

Wing Structure and the Aerodynamic Basis of Flight in Bats

Sharon M. Swartz^{*}, Jose Iriarte-Diaz[†], and Daniel K. Riskin[‡],
Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912

and

Arnold Song[§], Xiaodong Tian^{**}, David J. Willis^{††}, and Kenneth S. Breuer^{‡‡}
Division of Engineering, Brown University, Providence, RI 02912

Abstract Powered, flapping flight has evolved at least four times in the Animal Kingdom: in insects, birds, pterosaurs, and bats. Although some aspects of flight mechanics are probably common to all of these lineages, each of the four represents a unique solution to the challenges of maneuverable flapping flight at animal length scales. Flight is less well documented and understood for bats than birds and insects, and may provide novel inspiration for vehicle design. In particular, bat wings are made of quite flexible bones supporting very compliant and anisotropic wing membranes, and possess many more independently controllable joints than those of other animals. We show that the mechanical characteristics of wing skin play an important role in determining aerodynamic characteristics of the wing, and that motions at the many hand joints are integrated to produce complex and functionally versatile dynamic wing conformations.

I. Introduction

At the scale of micro air vehicles, bats exhibit extraordinary flight capabilities that arise by virtue of a variety of unique mechanical and neurophysiological features. Indeed, bat flight combines exceptional energetic efficiency and extraordinary maneuverability; for example, in the common body size range of large insects, small birds, and small bats, hovering flight in bats is 40% and 60% less costly metabolically than that of hawkmoths and hummingbirds respectively¹⁻³. To unravel the mechanistic basis of bat flight, and thereby to identify specific features that could be applied to human-engineered designs, we must identify the most functionally relevant components of the flight apparatus and ascertain their performance during normal flight behavior.

Given our goal of understanding those aspects of flapping flight that differ among bats, birds, and insects, we focus here on aspects of the structural design of bat wings that uniquely distinguish them. Bat wings possess 1) more than two dozen joints which can be controlled independently to some degree; 2) bones that deform adaptively during the characteristic motions of the wingbeat cycle⁴; 3) tremendously anisotropic wing membrane skin with both substantial variation and adjustable stiffness across the wing^{5, 6}; and 4) a distributed network of skin sensory organs believed to provide continuous information regarding flows over the wing surfaces^{7, 8}. The first three of these characteristics, the foci of this study, together produce wing surfaces whose geometry and kinematics are far more complex spatially and temporally than the classic literature regarding bat flight would suggest (Figure 1). Our

^{*} Associate Professor, Ecology and Evolutionary Biology, Box G-B206, Brown University, Providence RI 02912, and AIAA Member Grade for first author.

[†] Graduate Fellow, Ecology and Evolutionary Biology, Box G-BW, Brown University, Providence RI 02912 and AIAA Member Grade for first author.

[‡] Postdoctoral Researcher, Ecology and Evolutionary Biology, Box G-B206, Brown University, Providence RI 02912, and AIAA Member Grade for first author.

[§] Graduate Fellow, Division of Engineering, Box D, Brown University, Providence RI 02912, and AIAA Member Grade for first author.

^{**} Postdoctoral Researcher, Division of Engineering, Box D, Brown University, Providence RI 02912, and AIAA Member Grade for first author.

^{††} Postdoctoral Researcher, Division of Engineering, Box D, Brown University, Providence RI 02912, and AIAA Member Grade for first author.

^{‡‡} Professor, Division of Engineering, Box D, Brown University, Providence RI 02912, and AIAA Member Grade for first author.

long-term goal is to relate the detailed structure and motions of the bat wings to the production of aerodynamic force, and to understand how bats manipulate their flight apparatus to achieve steady flight, maneuvers, take-off and landing. This will ultimately require studies that incorporate kinematic analysis, experimental and theoretical fluid dynamics, materials science, and neurobiology, but important advances can be made in each of these subjects independently as we progress towards a more integrative understanding.

One primary obstacle to advancing our understanding of bat flight to date has been an absence of detailed kinematic information at high temporal resolution; such data can provide tests of the robusticity of existing fixed-wing models of bat flight, including assumptions concerning the nature of the wingbeat cycle, the relative uniformity of wing shape, rigidity of the wing, etc.⁹⁻¹² We explore here the dynamic anatomy of the bat wing in flight, with particular attention to those aspects of wing structure that are most likely to fundamentally influence aerodynamic performance. Specifically, we ask: 1) Does the entire wing move in synchrony through a two-phase (upstroke vs. downstroke) wingbeat cycle that can be linked directly to cyclic generation of aerodynamic force? 2) To what degree does the skeleton remain rigid during the movements of the wingbeat cycle? 3) To what extent does the skin of the wing membrane stretch and recoil during flight?

II. Study Design

Lesser short-nosed fruit bats, *Cynopterus brachyotis*, were the subjects of these studies. We chose this species for analysis because they thrive in captivity, respond well to handling and training, and, at 35-45 g body mass and 30-40 cm wingspan, are an appropriate size for windtunnel studies. This species is native to many forested areas of Southeast Asia, and possesses the highly developed visual system characteristic of most nocturnal vertebrates, but does not echolocate as do approximately three-quarters of bat species¹³. Study subjects were drawn from a captive-bred colony (Lubee Bat Conservancy; Gainesville, Florida). All subjects were female, eliminating sex-specific variation. For studies of straight (non-turning) flight, key anatomical landmarks of animal subjects were marked with an array of high-contrast markers on the undersurface of one wing (Figure 2, 3). Marker sites were chosen to allow reconstruction of motion of anatomical landmarks and to facilitate measurements of strain in wing bone and specific regions of the wing membrane during flight. All experiments were approved by the appropriate Institutional Animal Care and Use Committees.

