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Title: Advances in the study of bat flight: the wing and the wind³

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Advances in the study of bat flight: the wing and the wind

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Abstract

Bats are diverse, speciose, and inhabit most of earth's habitats, aided by powered flapping flight. The many traits that enable flight in these mammals have long attracted popular and research interest, but recent technological and conceptual advances have provided investigators with new kinds of information concerning diverse aspects of flight biology. As a consequence of these new data, our understanding of how bats fly has begun to undergo fundamental changes. Physical and neural science approaches are now beginning to inform understanding of structural architecture of wings. High speed videography is dramatically expanding documentation of how bats fly. Experimental fluid dynamics and innovative physiological techniques profoundly influence how we interpret the ways bats produce aerodynamic forces as they execute distinctive flight behaviors and the mechanisms that underlie flight energetics. Here, we review how recent bat flight research has provided significant new insights into several important aspects of bat flight structure and function. We suggest that information coming from novel approaches offer opportunities to interconnect studies of wing structure, aerodynamics, and physiology more effectively, and to connect flight biology to newly emerging studies of bat evolution and ecology.

Key words: flight, Chiroptera, biomechanics, wings, aerodynamics, energetics, locomotion, morphology

39 ***Introduction***

40 Bats possess a wide range of flight capabilities. They are remarkably maneuverable,
41 possess exceptional load carrying ability, and, depending on the species, can hover, fly
42 exceptionally fast, or modulate flight physiology to migrate (see *e.g.* Norberg 1976a; Stockwell
43 2001; McGuire et al. 2013). In the last twenty years, technological advances have provided
44 investigators with new kinds of data concerning diverse aspects of flight biology, and our
45 understanding of how bats fly has begun to undergo fundamental changes. The advent of high
46 speed videography, biomaterials approaches to understanding structural architecture of wings,
47 adoption of methods from experimental fluid dynamics, and incorporation of sophisticated
48 physiological techniques into studies of flight can profoundly influence how we interpret the
49 ways bats produce aerodynamic forces as they execute distinctive flight behaviors, as well as the
50 mechanisms underlying the supply and control of energy to enable flight over multiple time
51 scales. Here, we review how recent bat flight research has provided significant new insights into
52 several important aspects of bat flight mechanics and physiology. We close with some thoughts
53 on the role that improved understanding of flight has for interpreting bat ecology and evolution,
54 and some speculation concerning future advances in this field of study.

55 Much recent progress in the biology of flight of bats, like that in the biology of flight of
56 other animal groups, has arisen from technological advances in visualizing motion,
57 understanding structural materials, experimental fluid mechanics, and ground-breaking
58 techniques for the study of metabolic physiology. As organismal biology has gained powerful
59 new tools, we are able to generate substantial new data that would have been difficult or
60 impossible to obtain only twenty to forty years ago. Today, we are able to document, often with
61 very high temporal and spatial resolution, diverse aspects of bat flight. It is possible to visualize

the three-dimensional motions of the wing, thereby examining the external surface of the animal using visible light. Analysis of high-resolution 3D kinematics facilitates understanding of how force production is modulated to change speed, execute turns, perform landings, etc. (*e.g.* Iriarte-Diaz and Swartz 2008; Riskin et al. 2010; Wolf et al. 2010; von Busse et al. 2012), and allows exploration of how the wide range of body sizes seen in extant bats influences flight (Riskin et al. 2010). Similarly, as the techniques of experimental fluid dynamics have entered the toolbox of those studying animal flight, we have begun to describe wakes, the aerodynamic ‘footprints’ of flying bats. Through this fluid physics approach, we may better understand how the distinctive morphological features and patterns of motions of bat wings produce flight forces (*e.g.* Hedenström et al. 2007; Hubel et al. 2012; Hedenström and Johansson 2015). We also are now able to build and study mechanical models that capture, in simplified form, key aspects of the complex physical architecture of bat wings (Bahlman et al. 2013; 2014). These models allow researchers unprecedented power to tease apart roles of traits that are tightly interconnected in living animals, often in a manner that prevents effective analysis of function of specific characteristics.

