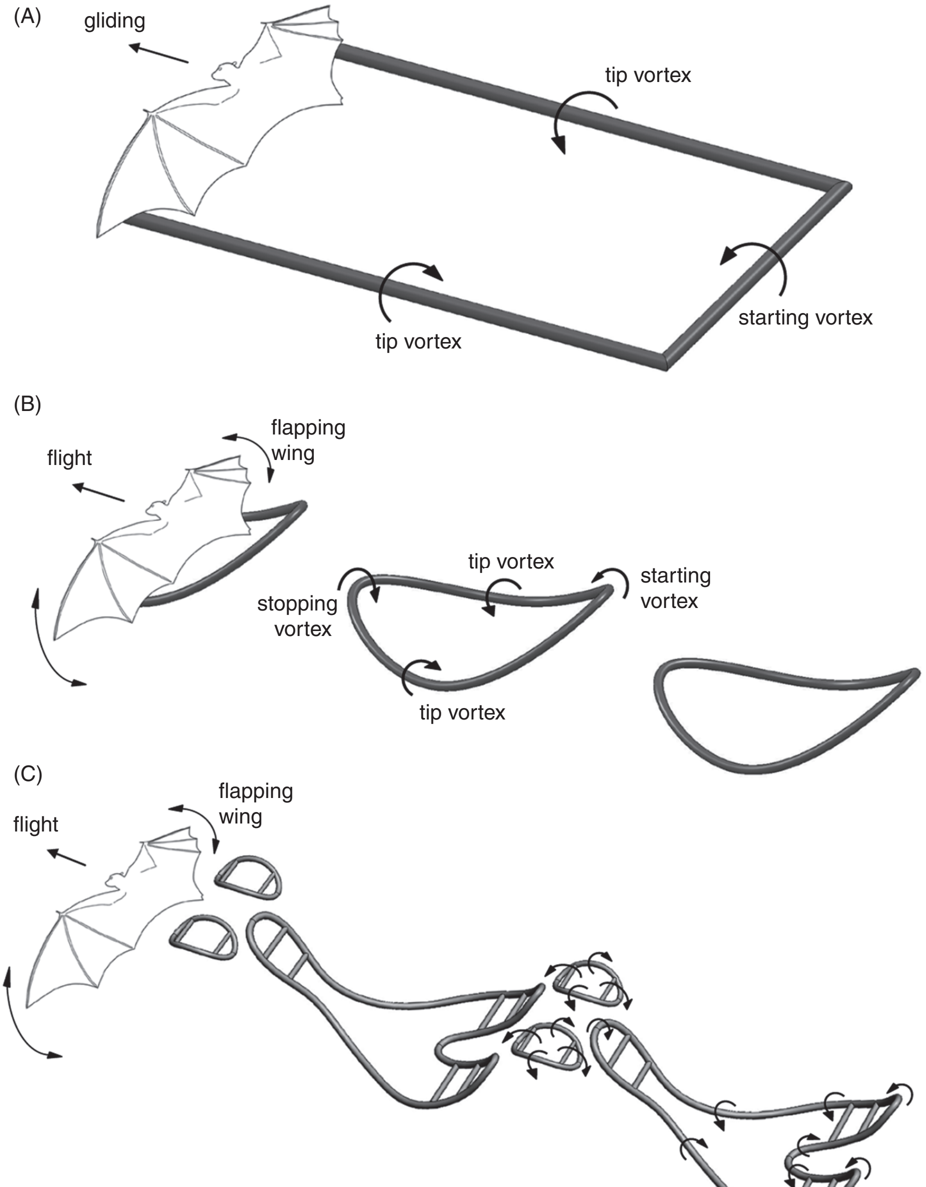

Figure 9.2 Schematic illustration of structure of vortex wakes for different kinds of flight. (A) Gliding or flight in fixed-wing aircraft produces relatively simple wakes that possess a starting vortex and a pair of nearly linear, parallel tip vortices where vorticity is shed from the wingtips as lift is produced by forward movement of the wing through the air. (B) In flapping flight, the path of the wingtip is much more complex spatially, such that even where the magnitude of vorticity is constant, the spatial

behind a flying animal. Most readers have some everyday experience that provides a useful heuristic for this concept; a fixed-wing airplane in flight leaves behind it two vapor trails, created by two *tip vortices*, one trailing the tip of each wing, that arise directly from the aerodynamic forces produced as the plane moves through the atmosphere. Newtonian mechanics assures us that for any force there is an equal and opposite reaction force, and the force generated on each wing is mirrored by its reaction force, experienced by the fluid surrounding the wing. The wake left behind the wing thus contains a complete "footprint" of its force production. Bats also leave an aerodynamic wake, albeit a wake that is much smaller and less intense than that of a jet aircraft, but, one which can persist for several meters, making it amenable to measurement using modern fluid mechanics diagnostic tools such as particle image velocimetry, or PIV.

An aerodynamic wake flow can be analyzed in terms of its *vortex structure* and its associated *circulation*. Vorticity is the local angular or rotational velocity of the fluid, and a vortex is somewhat subjectively defined as a concentration of vorticity. Tornados and the swirling motions of water draining from the bathtub are familiar everyday examples of vortices. These so-called "trailing vortices" are generated by every flying object, from large airplanes to birds and bats, although they have a very different character in small flyers, such as insects, due to the very low Reynolds numbers that characterize their flight. These vortices exist due to the fact that, to generate an upward force, lift, the animal uses its wings to direct air downwards, creating what is known as the "downwash." The downwash, in turn, interacts with the surrounding air to produce the trailing vortex wake (Figure 9.2). At high

Caption for Figure 9.2 (*cont.*) motion of the wingtip would lead to a more complex wake shape. However, lift changes continuously through the wingbeat cycle, hence the intensity of the wingtip vortex changes in parallel with its repositioning in space. One possible wake configuration for flapping flyers is a set of discrete vortex rings; this pattern would result if there is a period in each wingbeat cycle in which no lift is generated and vorticity falls to zero, producing a stopping vortex, leading to the closing of the trailing vortex into a ring. In this case, each wingbeat produces a ring with its own starting, wingtip and stopping vortices. This somewhat abstracted wake pattern has served as a starting point for discussions of the possibility of distinct gaits in animal flight, analogous to walking and running gaits in terrestrial locomotion. (C) Experimental techniques for wake visualization, such as particle image velocimetry, can be employed to describe natural wakes of flying bats and birds in detail to test hypotheses generated by theory, such as illustrated in (B). Here, a wake is generated by *Cynopterus brachyotis*, the lesser dog-faced fruit bat, flying at moderate speed, as documented by PIV (Hubel *et al.*, 2010). The realistic wake structure is far more complex than both the gliding and flapping models, showing many additional components in wake for each wingbeat than would have been predicted from theory alone.

Reynolds numbers, the dissipation of motion due to the viscosity of the air is weak, and these vortex structures can persist for a long time after the animal has flown by leaving a "footprint" in the air. The intensity and structure of these vortices directly reflects the way in which aerodynamic forces, including lift and thrust, were generated.

The total vortex strength, or circulation, Γ, of a vortex is directly related to the magnitude of the lift force of the vortex by the Kutta–Joukowski theorem as follows:

$$L = \rho U \Gamma w \tag{9.4}$$

where L is lift, ρ is air density, U is the speed of the object relative to the surrounding fluid and w is the wingspan. Quantitative analysis of wake vortices can thus give very specific information about aerodynamic force production.

There is more to a vortex than lift magnitude, however. The geometry of vortices contains important information about aerodynamic conditions. At high Reynolds numbers, Kelvin's circulation theorem requires that a vortex must have constant strength, and can neither start nor end in the flow, and hence vortex lines must either extend forever or form closed rings (Kundu and Cohen, 2008). This fundamental constraint has far-reaching consequences for the geometry of the vortex wake. For steady gliding flight, it requires that the two trailing tip vortices must have a constant and fixed magnitude. Furthermore, if the lift force increases and decreases as the wings flap down and up, the strength of the primary wake vortex must change accordingly. The technical constraints of Kelvin's theorem require that this waxing and waning of the vortex can only be accomplished by the introduction of "starting" and "stopping" vortices (Figure 9.2). In this way, the straight-line vortex pair that is characteristic of steady flight (e.g., gliding flight, or an airplane) can become a series of discrete vortex rings, characteristic of discrete wing flaps (Figure 9.2). More complex flapping kinematics, such as are common in bat flight, generate even more complex wake structures, and are the subject of active research at present (e.g., Hedenström *et al.*, 2007; Muijres *et al.*, 2008; Hubel *et al.*, 2009, 2010).