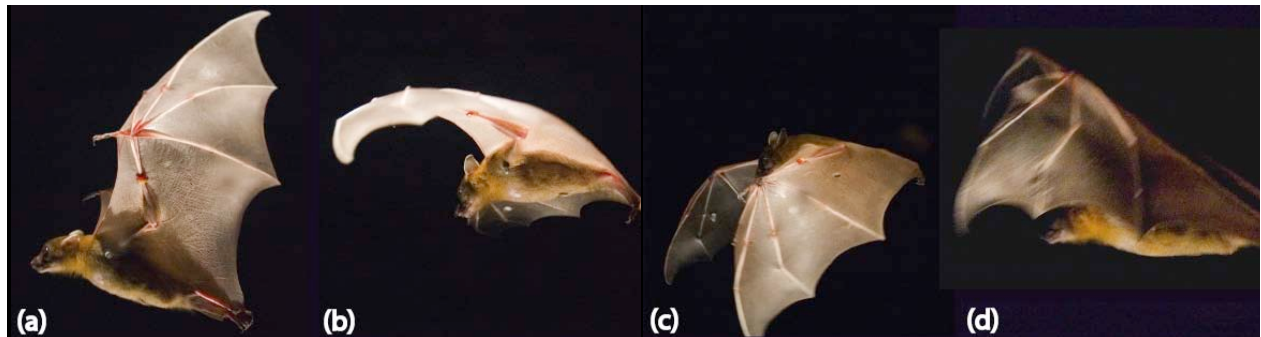


Figure 1. Sequence of images from typical wingbeat of *Cynopterus brachyotis* in slow flight. These lateral views show some portion of the complexity of 3D form of the wing during flight.

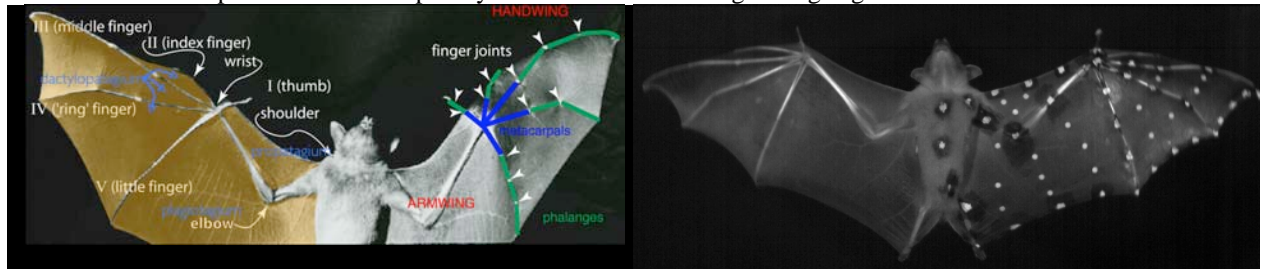


Figure 2. Anatomical structures of the bat wing

Figure 3. Bat with anatomical markers on body and wing bones and skin.

To obtain adequate anatomical detail over multiple wingbeat cycles at forward velocities at or greater than several body lengths per second, we required a windtunnel appropriate for biological research. The Harvard University – Concord Field Station (HU-CFS) windtunnel is an open-circuit tunnel with a closed jet with a 1.2x1.2x1.4m test section, able to operate at wind speeds up to 28.5 m/s (see ref. 14 for further detail regarding the

HU-CFS wind tunnel). We documented flights over a range of speeds; we report here on flights near the extremes of the recorded range, at 3 m/s, hereafter designated *slow* flight, and at 8.6 m/s, hereafter designated *fast* flight. Because of the challenges of accurately measuring flight speeds in the field, we do not know what fraction of the animals' true speed range these values represent, but they are capable of hovering for at least several seconds, and are likely able to fly faster than the highest speed we elicited in the wind tunnel, hence these values do not reach the extremes of flight performance in this species.

Animals were trained to fly in the windtunnel test section using positive reinforcement. Although individuals vary in their windtunnel performance abilities, several animals are capable of flying for many consecutive wingbeats without landing. This report focuses on extended flights of one such individual; future work will include comparisons among individuals. Preliminary investigation have also been unable to identify any significant differences in kinematics between windtunnel and free forward flight in this species.

Three high-speed digital cameras (Photron Fastcam 1280 x 1024 pixels, 1000 images per second) were employed to capture the wing and body motion. Post-processing of the high speed videos using the Direct Linear Transform (DLT) method merges the separate 2D camera views into a single 3D coordinate space and yields the unsteady three-dimensional motion of the entire wing-body system^{15, 16}. A DLT root mean square (RMS) error was calculated for each point at every frame. The RMS error varied from frame to frame, with median error 0.5 cm, 1.25% of the measurement range.

III. Results

A. Definition of the Wingbeat Cycle

The bat locomotor cycle is typically subdivided into a downstroke phase and an upstroke phase. Although authors vary in their definitions of these phases, most define downstroke as the portion of the wingbeat between the time the wingtip reaches its highest and lowest vertical excursions^{10, 11, 17, 18}.