The major advances in bat flight biology over the last few decades are revising our understanding of the mechanics and energetics of flight in bats, and can play a significant role in integrative understanding of bat ecology and evolution. New and emerging insights are helping to shape our ability to interpret the significance of wing shape and flight dynamics, and of the role of flight in shaping the biology of bats at multiple levels of structural organization and over many time scales (Nathan et al. 2008). Our growing appreciation of both the distinctive aspects of bat flight and those features of flight biology shared among bats and other groups of flying animals also contributes to the development of comparative biology of flight.

85 *Bat wing structure and motion*

86 Powered, flapping flight has evolved independently four times during the evolutionary
87 history of animals, and although powered in each instance by muscle, the architecture of wings
88 differs considerably differences among bats, birds, insects and pterosaurs (Figure 1). Primary
89 structural distinctions include major differences in both material composition and anatomy,
90 which lead directly to different challenges for wing shape modulation and control of motion
91 during flight. In insects, relatively stiff wings, composed primarily of chitin, rotate about a single
92 joint that articulates with the thorax, although that joint can be complex and entail multiple
93 degrees of freedom (*e.g.* Balint and Dickinson 2001; Vincent and Wegst 2004; Ninomiya and
94 Yoshizawa 2009). In contrast, the wings of birds and pterosaurs possess multiple synovial joints
95 between bones, adding the potential for dynamic control of changes in wing shape by flight
96 muscles. In bats, as in birds and pterosaurs, the basal form of the terrestrial vertebrate limb has
97 been modified by elongation of some bones, but distinctively, few forelimb bones are reduced or
98 lost, and the bat wing has many more bones and joints than that of birds or pterosaurs (Vaughan
99 1959; Norberg 1972). Bat wings have numerous mobile joints in the arm, forearm, and hand, as
100 was, presumably, the condition for limbs of bat ancestors before flapping flight evolved, and the
101 very large number of independent or semi-independent degrees of freedom of motion in the wing
102 skeleton confers potential for a great deal of three-dimensional wing shape change that can be
103 actively controlled by skeletal muscle (Figure 2). With growing ease and declining cost of high
104 resolution, high-speed kinematics, relationships between anatomy and three-dimensional shape
105 of the wing are becoming progressively clearer.

106 Recent work highlights several aspects of the structure of bat wings that were previously
107 underappreciated. New understanding of the specialized nature of wings has focused primarily

on skin and bones as materials, musculature within the skin, and sensory innervation. To better understand their functional dynamics, a number of studies have considered wing tissues from a solid mechanics perspective. This body of work demonstrates that wing skin and bones are distinctive in comparison to their homologs in non-volant mammals, and the highly derived mechanical characteristics of the constituents of wings strongly influences how wings function during flight.

Skin

Skin plays a key role in bat flight because it comprises the greatest part of the aerodynamic surface of the wing, simultaneously occupying a dominant functional role in thermo- and osmoregulation (Bassett and Studier 1988; Thomson and Speakman 1999; Voigt and Lewanzik 2011). It has long been recognized that the skin of bat wings possesses traits that are typical of most mammals at the tissue level, but also that it is distinctive among vertebrates in several ways that can be associated with flight, such as the possession of especially abundant, diverse and distinctive nerve endings (Gupta 1967; Quay 1970; Holbrook and Odland 1978; Marshall et al. 2015). Wing skin comprises a superficial epidermis and a deeper dermis on the dorsal and ventral surfaces, between which lies a central hypodermis that contains nerves, muscle fibers, blood vessels, and an intricate network of highly organized connective tissue bundles. The dermal and hypodermal layers are greatly reduced compared to the condition in non-volant mammals (Quay 1970; Holbrook and Odland 1978; Sokolov 1982). As a consequence, wing skin, although arising developmentally as a double layer, is significantly thinner than a single skin layer in other mammals of comparable body size, and is thus low in mass despite its large surface area (Swartz 1997; Madej et al. 2013). The fiber bundles of this soft tissue skeleton dominate its structure, and are readily visible even to the naked eye when the