A comment on efficiency is in order at this point. Since only the vorticity that lies in the direction of flight, the streamwise vorticity, is associated with the lift force, any non-streamwise component of vorticity, such as the starting and stopping vortices, represents fluid motion generated by the animal that is not used for weight support and is, in some sense, wasted energy. These non-streamwise vortex components are, however, unavoidable consequences of flapping flight, and therefore, from the standpoint of energy efficiency, are inherent disadvantages to any flapping mechanism of lift generation, particularly for long-range flight, such as migration. However, energy is not the only relevant currency for an organism, and flapping clearly confers other advantages, most notably the abilities to maneuver with ease and to fly in complex environments, where rapid changes in aerodynamic forces are advantageous. Besides, until flying animals evolve propellers or jets, there is no way to produce thrust in the air without flapping.

9.2.2 Drag and thrust

It is almost impossible to measure drag empirically on flying animals. Estimates of drag from live animals are also notoriously inaccurate. This is because we can only directly measure the net horizontal acceleration of an animal, which is the sum of thrust, the force that accelerates the animal forward, and drag, the force that decelerates the animal, and not their independent contributions. Moreover, attempts to use wind-tunnel tests to assess drag using dead specimens or models that recreate geometries of flying animals cannot reproduce the subtleties of a living, flapping animal, and are so destined to overpredict drag forces.

Although it might seem convenient to think of drag as a single entity, drag arises from several distinct sources, and their relative importance varies, depending on the physical situation. The four primary types of drag that influence flight are: (1) *skin friction drag*, drag associated with the viscosity of fluid flowing over a body; (2) drag due to lift, the so-called *induced drag*; (3) *form drag*, drag due to large-scale separation of flow from the object experiencing aerodynamic forces; and (4) *parasitic drag*, a catch-all phrase associated with minor flow separation over non-streamlined appendages such as legs, ears etc. Skin friction is an unavoidable consequence of the viscosity of air, and even for a perfectly streamlined object, represents about 40% of total drag. Drag due to lift, "induced" drag, is also unavoidable, and is due to the fact that any three-dimensional object that generates lift must also generate drag along with the vortex wakes created with the production of lift, as discussed above (Anderson, 2005). The downwash generated by the wake vortices "tilts" the lift force, slightly reducing the lift and thereby adding a small contribution to drag. Form drag is due to large-scale separation of the flow and the generation of large vortices. For well-streamlined bodies, including most bats in flight, this is usually minimal during the downstroke, but may be important during the upstroke. For species that fly for extended periods of time, it is likely that selection has led to streamlined body and wing anatomy and efficient flapping motions for steady forward flight, and that energy losses associated with form drag are relatively small; this is much less true for maneuvering flight and flight in other extreme conditions such as hovering or very fast flight.

9.2.3 Unsteady flow effects

The trailing vortex wake is not the only aerodynamic effect that we need to consider for the quantitative analysis of bat flight. Other kinds of fluid motions, grouped under the designation of unsteady effects, can occur for a wide variety of reasons, complicating the study of animal flight (for an excellent discussion of this subject geared for biologists, see Dickinson, 1996). Examples of unsteady effects include *stall* or *separation* – flight conditions in which large vortices can be shed from the wings and body, resulting in unstable changes in aerodynamic forces. Even when the wings are stationary, complex fluid motions can cause unsteady effects in some situations. The Reynolds number range typical of bat flight coincides with a critical aerodynamic transition between smooth and predictable *laminar* flow and chaotic *turbulent* flow, and unsteady effects often occur at those transitions. Most important, however, are the unsteady fluid effects induced by the flapping of the wings, which are necessary for sustained powered flight. The flapping motion generates time-dependent variations in the aerodynamic forces, which typically increase in strength during the downstroke, which is responsible for the bulk of the lift and thrust force generation, and decrease in strength during the upstroke, which, for bats appears to be a relatively passive recovery stroke. These effects are complex in nature, and are an area of intense research at the present. Unsteady effects have been the subject of considerable attention in the insect flight community since the 1970s. This body of work has demonstrated that unsteady phenomena such as delayed or dynamic stall, the Wagner effect and wake capture play a crucial role in aerodynamics in insects (Ellington, 1975; Maxworthy, 1979; Dickinson, 1994; Van den Berg and Ellington, 1997; Sane, 2003). Any complete model of bat flight aerodynamics will require consideration of unsteady effects, in addition to wake analyses.

One way to assess unsteady effects in a fluid is by the *Strouhal* number, *St*, a non-dimensional number that describes the importance of unsteady effects in relation to steady, inertial forces. The Strouhal number is defined as:

$$St = \frac{fA}{U} \tag{9.5}$$

where f is flapping frequency, A is flapping amplitude and U is flight speed. St values close to zero suggest that the flow is quasi-steady, and that steady aerodynamic theories should be largely applicable. A high value signifies the dominance of unsteady effects, while a value in the range of 0.2–0.3 means that both steady and unsteady effects are important. Bat flight is typically in the range of *St* of 0.2 to 0.6 (Taylor *et al.*, 2003; Riskin *et al.*, 2010) implying that unsteady effects play an important role. However, both the importance and the specific nature of unsteady effects in bat flight are yet to be fully understood.

9.3 Morphology

The structure of the limbs of bats is their most obvious specialization, and generations of bat researchers have uncovered characteristics of wing structure that influence flight performance (e.g., Humphry, 1869; Macalister, 1872; Vaughan, 1959; Norberg, 1972; Hermanson and Altenbach, 1985; Meyers and Hermanson, 1994; Sears, 2006). We focus here on those aspects of wing morphology most directly relevant to flight mechanics and aerodynamics, with most attention to work carried out in the last ten years. An excellent review of older literature can be found in Norberg (1990).

9.3.1 Compliant wings

One critical difference between bats and human-engineered aircraft, and, indeed, to a lesser extent, between bats and the other flying animals, is the degree to which the wing surface is deformable. Virtually all human-made aircraft have possessed rigid wings, with the few exceptions of the slightly deforming wings of gliders and a small number of highly experimental micro air vehicles (Shyy *et al.*, 1999; Lian *et al.*, 2003a, 2003b; Ansari *et al.*, 2006). For birds, the combination of robust skeletal structure and relatively stiff feather shafts confers substantial rigidity on all but the tips of bird wings, such that there is little movement within the wing itself during flight, other than bending at synovial joints (Hedrick *et al.*, 2004; Usherwood *et al.*, 2005; Tobalske *et al.*, 2007). Although insect wings can change shape during flight to some degree, their deformation is limited, and insect wings lack any joints distal to the body hinge (Combes and Daniel, 2001, 2003; Daniel and Combes, 2002; Bergou *et al.*, 2007). Bat wings, in contrast, possess very little innate stiffness. The wing consists of a compliant membrane of skin stretched across jointed bones that are themselves poorly mineralized and thus flexible. Bat wings likely function at variable, but generally quite low levels of stiffness throughout the wingbeat cycle during typical forward flight (Figure 9.3). It is possible that the skin is rarely stretched tightly, even over a wide range of diverse flight behaviors; future studies that focus specifically on the mechanics of the skin during flight will be needed before we will be able to fully address the range of stiffness bat wing skin experiences during normal functions.