1. Peak amplitudes along the wingspan

At slow speed (3 m/s), the wingtip oscillates at a mean of 8.8 cycles per second, with the wingtip decreasing height for an average of 56 ms (47%) of the 118 ms mean wingbeat period. At high speed (9 m/s), the wingtip oscillates at a mean of 9.9 Hz, with the wingtip moving downward for 51 ms of the 100 ms mean period (Figure 4, 5). Moving toward the body midline, the other primary anatomical landmarks along the wing's primary skeletal axis reach the extremes of their cyclical motion out of synchrony with the wingtip. On average, at slow speed the metacarpophalangeal joint of the third digit (third digit 'knuckle' or MCP III) reaches the bottom of its vertical cycle 6.9 ms after the wingtip, the carpus (wrist) reaches it nadir 1.3 ms later, and the shoulder is delayed by an additional 13.7 ms. At high speed, the respective delays are 3.4 ms for the MCP, 2.8 ms more for the wrist, and 19.4 ms for the shoulder. Hence, different spanwise regions of the wing undergo maximal displacements at different times and the relative delay of specific anatomical landmarks changes with velocity.

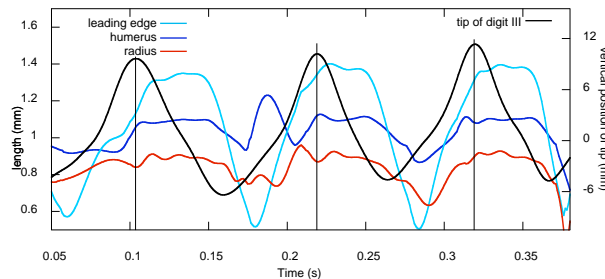


Figure 4. Non-coincidence of peak amplitude across wing (low speed). Peak vertical amplitude of different regions of the wing are achieved at different times. 0 represents the vertical position of the sternum, approximately at the animal's center of mass. Positive positions are above the sternum marker, negative below. Parts of the wing closest to the midline (i.e. the shoulder joint) reach their vertical peak before successively more distal (outboard) portions of the wing (wrist, followed by third metacarpophalangeal joint or 'knuckle' and the tip of the wing). Vertical excursion of

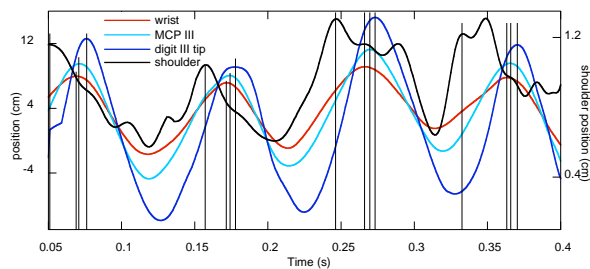


Figure 5. Non-coincidence of peak amplitude across wing (high speed). The pattern of temporal asynchrony of amplitude peaks observed at low speed (Figure 4) is maintained at higher velocities, despite increased complexity of the vertical motions of the shoulder. 10X magnification of shoulder motion (right Y-axis) compared to motions of other landmarks. The most prominent differences between velocities are in the amplitude of motion in the vertical direction. Motions in the side to side direction (not pictured) change little with speed, and motions in the fore-aft direction (not

the shoulder is given on the right Y-axis and is pictured) decrease in magnitude with increasing speed.

magnified 10X compared to other landmarks to show shoulder motions more clearly. Peaks are marked with thin vertical lines for comparison.

2. Peaks in amplitude in vertical and horizontal directions

In a simple wingbeat cycle of a rigid wing, the horizontal (both fore-aft and side-to-side/in-out) oscillations of a given anatomical landmark will be synchronized with the vertical oscillations. In *C. brachiotis*, the wingtip reaches its maximum excursions in vertical, fore-aft, and spanwise directions at quite different times in the cycle (Figure 4). This pattern is repeated for all skeletal landmarks, including the tip of the fifth digit (the primary chordwise skeletal support of the outboard portion of the wing) (Figure 6) and the metacarpophalangeal joints of both third and fifth digits (Figure 7). For some anatomical landmarks, such as the tip of digit III, vertical and side-to-side motions of nearly coincide, and for others, such as the tip of digit V and the MCP joint, these peaks are offset by 5-28% of the wingbeat cycle. For many landmarks, the peaks in fore-aft motion occur during the first third of upstroke, when the wing is near its lowest vertical position. For the fifth digit, however, fore-aft peaks may be nearly coincident with vertical peaks.

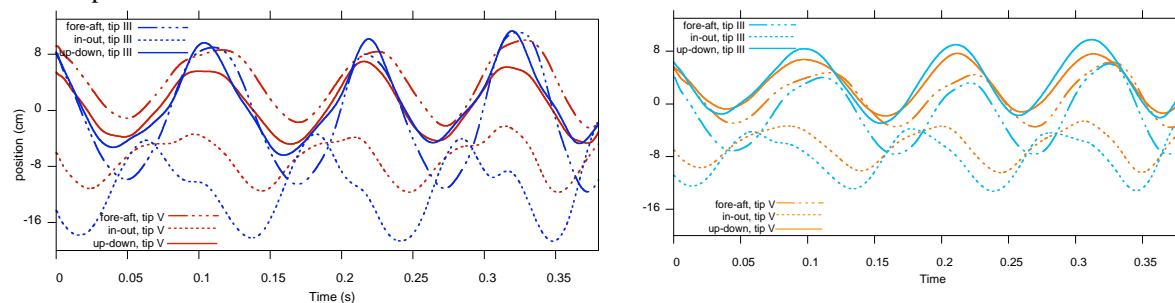


Figure 6 (left). Non-coincidence of peak amplitude in fore-aft, side to side, and vertical directions, wingtips. Peak amplitudes of the wingbeat for any given point on the wing are achieved at different times. Position of 0 represents the position of the sternum, near the CoM. Positive positions in the fore-aft direction are between the CoM and toes. In the transverse direction, 0 is on the body midline and values are increasingly negative toward the marked wingtip, and in the vertical direction, positive values are above the sternum marker, negative below. For both digits III (blue) and V (red), peaks in the three directions do not coincide, nor do peaks coincide in any one direction for the tips of digits III and V. From flight at slow speed; pattern is analogous for high speed flights.