131 wing is illuminated in visible or polarized light (Figure 3). The bundles contain a core of elastin
132 fibers, ensheathed by a network of collagen, which extend in a highly patterned network among
133 the bones of the arm, forearm and hand, and from these bones to the leading and trailing edge of
134 the wing (Holbrook and Odland 1978; J. J. Allen, pers. comm.). It has been proposed that elastin,
135 a highly elastic protein, could contribute to the ability of wing skin to resist puncture and limit
136 propagation of tears, and that elastin fibers may promote furling of wings following flight,
137 although details of the functional role of the wing skin elastin network remain uncertain
138 (Bhangoo and Church 1976; Holbrook and Odland 1978; Crowley and Hall 1994). Bat wing skin
139 is extraordinarily compliant and highly anisotropic, with greatest compliance along the wingspan
140 or proximodistal axis, and stiffness at least an order of magnitude higher parallel to the wing
141 chord (rostrocaudal direction) (Swartz et al. 1996; Cheney et al. 2015). In addition, skin of the
142 plagiopatagium is prominently wrinkled or corrugated, unless the joints of the armwing are
143 extended to a degree not achieved during normal flight conditions. It has long been observed that
144 the architecture of wrinkles and the elastin network appear interrelated (*e.g.* Crowley and Hall
145 1994), and recent work demonstrates that wrinkles arise because elastin bundles places the
146 matrix that surrounds them in compression, directly producing buckling (Figure 4) (Cheney et al.
147 2015). Elastin contributes importantly to mechanical performance in many vertebrate tissues,
148 including arterial walls, intervertebral discs, the walls and valves of the heart, and the sclera of
149 the eyes (Sacks and Chuong 1993; May-Newman and Yin 1995; Sacks and Chuong 1998; Vande
150 Geest et al. 2006; Eilaghi et al. 2010; O'Connell et al. 2012), and typically produces low stiffness
151 at low strains. In these materials, elastin, which is much less stiff than the other elements of
152 complex connective tissues such as collagen fibrils, is usually pre-stretched relative to these
153 components, and at low stresses the relatively compliant elastin is the primary load bearing

component (Woo et al. 1986; Brunon et al. 2010). As tissues elongate under tensile load, the stiffer elements contribute progressively more to load bearing, and the elastic modulus or stiffness of the material increases. Until very recently, however, it has been difficult to ascertain the extent to which this general understanding of soft tissues may apply to the skin of bat wings.

In the wing, elastin fibers provide skin with great compliance at low loads and with its great extensibility along the wingspan, parallel to the orientation of the fibers. The distinctive wrinkled geometry of the skin allows for great stretch at low stiffness; only after the wrinkles in the skin have unfolded does the stiffer matrix surrounding the elastin bundles play a prominent role in load bearing in wing skin (Cheney et al. 2015). The tremendous anisotropy of the skin is independent of the mechanical nature of the skin matrix, and is also driven by the embedded elastin fibers.

Understanding the materials nature of wing skin has substantial significance for interpreting bat wings as structures that interact with surrounding air to generate aerodynamic forces. Because the stiffness of wing skin is so low, the magnitude of aerodynamic forces experienced during flight readily changes the three-dimensional shape of the skin-based airfoil, which thus has far less predetermined 3D form than the wings of birds or insects. Investigations of skin-dominated bat wings, and of similar compliant wings in the human-engineered realm, demonstrate that membrane wings deflect when they experience aerodynamic loading, and passively adopt a lift-enhancing cambered shape (*e.g.* Rojratsirikul et al. 2010; Wu et al. 2011; Curet et al. 2013; Curet et al. 2014). In addition, the wrinkles in wing skin provide what has been termed ‘excess length’ (Rojratsirikul et al. 2010); this can be understood as potential aerodynamic surface that unfurls to varying degrees depending on the tension induced in the membrane by aerodynamic forces. Because wing skin has high compliance and an ability to

dynamically undergo changes in the degree to which it is wrinkled, it can change without substantial input of energy from the animal. When a large fraction of a wing surface is made of skin in which stiffness changes passively with load, with no requirement for tuning by the central nervous system, the mechanical response of the wing to varying flow conditions can be virtually instantaneous, without delays imposed by processing of sensory information and transmission of motor commands and subsequent activation of muscles. Moreover, compliant airfoils delay stall to higher angles of attack relative to those that are rigid and can alleviate the effects of gusts (Hu et al. 2008; Song et al. 2008). These traits likely contribute the bats' ability to maneuver at low forward flight speeds and to tolerate gusty or turbulent conditions (Swartz et al. 2008).