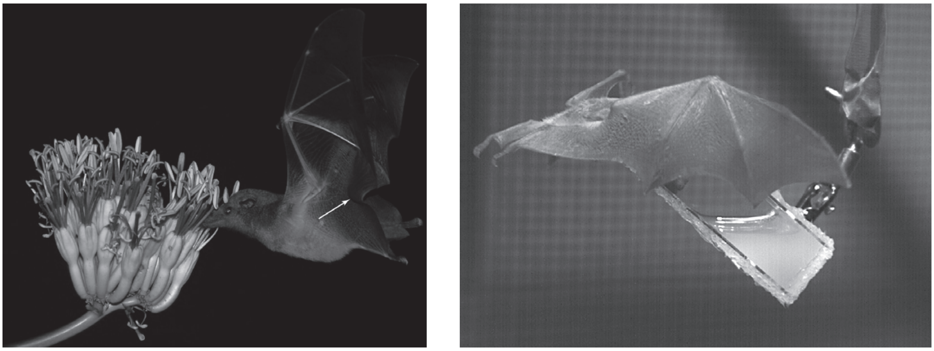

Figure 9.3 Left panel: *Choeronycteris mexicana*, the Mexican long-tongued bat, feeding at an agave flower, showing that even as the bat comes into the force-generating downstroke, the wing membrane is not taut, but experiences varying degrees of looseness depending on anatomical location. In this particular wingbeat, the plagiopatagium, the portion of the wing between the body and the hand skeleton, is so loose that a relatively large fold or flap is visible between the ankle and the tip of the fifth digit (white arrow). Photograph by Joseph Coelho, used with permission. See also color plate section. Right panel, *Glossophaga soricina*, Pallas's long-tongued bat, flying up to a nectar feeder in the lab, showing relatively relaxed, wrinkled skin in the arm- and handwing even during the middle of the downstroke, the portion of the wingbeat cycle in which aerodynamic forces are greatest. Photograph by Caroline Harper, used with permission.

9.3.2 Skin contribution

The greatest part of the surface area of the bat wing comprises skin. The skin is supported, tensioned and moved through space in a highly controlled fashion by the bones of the body, forelimb and hindlimb, and by the muscles associated with these bones. In addition, the armwing skin, or plagiopatagium, contains intrinsic musculature that takes both origin and insertion within the connective tissue of the membrane itself (Gupta, 1967; Quay, 1970; Holbrook and Odland, 1978). Wing membrane skin is similar to that of most other mammals, but both the epidermis and dermis are exceptionally thin, and the dermis greatly enriched in highly organized elastic fibers (Quay, 1970).

There are numerous characteristics of wing membrane skin that appear to relate directly to the modification of the wing as a flight organ. The reduction of skin thickness is substantial enough that it is likely to contribute not only to determining mechanical characteristics of the skin, but to also provide some significant weight savings, particularly in the distalmost portion of the wing (Swartz, 1997). Nerve endings in the wing membrane skin are especially abundant and diverse (Quay, 1970), and the specialized sensory hairs project a fraction of a millimeter from the wing surfaces to provide the central nervous system with, it is hypothesized, a detailed map of the state of flow over the wing (Zook, 2007; Sterbing-D'Angelo *et al.*, 2011). Wings carry out their aeromechanical roles at the same time as they play a central role in heat and water control (Basset and Studier, 1988; Thomson and Speakman, 1999). The reduction of skin thickness thus not only reduces the mass and thereby the energy required to accelerate and decelerate the wing during flapping, but also serves to greatly reduce surface-capillary diffusion distance, allowing for significant rates of skin gas exchange via the wing membrane. In this way, the wing may actually make a significant contribution to the oxygen budget of bats, with oxygen consumption and carbon dioxide production as much as 6–10% of whole-body values for resting, lightly anesthetized *Epomophorus wahlbergi* (Makanya and Mortola, 2007).

The mechanical properties of wing membrane skin are a major determinant of the behavior of bat wings as compliant airfoils (Swartz *et al.*, 1996). In particular, wing membrane skin of all species tested to date show particularly low stiffness in the spanwise direction, the direction from the body to the wingtip, in both the plagiopatagium, and the dactylopatagium (Figure 9.4). In contrast, the skin is up to two orders of magnitude stiffer when stretched in the chordwise direction. The stress–strain relationship for wing membrane skin is highly non-linear, but in general, this trend holds true at all parts of the stress–strain curve – at low, intermediate and high strains.

One critical way in which the compliance of the bat wing membrane is functionally significant in comparison with rigid fixed wings is that compliant wings self-camber in the presence of a pressure difference between the upper and lower surface of the wing. This self-cambering produces a faster increase in lift with increasing angle of attack, along with increased resistance to stall and loss of lift at high angles (Song *et al.*, 2008). These benefits likely offer bats and mammalian gliders an advantage in both lift generation and flight stability during rapid maneuvering, in comparison to the more rigid wings of birds or insects.

9.3.3 Bone contribution

The wing skeleton also contributes to the compliance of the bat wing, especially by the flexion, extension, abduction and adduction of the joints of the handwing. The primary mechanical function of bones in all vertebrates is to provide stiffness, however a few animals, bats among them, use bones of relatively low stiffness to perform locomotion via controlled deformation. In these cases, the low stiffness of the bone can arise by virtue of low mineralization, unusual geometry – such as extremely slender, elongated shapes – or both.

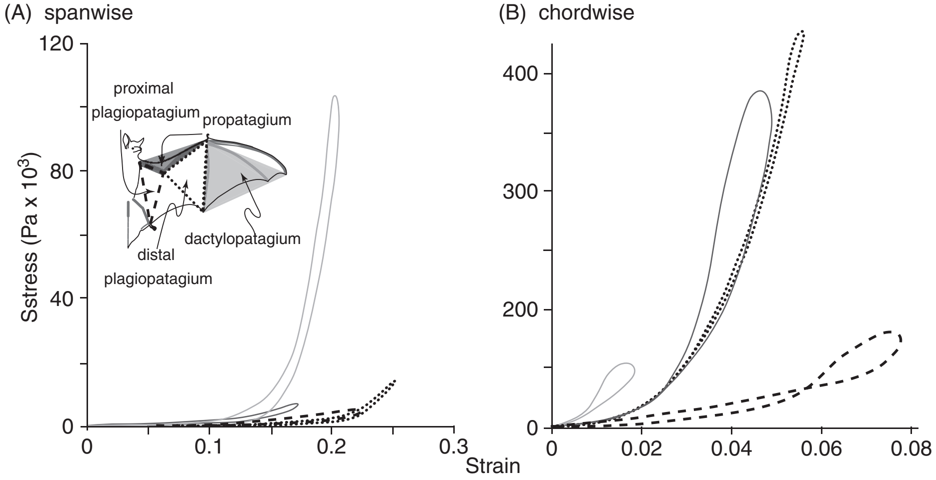

Figure 9.4 Mechanical characteristics of wing membrane skin of *Pteropus poliocephalus*, the gray-headed flying fox. The stiffness, given by the slope of the stress–strain trace, differs among regions of the wing membrane, and for each wing region differs greatly depending on whether the skin is tested from proximal to distal or spanwise (A) vs. from leading to trailing edge or chordwise (B). Adapted from Dumont and Swartz (2009). See also color plate section.

The avian furcula is one such example; the "wishbone" spreads laterally and then recoils with each wingbeat (Jenkins *et al.*, 1988). The hand skeleton of bats appears to be another example, in which relatively poorly mineralized bones that are also greatly elongated can undergo considerable deformations (Swartz *et al.*, 2005).

Typically, the mechanical properties of the compact bone tissue of mammalian long bones vary little among species (Currey, 1984, 2002). The bones of the bat wing, however, seem to represent a major exception to this pattern. Although the bat humerus is similar in mechanical properties to other mammals, the radius, metacarpals, proximal phalanges and distal phalanges each show progressively lower mineralization and hence stiffness (Papadimitriou *et al.*, 1996; Swartz *et al.*, 1998; Swartz and Middleton, 2008) (Figure 9.5). In combination with the structural geometry of the bones of the handwing (see below, wing bone cross-sectional geometry), the distal wing bones are therefore highly deformable, and preliminary evidence suggests that metacarpals and phalanges undergo significant bending during flight, even when animals do not attain high speeds or exhibit extreme maneuvers (Swartz *et al.*, 2005; Swartz and Middleton, 2008).