Figure 7 (right). Non-coincidence of peak amplitude in fore-aft, side to side, and vertical directions, inner portion of wing. The pattern observed at low speed (Figure 3) is maintained at higher velocities, despite increased complexity of the vertical motions of the shoulder. 10X magnification of shoulder motion (right Y-axis) compared to motions of other landmarks.

3. Speed effects

As *C. brachiotis* bats increase flight speed, wingbeat period decreases, and the maximum vertical excursion of the wingtip increases (Figure 8). In addition, numerous smaller-scale changes in the details of wing kinematics occur. For example, motions of the shoulder change with speed, going from relatively simple to more complex vertical trajectories. Although the wingtip excursion increases with speed, the shoulder shows an overall decrease in peak excursion in fore-aft, side to side, and vertical directions (Figure 9).

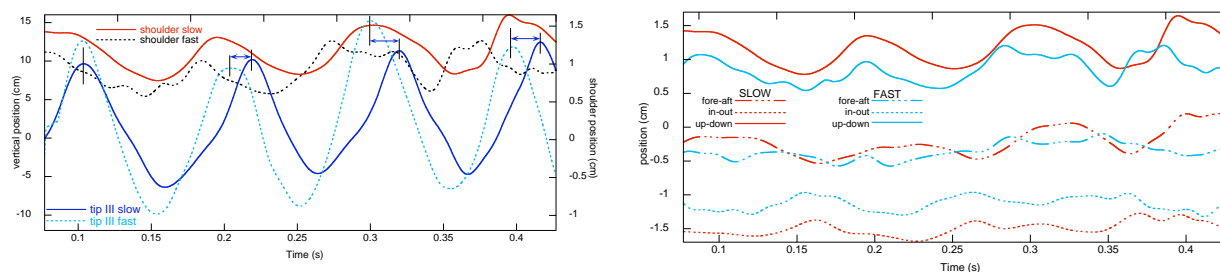


Figure 8. Kinematic changes with flight speed. Motions of the wing tip (tip of digit III) change with increasing flight speed. Wingbeat period decreases with speed, as indicated by wingbeat traces from 3 and 9 m/s flights aligned by timing of the first peak in vertical position. Time between peaks at slow vs. fast flight increase (double-headed arrows). Motions of the shoulder also become more complex with increasing speed, indicated here by greater complexity in vertical shoulder trajectory (red vs. black).

Figure 9. Shoulder motions change with speed. Motions of the shoulder in all three directions change with increasing flight speed. At high speed, the shoulder remains closer to the animal's CoM (near the 0 position on the y-axis), despite greater excursion of the wingtip (see Fig. 8).

B. Skeletal Deformation

Changes in Bone Deformation through Wingbeat Cycle

Measurements of distance between the endpoints of the elongated, slender bones of the wing clearly demonstrate substantial bending during the wingbeat. These changes appear to be directly related to patterns of wing motion, with bone length maxima and minima occur at regular points in the wingbeat cycle (Figure 9, 10). For example, the distal phalanx of the third digit is bent throughout the nearly the entire cycle, reaching its nominal resting length for only brief periods during upstroke (Figure 10); the loading-induced curvature is so great that the straight-line end-to-end length of this bone is only 45-55% of its resting length during much of the wingbeat (Figure 9). Large deformations of the skeleton are not observed solely in the wingtips. The third metacarpal, for example, is bent to less than 55% of its original length in most wingbeats, even in slow flight (Figure 11). There is noticeable difference among distinct regions of the wing, with the bones of the third digit undergoing much larger deformations than the bones of the fifth digit, oriented in the chord-wise direction. For most bones, the magnitude of deformation varies with speed; in the metacarpals and phalanges, strain magnitudes appear to decrease with increasing speed.

Figure 10. Bone length changes. Length of the distal phalanx of the third digit (red), the last bone of the wingtip, changes in synchrony with the wingbeat cycle in fast flight. Bone length is maximum (resting length) only during a small portion of the upward motion of the wingtip.

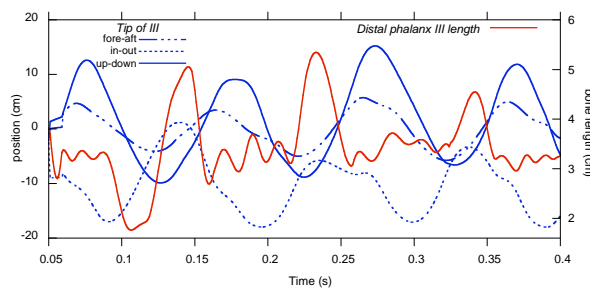
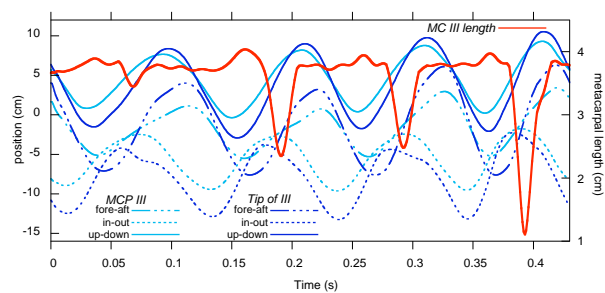


Figure 11. In slow flight, the length of the third metacarpal, the first spanwise bone from the wrist, changes during the wingbeat, with greatest deformations occurring during the middle portion of the upward motion of the tip. Deformations of this bone are less than for the wingtip.



C. Membrane Deformation

Measurement of the deformation of regions of the wing membrane show a strong dependence of membrane deformation on direction of measurement, as well as clear differences in deformation patterns among anatomical

regions of the wing (Figure 12-14). For slow flight, wing skin elongates parallel to leading or trailing edges more than in the chordwise or oblique directions in the propatagium ('leading edge flap, Figure 12), the plagiopatagium or armwing (inboard portion of the wing, Figure 13), and all sections of the dactylopatagium or handwing (outboard portion of the wing, Figure 14 and 15), although the magnitude of this effect is rather small in the region of the wing bounded by the fourth and fifth digits (Figure 15). Most skin regions are at or near their greatest stretch during the second quarter of the wingtip's downward motion. In the handwing, relatively full stretch is first achieved earlier in the wingbeat cycle, well before the wingtip has reached its greatest vertical excursion (Figure 14, 15). These regions of the wing also show significant increases in skin stretching at the beginning of the upward motion of the wingtip, although in the propatagium and armwing upward motion of the wingtip typically corresponds to a decrease in skin tension (Figure 12, 13).

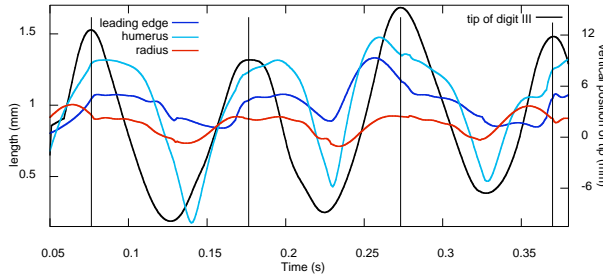


Figure 12. Propatagium ('leading edge flap') wing membrane length changes. Distances between wing markers change during the wingbeat and depend strongly on orientation within the plane of the wing. Length changes are greatest in the direction parallel to the leading edge of the membrane (light blue) and lower at directions parallel to the bones of the arm, the humerus (closer to the midline) and the radius (adjacent to the wrist).

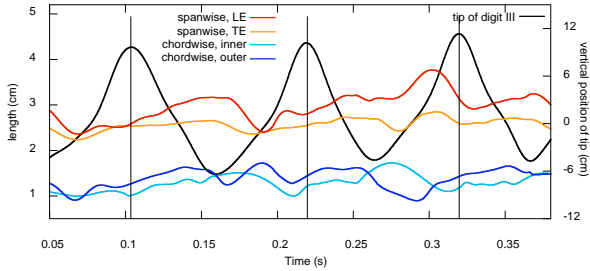


Figure 13. Differences in skin stretch in spanwise and chordwise directions. In slow flight, the skin of the plagiopatagium, the wing region closest to the body, stretches differentially in chordwise (blue) vs. spanwise (red, orange) directions. Larger strains are observed in the spanwise direction, the direction in which the skin is much less stiff, and the spanwise skin stretch occurs through much of the cycle with the exception of the early half of the wingtip's upward motion.

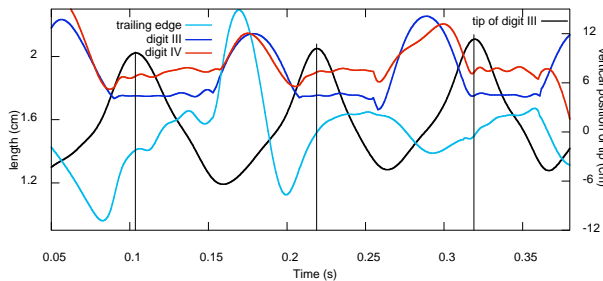


Figure 14. Dactylopatagium or handwing membrane length changes. The skin at the trailing edge of the portion of the handwing closest to the wingtip undergoes the largest deformations observed in the wing membrane (light blue), more than doubling in length between shortest and most stretched conditions. Greatest stretch occurs late in downstroke in both spanwise (light blue) and chordwise (blue, red) directions.

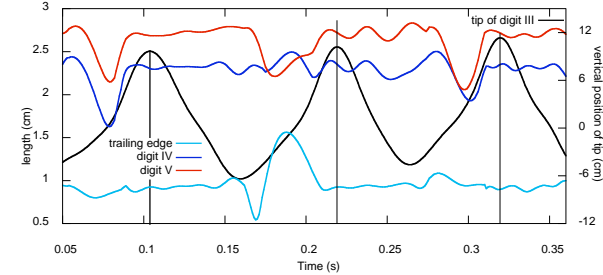


Figure 15. Medial dactylopatagium or handwing membrane length changes. Like the skin of the adjacent wing region, here the greatest length changes occur in the skin parallel to the wing's trailing edge (light blue), with a brief interval of high stretch in the middle part of the wingtip's upward motion.