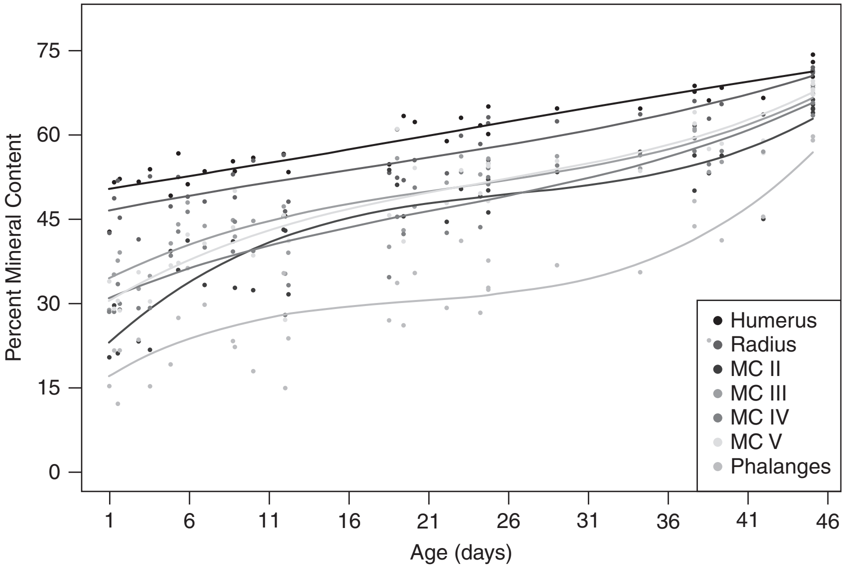

Figure 9.5 Ontogenetic pathway to adult variation in wing bone mineralization in *Tadarida brasiliensis*, the Brazilian free-tailed bat. Unlike typical mammalian limb skeletons, bat wing skeletons show great variation among bones in mineralization levels, with much greater mineralization in the proximal skeletal elements than the distal elements at all ages, from birth to skeletal maturity at 46 days. Within each bone, there is a steady increase in mineralization during lactation and eventual weaning. Adapted from Papadimitriou *et al.* (1996), Swartz and Middleton (2008). See also color plate section.

Although we do not yet have full understanding of the role of flexible bones on the mechanics and energetics of bat flight, evidence obtained to date suggests several intriguing possibilities. The flexibility of the distal wing bones arises through reduction in bone mineral, and as a consequence, the density and mass of these bones is reduced relative to their primitive condition. Because the metabolic cost of accelerating and decelerating limbs can be a significant portion of the total metabolic cost of locomotion, particularly for animals with large limbs, such as bats, the reduced mass of the distal wing skeleton that results from decreased mineralization significantly reduces wing mass and thus the energetic cost of locomotion, especially at high wingbeat frequencies. Flexible bones also may deform under aerodynamic loading, so it is possible that these bones can passively align with dynamically changing patterns of airflow, and the most distal portions of the wing, the region of the wing that moves most rapidly, could, by passive wing rotation, decambering and/or deformation, reconfigure in a manner that might decrease drag and local turbulence.

9.4 Wing geometry

9.4.1 Aspect ratio and wing loading

In aircraft aerodynamics, the wing loading and aspect ratio of a plane convey important information concerning an aircraft's energetics and ability to maneuver. To the extent that bats operate like fixed-wing aircraft, bats with higher aspect ratios, the mean ratio of wingspan to chord, should have decreased induced drag and therefore are predicted to enjoy a decreased energetic cost of flight (Norberg and Rayner, 1987; Norberg, 1990) – conversely, as aspect ratio increases, theory suggests that maneuverability of bats should decrease. As a result, the shapes of bat wings are often used to infer the relative importance of fast flight in open habitats (high aspect ratios) to maneuverability in cluttered habitats (low aspect ratios). Although some support for this relationship has been shown through field studies (Aldridge and Rautenbach, 1987), other studies have failed to demonstrate that relationship (Saunders and Barclay, 1992; Stockwell, 2001).

Wing loading, computed as body mass per unit of fully extended wing area, is also directly related to flight performance in aircraft in a manner that has invited comparison for winged animals. Animals with increased wing loading are expected to fly at higher speeds than animals with low wing loading, to generate enough lift to fly. Also, increased wing loading should increase the cost of flight and decrease maneuverability, so animals should have wing loadings as low as other biomechanical requirements of their lifestyles will allow. In general, wing loading scales positively with body size, so large animals have higher wing loading than small animals do (because weight increases faster than area as body size rises). Recent experiments with pteropodids demonstrate that the largest bats overcome their relatively higher wing loading by extending their wings more fully and using higher angles of attack during the downstroke than small bats do (Riskin *et al.*, 2010).

It is important to note, however, that many of the assumptions involved in the clear relationship of aspect ratio and wing loading on the one hand and aircraft flight performance on the other do not apply to flapping flight in bats. Not only do the large-scale changes in wing form produced by flapping dynamics fundamentally change the expectations of performance based on wing shape alone, bats fly at Reynolds numbers much lower than those of aircraft and therefore unsteady aerodynamic effects can be very important in their flight. As a consequence, simple extrapolation of aircraft performance expectations to bat wing shapes may not apply in a straightforward manner. We suggest that this is a subject that would benefit greatly from more attention as new studies seek to better understand how wing form and the details of flapping motion work synergistically to determine natural flight performance in bats.

9.4.2 Wing bone cross-sectional geometry

The cross-sectional geometry of a bone, like that of any other beam, plays a major role in determining the nature of its response to mechanical forces, along with its material stiffness or elastic modulus (Wainwright *et al.*, 1976; Currey, 1984). The shafts of typical limb long bones of mammals are elliptical in cross-sectional shape, varying from nearly circular to possessing a major axis roughly twice the minor axis, and the bone cortex is most often 25 to 75% of the bone diameter (Currey and Alexander, 1985). The wing bones of bats, however, differ from the customary mammalian pattern (Swartz *et al.*, 1992). The bones of the armwing are extremely thin-walled, with cortices less than 25% the magnitude of bone diameter, and with the outer diameter significantly expanded relative to those of non-volant mammals of comparable body size (Swartz *et al.*, 1992; Swartz and Middleton, 2008). In contrast, the metacarpals and phalanges are thick-walled or even completely solid (cortical thickness is 68–100% of bone diameter for phalanges). Although the metacarpals may be expanded in outer diameter relative to those of non-volant mammals, the phalanges, unlike the remainder of the wing bones, do not show this pattern (Swartz and Middleton, 2008).

These distinctive aspects of bone geometry suggest substantial functional differentiation in mechanics of the armwing and handwing. The geometry of the humerus and radius is most consistent with resisting loading in torsion, or bending loads applied from multiple different directions. Although there is little direct information concerning the loading of the bat wing during flight, the few hints available suggest that torsion and bending are indeed the predominant loading regimes in this part of the skeleton (Swartz *et al.*, 1992). In contrast, the low second moments of area, coupled with low stiffness, suggest that the bones of the handwing, unlike the long bones of terrestrial mammals, are specialized to maximize rather than minimize their deformation with respect to bending loads. As these elongated, slender bones interact with their fluid surroundings, their geometry will tend to promote deflection rather than resisting bending, perhaps contributing to an adaptive wing reconfiguration (see above).

9.4.3 Sensory hairs

One way in which the surface of the bat wing differs from the skin surface of other parts of the bat body and from the skin surface of the limbs of all other mammals is the presence of distinctive hairs that perform a somatosensory function. These hairs, quite different in size and morphology from pelage hairs, emerge from small dome-shaped structures on both the dorsal and ventral wing surfaces, singly, but also in pairs or in small clusters (Crowley and Hall, 1994; Zook, 2007; Sterbing-D'Angelo *et al.*, 2011) (Figure 9.6). The domes comprise a cluster of supporting cells around the hair follicle, including Merkel cells, cells often known as "touch cells" that are believed to act as intermediates between an initial stimulus and afferent neuron impulses. The sensory hairs are distributed in a highly patterned fashion, with high densities along the wing bones, the intrinsic wing muscles (mm. plagiopatagiales), and in the regions of the wing's leading and trailing edges. Electrophysiological recordings from the primary afferent nerves of the hair-dome apparatus in *Antrozous pallidus* and *Eptesicus fuscus* demonstrate high sensitivity to air-puff and direct touch stimuli, but little or no response to direct touching of the wing membrane between the domes or stretching of the membrane (Zook, 2005; Sterbing-D'Angelo *et al.*, 2011). These responses are completely surface specific; that is, ventral hairs show no response to stimuli on the dorsal wing surface, and vice versa, although wing membranes are extremely thin, usually between 0.03 and 0.08 mm (Studier, 1972; Swartz *et al.*, 1996).

This morphological and physiological information suggests that the function of the hair cell network is to provide bats with a detailed, real-time map of flow conditions on the wing during flight. Each hair is well suited to be able to monitor airflow in its immediate vicinity, albeit in a simple manner. A large number of simple measurements, however, obtained from relevant locations distributed throughout the wing's surface, may provide the central nervous system with the requisite raw data to produce an integrated map of airflow patterns over the wing as a whole, suggesting fine-scale adjustments to kinematics, wing membrane tension etc. must be made to deal with flow turbulence at particular anatomical locations on the wing (Dickinson, 2010).

9.4.4 Flight muscle

The distinctive anatomical specializations of the musculature of the wing for flight have been the subject of intense scientific interest since at least the middle of the nineteenth century (Humphry, 1869; Macalister, 1872; Miller, 1907; Vaughan, 1959, 1966; Norberg, 1970, 1972; Strickler, 1978; Altenbach, 1979). In addition to the unusual and, in some cases, unique gross morphology of bat musculature, the flight muscles of bats have notable physiological and/or biochemical characteristics (see Hermanson, 1998 for an excellent review).

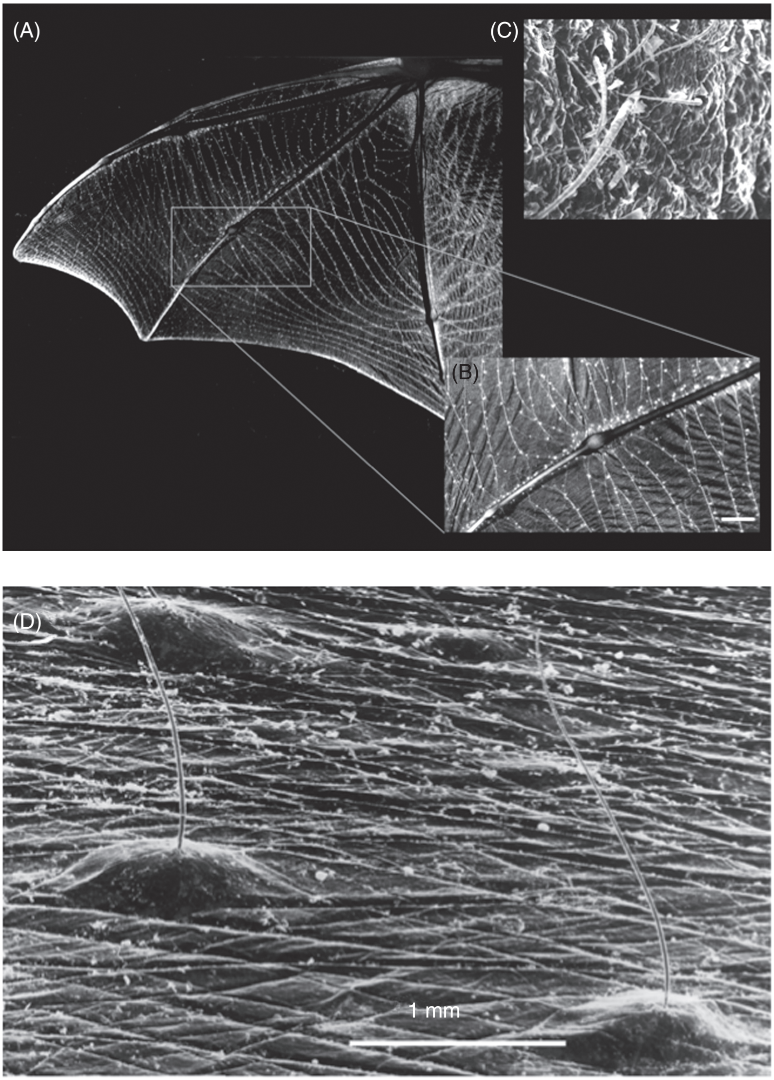

Figure 9.6 Sensory hair cells on the wing of *Antrozous pallidus*, the pallid bat (A)–(C) and *Pteropus poliocephalus* (D). (A)–(C) adapted from Zook (2007); (D) adapted from Crowley and Hall (1994). See also colour plates section.

Direct measurement of the patterns of muscle activation during normal flight in several bat species has shown complexities to these patterns that could not have been predicted from anatomical analysis alone. For example, Vaughan first hypothesized that the pectoralis, serratus ventralis and subscapularis muscles together drive the powered downstroke in bats, and although all subsequent studies have concurred, experimental measurement of muscle activity patterns have shown that electrical activity begins in the pectoralis not only before activity in the other muscles, but significantly before the onset of downstroke, leading the upstroke–downstroke transition by approximately 20 ms in *Antrozous pallidus* and *Artibeus jamaicensis* (Hermanson and Altenbach, 1981, 1983, 1985). It is likely that this pattern arises because the pectoralis undergoes eccentric contraction, electrical activity during lengthening and thus experiences enhanced force generation relative to an isometric or shortening contraction. In contrast to predictions that downstroke muscle activity should persist throughout the majority of the downstroke, measurements from *A. pallidus, A. jamaicensis* and *Eptesicus fuscus* show that the trio of downstroke muscles cease electrical activity approximately halfway through the downstroke, and that the remainder of the downstroke must therefore occur via the momentum gained in the first half of the cycle (Altenbach and Hermanson, 1987). Studies of upstroke musculature have demonstrated, similarly, that this portion of the wingbeat cycle is actively controlled by a combination of muscles, the trapezius, deltoideus, supraspinatus and infraspinatus, commencing electrical activity not at the onset of upstroke, but about halfway through downstroke (Hermanson and Altenbach, 1983, 1985). This allows bats to control upstroke in an active and precise manner, rather than passively, trading energetic costs of muscular activation for greater control of wing motions in this portion of the wingbeat cycle.

In comparison to comparable locomotor systems in other vertebrates, there is little variability in the composition of the flight muscle tissue of bats (Hermanson, 1998). There appear to be only two variants of pectoralis fiber type composition, a unitypic and a bitypic form. It has been proposed that these two forms could represent single and dual gear flight motors (Hermanson and Foehring, 1988; Hermanson *et al.*, 1993), with frugivores that occasionally employ hovering flight benefiting differentially from multiple fiber types in comparison to insectivores. This hypothesis is consistent with the presence of bitypic pectoralis muscles in *Artibeus jamaicensis* and *A. literatus*, and the unitypic character of insectivorous vespertillionids (Hermanson, 1998). The vampire bats studied to date, *Desmodus rotundus* and *Diaemus youngi*, and two mormoopids, *Mormoops megaphylla* and *Pteronotus parnellii*, however, are also bitypic. The complexity of the muscle fiber type distribution suggests that multiple factors may operate to exert selective pressure on fiber architecture, and that we have not yet fully explored the function of even the largest and most important of the flight muscles.

9.5 Flight performance

The kinematics of the bat wing are complex, among the most complex motions of those of any vertebrate limbs. Because there are so many joints in a bat wing, some of which, such as the shoulder, can be moved in more than one direction, bats have more than 20 degrees of freedom per wing, so even describing a wingbeat cycle is a considerable challenge (Riskin *et al.*, 2008). On the downstroke, bats extend their wings, and move them downward and forward, or ventrally and anteriorly in anatomical terminology (Norberg, 1976, 1990; Swartz *et al.*, 2005; Riskin *et al.*, 2008). On the upstroke, the wings are folded to varying degrees, and move dorsally and posteriorly. As the wings move through a locomotor cycle, the postures of the different finger bones change, causing complex changes in the three-dimensional curvature of the wing over the course of the cycle; these include changes in the degree to which the wing is cambered at different points along the length of the wing and at different times in the cycle (Swartz *et al.*, 2005). Furthermore, the wing bends and twists as it is flapped, so that by the time the wingtip has finished the downstroke, the wrist is already well into the upstroke (Norberg, 1976).