IV. Discussion

A. Defining the wingbeat cycle

Descriptions of all types of animal locomotion partition typical cyclic motions into phases such as stance and swing, propulsion and recovery, and upstroke and downstroke; these descriptors are non arbitrary, but instead have significant meaning in the mechanics, energetics, and even neural control of locomotion^{19, 20}. This kind of framework, although most developed for terrestrial locomotion, has been successfully applied to the flight of birds, insects, and bats^{17, 21-24}. For insects, in which the wing is a single, unjointed structural unit, it is clearly possible to

unambiguously distinguish upstroke and downstroke. And, the most widely accepted notion of gait in vertebrate flight is rooted in the notion that the wingbeat cycle of birds and bats can be subdivided into upstroke and downstroke and that these phases are not only distinct kinematically but also differ fundamentally in aerodynamic force production²⁵. Bird wings possess several joints that can be controlled independently, and bird flight research has successfully conceptualized the wing as a quite rigid, nearly planar structure that moves as a whole or in two to three parts, through space. In these contexts, the notion of a distinct up- vs. downstroke is clearly meaningful, and additional aspects of wing motion, such as rotation about the wing's long axis, can be understood in an upstroke/downstroke framework.

In bats, however, seven to eight independently controllable joints are interposed between the body axis and the wingtip, and the separate fingers of the primitive mammalian hand structure retain significant autonomy. Moreover, wing membrane skin is exceptionally compliant⁶, and bones may bend under aerodynamic loading. Together, these characteristics produce wings with great potential to take on a rich diversity of three-dimensional conformations that can reconfigure dynamically in many complex ways. Here, we find no non-arbitrary way to subdivide the wingbeat into upstroke and downstroke. The upward motion of the humerus at the shoulder joint occurs before those at the wrist, which are, in their turn, before those of the fingers and finally the wingtips. The motions of the third digit, the wing's primary spanwise support, and the fifth digit, the chordwise support, are not synchronous. And, perhaps most importantly, the vertical, side to side, and fore-aft motions of any one wing joint may be nearly completely out of phase.

The terms 'upstroke' and 'downstroke' as used in the animal flight literature are thus rather misleading when applied to bat flight. The vertical motion of the wingtip has no special anatomical or functional significance; we could arbitrarily partition the wingbeat cycle by the vertical motion of the shoulder or wrist, the maximum and minimum values of tip fore-aft motion, etc. When it is useful to think of subdivisions within the wingbeat, we propose that it will be necessary to select criteria based on the nature of the question at hand, and to communicate definitions in a clear, unambiguous manner. This issue may take on particular importance in considering issues such as the potential existence of flight gaits. Answering questions about whether lift is restricted to the downstroke at low speeds requires a clear definition of downstroke that relates in a meaningful way to the hypothesized mechanistic basis for distinct gaits. We believe that it is unlikely that bat flight will be readily analogized to terrestrial locomotion, in which each limb alternates between a propulsive support and a non-propulsive swing phase. Instead, better progress may be made by viewing force production during bat flight as continual but constantly changing in magnitude and orientation.

B. The role of bones

Most researchers believe that the primary mechanical function of the bones of the vertebrate limb is to resist and transmit loads. Bones thereby function as rigid levers about which muscles can exert moments; these moments cause relative rotations and translations of adjacent bones at joints, and the geometry of these relative motions is constrained by the three-dimensional configurations of mating joint surfaces. To date, analyses of bird and bat flight have largely assumed that this view, derived primarily from research on medium to large terrestrial vertebrates, will apply to aerial vertebrates as well. Our results show that wing bones of bats achieve their mechanical functions in a more flexible and dynamic fashion, deforming and recoiling with every wingbeat.

Given that bat wing bones vary in external dimensions, cross-sectional geometry, and mineralization^{4, 26, 27}, and that aerodynamic forces vary throughout any given wingbeat cycle, with velocity, etc., there is a large domain of possible patterns of skeletal deformation during flight. Some particularly robust bones, such as those of the arm and forearm, undergo little or no deformation, while the slender, tapered, and poorly mineralized bones on the wingtips may never reach full resting length during flight. These dynamic patterns of bone bending will be a key determinant of the three-dimensional conformation of the wing at a particular moment in the wingbeat cycle, and the interactions of the mechanics of the wing skeleton with relevant aerodynamics may be a particularly important area of future study.

C. The role of skin

The wings of traditional human-engineered aircraft are rigid and thus characterized by a constant camber. The skin of the bat wing, however, is highly compliant^{5, 6}, and thus can undergo substantial changes in shape and camber when experiencing variable aerodynamic forces. Recent work from our group and others has shown that at biologically relevant Reynolds numbers, even a low degree of compliance can have substantial effects on aerodynamic performance of simple airfoils²⁸⁻³⁰. The work presented here shows that bat wing membrane skin is not fully stretched through the downstroke, nor is it at maximum stretch for all wing regions simultaneously. In fact, although these measurements convey the maximum length between markers achieved during a particular flight, we

do not presently know whether this approaches the maximum stretch the skin can withstand, or even if flight brings the wing skin into the linear region of the J-shaped skin stress-strain relationship⁶. Future work that documents the lengths between skin markers at full extension will help to clarify these issues.