9.5.1 Changes in kinematics with speed and acceleration

Terrestrial animals employ distinct gaits at different speeds, like walking and running in humans, for example (Alexander, 2003; Biewener, 2003). In contrast, there is no evidence for an abrupt, discontinuous pattern of kinematic change with speed for flying bats. The kinematic transitions among speeds are gradual. For this reason, we prefer not to employ the term gait in the description of wing kinematics in bats.

One way to understand the link between kinematics and aerodynamic force production is to examine which kinematic parameters change during steady flight over a range of speeds. When an animal flies at a constant velocity, without climbing, falling, speeding up or slowing down, this is often referred to as steady flight. We note, however, that this does not imply that the operative aerodynamics are steady; steady flight, in this sense, can certainly involve unsteady aerodynamics. When a bat performs steady flight, over a complete wingbeat cycle, the amount of lift required is equal to its weight, and it must produce just enough thrust to overcome drag. Consider steady flight at a low speed compared with steady flight at a high speed. At both speeds, the amount of lift required is the same: it must equal the animal's body weight. At high speeds, however, the requirement for thrust is increased because the drag forces are substantially higher than during slow flights. As mentioned before, the absolute values of drag and thrust cannot be known, but they both increase exponentially with flight speed. Changes in kinematics with speed, therefore, can indirectly tell us how bats modulate the coefficient of lift, thrust and drag.

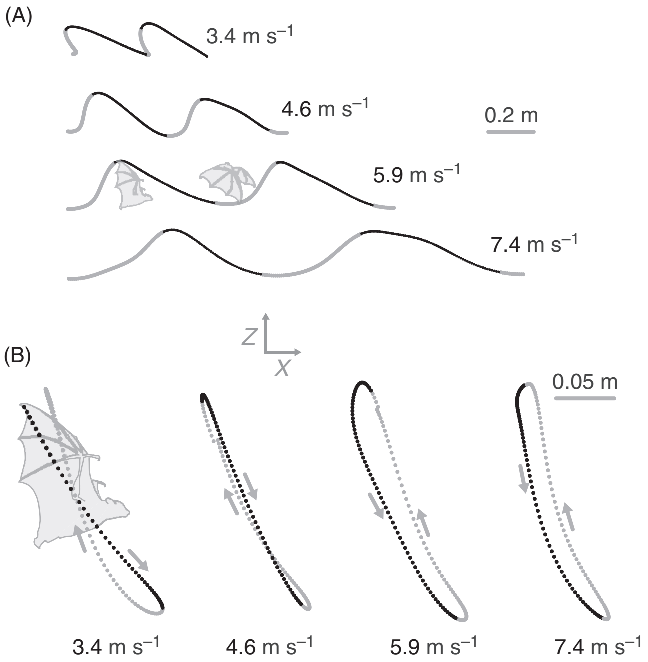

Figure 9.7 Lateral view of wingtip motions during flight at different speeds in *Cynopterus brachyotis*, the lesser dog-faced fruit bat. (A) In a world-based frame of reference, the distance traversed by both body and wingtip over each wingbeat increases with increasing forward flight speed; downstroke portions of wingtip motions given in black, upstroke in gray. (B) In the frame of reference of the bat's body, the change in the stroke plane angle with increasing flight speed is clear. At lower flight speed, to the left, stroke plane angle is relatively low, and as flight speed increases the stroke plane becomes increasingly vertical. Adapted from Iriarte-Díaz *et al.* (2011).

One aspect of wing kinematics that changes with flight speed in most bat species is the stroke plane angle (Figure 9.7). In lateral view, the movement of the wingtip of a bat with respect to its body traces a diagonal line, going posteriorly and dorsally on the upstroke, and ventrally and anteriorly on the downstroke. At lower speeds, there is considerable wingtip movement in the fore–aft direction, so the path of the wingtip is quite slanted from vertical. At higher speeds, the fore–aft component of that movement is diminished, and the line traced by the wingtip is almost vertical. Why does the stroke plane become more vertical as speed increases? Recall that lift is generated when the air moves over the wing with some speed U, and that the amount of lift generated increases with U^2. When a bat flies fast, the relative velocity of air with respect to the wing is high and high U generates substantial lift. At low forward speeds, much less lift is generated, and reaching an adequate lift magnitude to balance body weight is a physical challenge. Thus, by modulating wing kinematics to include a significant forward component in the downstroke during slow flight, there will be an additional component of relative forward motion of the wing with respect to the air that will generate extra lift in proportion to the square of its magnitude. When bats fly slowly, they also increase the camber and angle of attack of the wing, probably also to improve lift (Riskin *et al.*, 2010).

Of course, bats do not always fly at steady speeds. They often accelerate vertically or horizontally, and the magnitudes of those accelerations reflect, respectively, the total lift force or the sum of thrust and drag forces. Based on measurements of kinematic changes with those accelerations, one study on pteropodid bats demonstrated that bats increase lift forces by extending their wings more fully, increasing wingbeat frequency, increasing angle of attack and increasing camber. To increase horizontal acceleration, bats extended their wings more fully on the downstroke, drew their wings in more fully on the upstroke, increased stroke amplitude and decreased stroke plane angle (Riskin *et al.*, 2010).

9.5.2 Hovering flight

Few animals, such as some insects and a few bird species such as hummingbirds, have evolved the ability to sustain hovering flight, where the body is maintained still in air by the aerodynamic forces produced by flapping the wings. Nectar-feeding bats are also able to sustain hovering and they are among the largest animals to do so. Interestingly, among animals of comparable body size, the hovering flight of nectar-feeding bats is 40 and 60% less costly metabolically than that of hawkmoths and hummingbirds, respectively (Winter, 1998; Winter and von Helversen, 1998; Voigt and Winter, 1999), suggesting that bats have more efficient mechanisms of lift generation than members of the other groups.

The kinematics of hovering in bats differ from those of insects and hummingbirds. Insects and hummingbirds hover with fully extended wings during both downstroke and upstroke, and move the wings in a primarily horizontal stroke plane. Insects generate roughly equal amounts of lift between the upstroke and the downstroke, in what is called a "symmetrical" or "normal" hovering. Hummingbirds, however, perform "asymmetrical" hovering, producing only 25% of the lift during the upstroke, despite the relatively symmetrical up- and downstroke wing kinematics (Warrick *et al.*, 2005). Unfortunately, we still lack experimental measurements of lift generation during hovering in bats, but based on wing kinematics and relatively simple modeling of wing aerodynamics (Norberg, 1976), bats seem to also perform asymmetric hovering with most of the lift generated during the downstroke.

In the 1970s, studies of the mechanics of hovering flight in bats based on the use of kinematics and aerodynamic theory showed that the aerodynamic force generated during hovering could not be explained by quasi-steady aerodynamics, and that unsteady mechanisms must be used to produce enough lift to sustain flight (Norberg, 1976). Recently, studies using PIV (particle image velocimetry) methods conclusively document that slow-flying bats can increase lift generation as much as 40% by using attached leading-edge vortices (Muijres *et al.*, 2008) similar to those used by insects (e.g., Fry *et al.*, 2005) and hummingbirds (Warrick *et al.*, 2005), although the use of other unsteady mechanisms, such as rotational circulation and delayed stall could also be involved (Dickinson *et al.*, 1999). Why hovering flight in bats is energetically cheaper than that of insects and birds of similar size, however, is still unclear.

9.5.3 Thrust on the upstroke?

At any speed, the tip of the wing moves upwards and backwards relative to the body during the upstroke. But if the speed of the body is low enough, the tip can sometimes even move backward relative to the still air during the upstroke (e.g., Figure 9.7A, top illustration). This has been called "tip-reversal upstroke" (Aldridge, 1987a), and tip-reversal upstrokes have been thought by some to provide additional thrust to slow-flying bats. There are at least two possible mechanisms by which tip reversal may provide aerodynamic force; the wingtip could push air backward like a canoe paddle, or the bat may oversupinate the wingtip to produce a positive angle of attack at the tip and thereby produce lift locally. Support for the hypothesis that tip reversal is aerodynamically useful comes from the observation that when a bat performs a tip-reversal upstroke, markers on its body accelerate forward. If markers placed on a bat's body track the position of the center of mass, then their forward acceleration implies that net thrust exceeds drag during upstroke.

Recent work demonstrates that for *Cynopterus brachyotis* (Pteropodidae), although the trunk skeleton accelerates forward on the upstroke during slow flight, its acceleration can be partially explained by inertial effects due to the flapping motion of the wings (Iriarte-Díaz *et al.*, 2011). When the wings swing backward, approximately 20% of the bat's mass moves backward relative to the center of mass. To balance this, other portions of the body must move forward relative to the center of mass; this is reflected in the forward acceleration of the body markers. The detailed changes of the distribution of mass in the body and wings of a flying bat show that although markers on the body accelerate forward during tip-reversal upstroke, the center of mass does not (Iriarte-Díaz *et al.*, 2011). For slow-flying *C. brachyotis*, there is no net thrust on the upstroke. Such mass models have not yet been computed for other species, but considering that the forward acceleration of markers on the sternum, taken as evidence of net thrust on the upstroke for other bats, is also present in *C. brachyotis*, it would seem that all of the net thrust and lift generated by bat wings during slow flight is on the downstroke.

9.5.4 Wake structure

In recent years, researchers have focused attention on the wakes left behind flying organisms (Rayner *et al.*, 1986; Spedding, 1987; Spedding *et al.*, 2003; Birch *et al.*, 2004; Warrick *et al.*, 2005; Johansson *et al.*, 2008). As mentioned previously, a wake preserves, in its three-dimensional structure, the history of the forces generated as a solid object, such as an animal, moves through a fluid, such as air or water. Animal wakes have been studied to discern various aspects of force production, first qualitatively, using techniques such as smoke visualization (e.g., Vandenberg and Ellington, 1997; Srygley and Thomas, 2002) and photographic analysis of wakes created in volumes of neutrally buoyant helium bubbles (e.g., Rayner *et al.*, 1986), and more recently using particle image velocimetry or PIV (e.g., Hedenström *et al.*, 2007, 2009; Hubel *et al.*, 2009, 2010). To date, only three bat species have been studied using PIV: two nectar-feeding bats, *G. soricina* and *Leptonycteris curosae*, and a fruit bat, *C. brachyotis*. The wake structure in bats seems to be consistent among species and shows considerable differences to wakes in birds. Similar to the wake observed behind birds during slow flight, bats shed trailing vortices from the wingtip, but in addition, there is a secondary streamwise vortex shed by the body, forming a vortex ring for each wing (Hedenström *et al.*, 2007; Hubel *et al.*, 2010) (Figure 9.2). This secondary vortex structure is much stronger in *G. soricina* (*c.* 50% of the tip vortex strength) than *C. brachyotis* (8% of the tip vortex strength). Wake structure analyses show a continuous change in circulation with speed, indicating a gradual change in aerodynamic force generation instead of the discontinuous change expected with distinct gaits (Hedenström *et al.*, 2007).

9.5.5 Kinematic differences among species

It is well known that the wing shapes of bats vary among species (Norberg and Rayner, 1987), but very little is known about the diversity of wing kinematics among species. Most of what we know about bat wing kinematics comes from just a few species, but these span a range of body sizes and ecological roles. One important result from kinematic analyses carried out to date is that the flight performance of a bat species often differs from what is expected based on its morphology alone. This is an important point, but one that is rarely acknowledged, since it is often convenient to infer performance based on morphology alone.

For example, from arguments based on the aerodynamics of large fixed-wing aircraft, turning performance should be superior in bats with low wing loading compared to those with high wing loading. In keeping with this prediction, Aldridge (1987) found that maximum turn curvature was inversely proportional to wing loading among five insectivorous species that made banking turns. However, one of his species, *Rhinolophus ferrumequinum*, was able to perform a tighter turn than expected based on its wing loading, by dropping its flight speed to near zero while turning. Instead of making a banked turn, this species flew "like a helicopter." This, and a few other interspecific studies (e.g., Aldridge, 1987a; Stockwell, 2001; Riskin *et al.*, 2009, 2010) have demonstrated that variation in morphology can be modulated by kinematics.

Evidence that bat species vary substantially in the details of wing motions comes from data sources outside of kinematics per se (Hermanson and Altenbach, 1983, 1985). The timing of activity of the flight musculature in two species of similar body size, *Artibeus jamaicensis*, a frugivorous phyllostomid, and *Antrozous pallidus*, an insectivorous vespertilionid, directly assessed using electromyography, shows numerous differences. Many of the flight muscles fire once per wingbeat cycle in *Antrozous*, at the end of the downstroke only, but are biphasic in *Artibeus*, firing at the end of both downstroke and upstroke. This may reflect the use of a derived shoulder-locking mechanism, present in vespertilionids, but less well developed in phyllostomids, that is believed to arrest the motion of the wing at the end of upstroke passively. If the skeleton can block the abduction of the humerus, there is less need for muscle activity to actively resist the upward inertia of the wing. This kind of interspecific variation in muscle activity pattern clearly demonstrates that not all bats control their wing kinematics the same way and the investigators inferred that this kind of variation in activation pattern may also underlie patterns of variation in maneuverability in frugivorous compared with insectivorous bat species. It is clear that we have only begun to understand the motor control of the bat wing, and that further explorations of this subject may have a great deal to teach us about bat flight. In the meantime, even our limited understanding makes clear that it is worthwhile to remember that a bat's flight performance cannot be predicted from its wing shape alone.

9.5.6 Maneuvering: changing direction during flight

The ability to quickly alter flight direction and speed is fundamental for bats to successfully navigate three-dimensionally complex environments, to capture prey and to avoid predators. Despite this, maneuverability and the mechanisms underlying maneuvering abilities have yet to be thoroughly investigated. A flying organism has six degrees of freedom of movement: translation in three dimensions in space and rotation around three orthogonal axes centered on the center of mass. Flying maneuvers require the translation of the center of mass in space plus rotations of the body around three axes, termed yaw, pitch and roll.

In its most basic form, a turning maneuver requires that the forces experienced by the two sides of the body be asymmetrical; that is, the organism is subjected to a sideways or centripetal force that will drive it through the turn. Force asymmetry for turns can be achieved in multiple ways, but the most commonly described method of turning is the banked turn. In this kind of turn, an animal rolls into a bank, which reorients the lift vector by tilting it towards the direction of the turn (Figure 9.8). The tilting of the lift vector produces a centripetal force component that deflects the organism through the flight path. When the turn is complete, the body can reverse the process and return to an unbanked position such that centripetal force is no longer produced. Human-engineered aircraft employ this mechanism, it has been observed in insects and birds, and it has been proposed for bats. If a flying organism performs a banked turn, then for any given lift coefficient and bank angle, the turning radius depends directly on the wing loading or body weight per unit wing area; there is some evidence consistent with this relationship from bats in both field and obstacle-course settings (Aldridge, 1986; Aldridge and Rautenbach, 1987; Stockwell, 2001).