The skin stretching we observe clearly varies with orientation within the plane, or more accurately, the surface, of the wing, and across specific anatomical regions. In particular, the strains along the leading and trailing edges and in the spanwise direction away from the wing edges are greater than those in the chordwise direction. At least two phenomena, not mutually exclusive, may contribute to this pattern. First, the distribution of pressure on the wing surface is complex and dynamically evolving, and could differentially stress the membrane in different directions; even a simple pressurized cylinder will have different wall stresses in the longitudinal and circumferential directions. Second, deformations are constrained by the mechanical characteristics of the material, and bat wing membrane skin is highly anisotropic, with stiffness in the chordwise direction typically more than 100-fold greater than that in the spanwise direction. Hence, even with a uniform pressure distribution, we would expect greater spanwise stretching. Indeed, it is perhaps more remarkable that the spanwise and chordwise skin strains are so similar, given the extreme anisotropy of the membrane.

These results further suggest that the manner in which biologists traditionally measure wing area from bats^{31, 32} may not capture the relevant surface areas for understanding aerodynamics. The wings of bats do not appear to reach a fully extended condition, even when the wingtip is at shoulder height. Future comparative studies will help clarify how wing area may vary for an individual depending on the flight behavior, and how these patterns vary among bat species, and such studies could help define more useful and physically relevant measures of wing size and shape.

Further variations in wing area may arise through passive interactions between aerodynamic forces and mechanical characteristics of wing skin, or may perhaps be actively controlled by the precise positioning of wing bones with respect to one another and/or position of the hindlimbs. Ongoing kinematic analysis not detailed here shows that the hindlimbs of these bats change posture during flight, moving apart from one another during the part of the cycle when the wing mostly moves downward, and coming together during the mid-body (sagittal) plane during the wing's upward motion. Moreover, activity of intrinsic wing musculature has the potential to modulate membrane mechanical characteristics, and to change how the membrane deforms by changing its stiffness and/or anisotropy. Kinematic analysis alone cannot distinguish whether this motion is actively controlled by activity in the muscles surrounding the hip joint or is a passive consequence of tension within the membrane pulling the hindlimbs more forcefully during some parts of the wingbeat cycle. However, this question could be resolved by direct measurement of the electrical activity of hip and thigh musculature during flight using electromyography.

The patterns of skin stretching that we observe here suggest that local curvature in the wing membrane may be highly variable. In a sense, there is potential for camber to vary along the wing's length and throughout the wingbeat cycle. Documenting these patterns and exploring their potential aerodynamic significance remain significant challenges for the future.

V. Conclusion

Bats are distinctive in several important ways that we believe will prove crucial to understanding the mechanistic basis of bat flight. First, the complex, highly multijointed structure of the wing gives rise to considerable kinematic and mechanical complexity that may be relevant for aerodynamics. We propose that one important part of exploring this complexity will be to develop effective methods for describing bat wing motions in flight; although insects and birds are characterized by wingbeat cycles with distinct up- and downstrokes at a particular stroke angle and amplitude, such descriptors may fail to capture relevant aspects of how bats move their wings. Although novel descriptors of flight may complicate comparisons among bats and the other flying animals, we suggest that the complexity of the dynamic spatial configurations of bat wings is critical to the generation of aerodynamic forces, and that oversimplifying the real complexity of bat wing motions will limit our ability to unravel the mechanistic basis of bat flight.

Both kinematic patterns and the relative wing rigidity clearly differ among the three extant lineages of flying animals, and the ways in which bat structure and motion are unique may have important consequences for flight performance. Just as bird flight dynamics are importantly influenced by the interactions of aerodynamic forces and primary feathers, particularly toward wingtips, we must begin to think of the interaction between forces and wing bone bending as important elements in the overall picture of bat flight. Perhaps even more importantly, the skin of bat wings behaves in a highly compliant fashion that is distinct from how wing surfaces of insects and birds operate.

Acknowledgments

All experiments were conducted at the Concord Field Station (CFS) at Harvard University and we express our thanks to the CFS staff, especially Andy Biewener. We are, as always, grateful to Ty Hedrick for his assistance and for the use of his kinematics digitizing code. Bats were provided through the generous support of the Dr. Allyson Walsh and the Lubee Bat Conservancy. This work is supported by the Air Force Office of Scientific Research (AFOSR), monitored by Drs. R. Jeffries and W. Larkin, the Brown University UTRA program, and the NSF-ITR program.