However, growing evidence suggests that differences in turning techniques (e.g., gliding vs. flapping turns; Aldridge, 1987b) and changes in wing posture throughout the turn (Lentink *et al.*, 2007) can substantially alter the turning performance in ways that cannot be predicted by simple morphological parameters. The only study that has evaluated the kinematics of turning in bats suggests that turning performance is highly dependent on flight kinematics (Iriarte-Díaz and Swartz, 2008). Detailed analysis of the wings and body motion of fruit bats performing 90° turns showed that during the upstroke portion of the wingbeat cycle the body rotates in the direction of the turn, without significant changes in flight direction. This body rotation allows the bat to use part of the thrust produced during the downstroke to enhance centripetal force, allowing the bat to perform tighter turns than predicted by wing morphology alone (Iriarte-Díaz and Swartz, 2008). At least as importantly, turning is almost certainly one area of flight behavior in which the

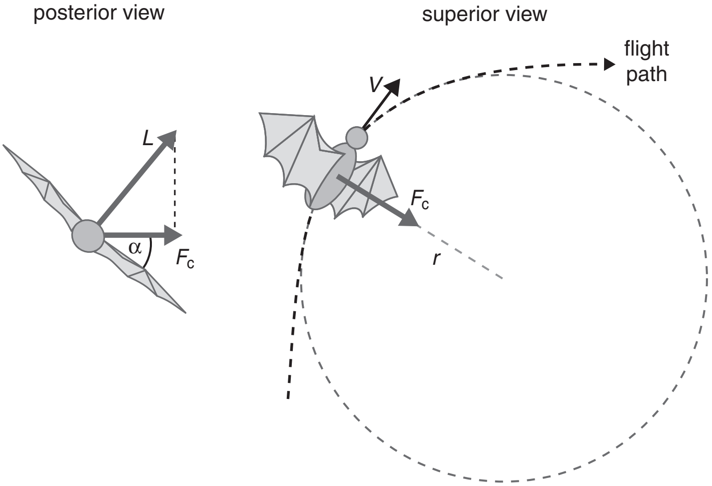

Figure 9.8 Forces required to turn during flight. If a bat banks during a turn, illustrated on left, the lift force, *L*, is rotated in such a way that is has a force component directed in the direction of the turn, *Fc*, which will propel the bat in the appropriate direction. The effect of this kind of turn, the turning radius, for a given velocity, *V*, and centripetal force, *Fc*, depend on the wing loading of the bat.

sensory input to the motor system is a crucial determinant of motor performance. The rate at which the bat receives information about changes in its three-dimensional position and accelerations, whether input to the central nervous system from the visual system, the auditory system, the vestibular apparatus or directionally sensitive wing hair sensors, has the potential to play a major role in controlling maneuvering abilities. One of the major challenges for future research is to separate sensory from mechanical and aerodynamic effects in limiting the capacity of bats to carry out extreme movements.

9.5.7 Landing: maneuvering to stop

In contrast to birds, which approach landing by simply reducing flight speed, bats face a biomechanical challenge as they must rotate their bodies in mid-air to roost head-under-heels, by performing elaborate acrobatic maneuvers. In a recent study, Riskin *et al.* (2009) found differences in the kinematics and kinetics of landing among three bat species: *Cynopterus brachyotis*, *Carollia perspicillata* and *Glossophaga soricina*. *C. brachyotis* employs a "four-point landing," using all four limbs to make contact with the substrate at impact by pitching up the body until the ventral side of the body faces the ceiling. The other two species use "two-point landings" to contact the ceiling using only the hindlimbs by simultaneously rotating their bodies in yaw, pitch and roll. Impact forces against the ceiling were four times larger during four-point landings than those recorded in two-point landings, and the authors postulated that the differences between these two landing styles could be explained by differences in the roosting habitats used by each species (Riskin *et al.*, 2009). *C. brachyotis* is a foliage-roosting species, whereas the other two species examined roost in caves. A surface such as leaves can absorb the impact energy of landing more effectively than can a rocky cave surface, and consistently, those species that roost in caves use two-point landings with low impact forces. However, differences in landing style might alternatively be explained by phylogenetic considerations: the four-landing species was a pteropodid while the two-point landing species were phyllostomids. Further analyses using more taxa distributed across the bat phylogeny are necessary to resolve this point.

9.6 Conclusion

We are fortunate to be at a turning point in the study of bat flight. Technological advances have made imaging the complex motion of bats far easier than at any time in the past, and are enabling researchers to gain insights into the aerodynamics of flight in ways that were unimaginable only a decade ago. Simultaneously, better collaborations among biologists and engineers are facilitating integrative research programs that are beginning to fruitfully apply the rich, powerful analysis methods of aeronautical engineering to the far more complex and subtle machinery of the bat flight apparatus. Once the early and most challenging steps are taken, we can look forward to an increased pace of advancement, and we predict that the next ten years will see a great increase in studies of bat flight. We can look forward to much better understanding of the ways in which bat flight is truly unique and unlike that of planes, birds or insects, and of the ways in which this special mode of flight has diversified over bat evolution.

9.7 Glossary

Angle of Attack. The angle at which the wing is inclined relative to the local air velocity. Lift increases as the angle of attack increases, up to a critical angle where the aerodynamic forces "stall" and lift declines and drag rises precipitously (Figure 9.1).

Camber. The front to back curvature of the wing, defined as the maximum height of the wing arc, divided by the chord length (Figure 9.1).

Circulation. The average vorticity contained in a defined area. In classical aerodynamics, all of the vorticity is confined to well-defined vortices, and hence the circulation of the flow is defined completely by the strength of vortices.

Lift, Drag. Aerodynamic forces acting perpendicular to, and parallel to the direction of the flow, respectively.

Reynolds Number. A dimensionless number, defined as $\rho Uc/\mu$, where ρ is the fluid density, U is the flight speed, c the wing chord and μ the fluid viscosity. The Reynolds number indicates the relative importance of inertial forces compared with viscous forces. Bat flight is typically characterized by a Reynolds number of approximately 10 000–50 000, which is considered a low number for aerodynamic flows.

Starting and stopping vortices. Vortex structures, oriented in the spanwise direction, associated with the beginning of the downstroke and the end of the upstroke, respectively. These vortices connect to the trailing streamwise wake vortices.

Stroke plane angle. Angle between the lateral projection of the displacement of the wingtip with respect to the body and the horizontal, indicating the main direction of the flap.

Strouhal Number. A dimensionless number, defined as fA/U where f is the flapping frequency, U is the flight speed and A the flapping amplitude. The Strouhal number indicates the relative importance of unsteady fluid dyanamic effects. Small numbers ($St < 0.1$) usually indicate that the flow is relatively steady, while large numbers ($St > 3.0$) suggest that unsteady effects dominate. Bat flight, and indeed most biological fluid locomotion, is characterized by a Strouhal number between 0.2–0.4, indicating that steady aerodynamics are important, but that unsteady forces cannot be ignored.

Vortex. A concentration of aligned vorticity. Common examples of vortices are tornadoes and the "bathtub vortex," caused as water drains from a tank.

Vorticity. The local rotational or angular speed of the fluid.

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10

Toward an integrative theory on the origin of bat flight

NORBERTO P. GIANNINI

> In bats . . . we perhaps see traces of an apparatus originally constructed for gliding through the air rather than for flight. Darwin (1859, p. 181)

10.1 Introduction

It is easy to grasp why bats are so successful: a small nocturnal mammal in possession of powered flight can explore resources in a relatively low-risk environment at spatial scales orders of magnitude larger than that of non-volant mammals of comparable size. As an example, the median home range of the 8–11 g vespertilionid *Chalinolobus tuberculatus* can be as large as 1500 ha (O'Donnell, 2001); this is the average area used, for instance, by a 300 kg herbivore, the Wapiti (*Cervus elaphus canadensis*; Calder, 1996). Acquisition of powered flight represented an immediate advantage to the bat lineage. As attested by the fossil record, bats reached nearly worldwide distribution early in their evolution. By the Early Eocene, bats suddenly appear in all the major landmasses they inhabit today (Gunnell and Simmons, 2005; Tejedor *et al.*, 2005; Eiting and Gunnell, 2009). This suggests that powered flight may have played a key role in the fast expansion of bats, thereby contributing to their spectacular diversification.

Beyond the presence of wings, adaptations to powered flight encompass most organ systems, including: full flexion and extension of whole wing (including hyperabduction of digits) automated via tendon rearrangements (Norberg, 1972); energy-saving locking mechanisms such as vertebral column rigidity (Vaughan, 1959); locking mechanisms in each forelimb joint to prevent hyperextension or rotation of the wing (Vaughan, 1959); concentration of forelimb muscle mass towards the center of gravity to reduce inertial power (Vaughan, 1970); leading-edge camber adjustment by pronation of hand, assisted by tension of propatagium via m. occipitopollicalis and stiffened dactilopatagium minus (Norberg, 1969); trailing-edge camber adjustment by

Evolutionary History of Bats: Fossils, Molecules and Morphology, ed. G. F. Gunnell and N. B. Simmons. Published by Cambridge University Press.