References

1. Voigt, C.C. and Y. Winter, *Energetic cost of hovering flight in nectar-feeding bats (Phyllostomidae : Glossophaginae) and its scaling in moths, birds and bats*. Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology, 1999. **169**(1): p. 38-48.
2. Winter, Y., *Energetic cost of hovering flight in a nectar-feeding bat measured with fast-response respirometry*. Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology, 1998. **168**(6): p. 434-444.
3. Winter, Y. and O. von Helversen, *The energy cost of flight: do small bats fly more cheaply than birds?* Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology, 1998. **168**(2): p. 105-111.
4. Swartz, S.M., K.L. Bishop, and M.-F. Ismael-Aguirre, *Dynamic complexity of wing form in bats: implications for flight performance*, in *Functional and evolutionary ecology of bats*, Z. Akbar, G. McCracken, and T.H. Kunz, Editors. 2005, Oxford University Press: Oxford.
5. Swartz, S.M., *Skin and bones: the mechanical properties of bat wing tissues*, in *Bats: Phylogeny, Morphology, Echolocation, and Conservation Biology*, T.H. Kunz and P.A. Racey, Editors. 1998, Smithsonian Institution Press: Washington, D. C. p. 109-126.
6. Swartz, S.M., et al., *Mechanical properties of bat wing membrane skin*. J. Zool., 1996. **239**: p. 357-378.
7. Crowley, G.V. and L.S. Hall, *Histological observations on the wing of the grey-headed flying fox (Pteropus poliocephalus) (Chiroptera:Pteropodidae)*. Australian Journal of Zoology, 1994. **42**: p. 215-236.
8. Zook, J.M., *Mechanoreceptors of the Chiroptera wing*. Seventh Int Bat Res Conf, Third European Bat Res Symp, 1985.
9. Bullen, R. and N.L. McKenzie, *Bat airframe design: flight performance, stability and control in relation to foraging ecology*. Australian Journal of Zoology, 2001. **49**(3): p. 235-261.
10. Norberg, U.M., *Vertebrate flight: mechanics, physiology, morphology, ecology and evolution*. 1990, Berlin: Springer-Verlag.
11. Rayner, J.V.M., *Vertebrate flapping flight mechanics and aerodynamics and the evolution of flight in bats*, in *Bat flight - Fledermausflug, Biona Report*, W. Nachtigall, Editor. 1986, Gustav Fischer: Stuttgart. p. 27-74.
12. Thomas, S.P. and R.A. Suthers, *The physiology and energetics of bat flight*. J. exp. Biol., 1972. **57**: p. 317-335.
13. Nowak, R.M., ed. *Walker's Mammals of the World. 5th Edition*. 1991, John Hopkins University Press: Baltimore.
14. Hedrick, T.L., B.W. Tobalske, and A.A. Biewener, *Estimates of circulation and gait change based on a three-dimensional kinematic analysis of flight in cockatiels (Nymphicus hollandicus) and ringed turtle doves (Streptopelia risoria)*. Journal of Experimental Biology, 2002. **205**: p. 1389-1409.
15. Hatze, H., *High-precision three-dimensional photogrammetric calibration and object space reconstruction using a modified DLT-approach*. J. Biomechanics, 1988. **21**: p. 533-538.
16. Tobalske, B.W., T.L. Hedrick, and A.A. Biewener, *Wing kinematics of avian flight across speeds*. Journal of Avian Biology, 2003. **34**(2): p. 177-184.
17. Norberg, U.M., *Aerodynamics, kinematics and energetics of horizontal flapping flight in the long-eared bat Plecotus auritus*. Jour. Exper. Biol., 1976. **65**: p. 179-212.
18. Vaughan, T.A., *Flight patterns and aerodynamics*, in *The Biology of Bats*, W.A. Wimsatt, Editor. 1970, Academic Press: New York. p. 195-216.
19. Alexander, R.M., *Principles of Animal Locomotion*. 2003, Princeton: Princeton University Press. 371.
20. Biewener, A.A., *Animal Locomotion*. 2003, Oxford: Oxford University Press. 256.
21. Aldridge, H., *Kinematics and Aerodynamics of the Greater Horseshoe Bat, Rhinolophus-Ferrumequinum, in Horizontal Flight at Various Flight Speeds*. Journal of Experimental Biology, 1986. **126**: p. 479-497.
22. Norberg, U.M., et al., *The cost of hovering and forward flight in a nectar feeding bat, Glossophaga soricina, estimated from aerodynamic theory*. Journal of Experimental Biology, 1993. **182**: p. 207-227.
23. Watts, P., E.J. Mitchell, and S.M. Swartz, *A computational model for estimating the mechanics of horizontal flapping flight in bats: Model description and validation*. Journal of Experimental Biology, 2001. **204**(16): p. 2873-2898.
24. Rayner, J.M.V., G. Jones, and A. Thomas, *Vortex Flow Visualizations Reveal Change in Upstroke Function with Flight Speed in Bats*. Nature, 1986. **321**(6066): p. 162-164.
25. Rayner, J.M.V., G. Jones, and A. Thomas, *Vortex flow visualizations reveal change in upstroke function with flight speed in bats*. Nature, 1986. **321**: p. 162-164.
26. Papadimitriou, H.M., S.M. Swartz, and T.H. Kunz, *Ontogenetic and anatomic variation in mineralization of the wing skeleton of the Mexican free-tailed bat, Tadarida brasiliensis*. J. Zool., 1996. **240**: p. 411-426.

27. Swartz, S.M., *Allometric patterning in the limb skeleton of bats: implications for the mechanics and energetics of powered flight*. J. Morph., 1997. **234**: p. 277-294.
28. Shyy, W., M. Berg, and D. Ljungqvist, *Flapping and flexible wings for biological and micro air vehicles*. Progress in Aerospace Sciences, 1999. **35**(5): p. 455-505.
29. Levin, O. and W. Shyy, *Optimization of a low Reynolds number airfoil with flexible membrane*. Cmes-Computer Modeling in Engineering & Sciences, 2001. **2**(4): p. 523-536.
30. Lian, Y.S., et al., *Membrane wing aerodynamics for micro air vehicles*. Progress in Aerospace Sciences, 2003. **39**(6-7): p. 425-465.
31. Norberg, U.M. and J.M.V. Rayner, *Ecological Morphology and Flight in Bats (Mammalia, Chiroptera) - Wing Adaptations, Flight Performance, Foraging Strategy and Echolocation*. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 1987. **316**(1179): p. 337-419.
32. Pennycuik, C.J., *Bird flight performance: a practical calculation manual*. Vol. 63. 1989, Oxford: Oxford University Press.