Bones

The great elongation of many of the bones of the forelimb is often considered among the most obvious of specializations of bats for flight (*e.g.* Vaughan 1970c). Because wings possess many elongated bones, typically an advantage for a vertebrate wing with a large aerodynamic surface, the wing skeleton can easily contribute substantial weight to a flying animal. In flying animals, then, multiple competing constraints on limb bone design are particularly striking: elongated bones provide large aerodynamic surfaces, and robust or highly mineralized bones confer high strength to resist large forces, but require that the animal invest body mass in the wings and incur energetic costs in flight. In contrast, reduction in bone mass, which can be achieved by smaller size or reduced mineralization, reduces the energetic cost of flight but may lead to smaller wing surfaces or greater risk of bone failure (Swartz 1997; Swartz and Middleton 2008; Dumont 2010; Riskin et al. 2012). Although the tissue of limb bones is far less evolutionarily labile than bone geometry, and mineralization levels and hence mechanical properties of compact bone tissue of mammalian limb bones varies relatively little (Currey

2002), the bones of bat wings are a distinctive exception to this generalization. During the evolution of bat wings, selection appears to have acted to reduce mass and/or stiffness and/or brittleness in the bones distal to the wrist, the metacarpals and phalanges: mineralization decreases in proximal to distal gradient, with very low mineral in distalmost bones (Papadimitriou et al. 1996; Swartz and Middleton 2008). From a beam mechanics perspective (e.g. Currey and Alexander 1985), the humerus and radius are well suited to resist deformations in bending or torsion, due to both structural geometry and high mineralization (Swartz and Middleton 2008; Dumont 2010). Metacarpals and phalanges, however, are among the least mineralized of mammalian bones, and unlike all other vertebrate wing bones, are not hollow, and thus their structural architecture promotes bending rather than resisting it. Low mineralization of distal wing bones reduces the mass moment of inertia of the wing and can thus also decrease the inertial cost of flight, especially at high wingbeat frequencies. Full understanding, however, of the mechanical and energetic consequences of modulation of bone geometry and material properties in bat wings awaits more in-depth study.

Muscles

Bat wings possess a full complement of skeletal muscle spanning synovial joints between bones of the wing, although the relative sizes and specific attachment sites of individual muscles may differ markedly from the condition in various terrestrial mammals (Vaughan 1970b). In addition, bat wing membrane skin is invested with skeletal muscles that, in addition to passive connective tissue elements, add a layer of complexity to the mechanical behavior of wing tissue and provide a mechanism by which bats can actively control membrane properties for aeromechanical purposes. We have recently begun to appreciate the importance of these unique muscles to bat flight. Among these, relatively large muscle bundles originate on the wing

skeleton and insert into the membrane network; these vary among taxa, but always include the m. occipitopollicalis in the leading edge of the wing membrane, and can include a m. coracocutaneous, and/or a m. humeropatagialis, (Vaughan 1959, 1970a; Strickler 1978; Thewissen and Babcock 1991). Smaller muscles comprise the intrinsic or intramembranous muscles, which originate and insert within the connective tissue of the membrane itself, and do not attach directly to bones. These include the mm. plagiopatagiales, restricted to plagiopatagium or armwing, where they run parallel to digit V (Gupta 1967; Swartz et al. 1996; Cheney et al. 2014a). All bat species closely examined to date possess these muscles, and they vary greatly among bat species in cross-sectional area, length, and number (Ackert 1914; Gupta 1967; Quay 1970), with no obvious correlation between the morphology of these muscles and other aspects of wing structure, flight mode, feeding ecology, etc.

Although it has long been suggested that these muscles play a role in the control of wing shape (*e.g.* Vaughan 1959), until recently there have been no empirical studies of the function of the muscles within the wing membrane skin. This is largely due to the technical challenges of recording activity from very small muscles contained within soft skin wings that flap at large amplitudes, typically at rates over ten wingbeats per second. Indeed, the quite limited cross-sectional area of the muscles, even summed over a complete array of the span of an armwing, could suggest a primarily proprioceptive function, such as has been reported from some other vertebrate muscles (Peck et al. 1984). However, EMG recordings from the plagiopatagiales of *Artibeus jamaicensis* (Leach, 1821) have now demonstrated that the muscles are activated during each wingbeat cycle, with recruitment intensity increasing late in upstroke, remaining elevated, then decreasing late in downstroke during flight at both slow and moderate speeds (Cheney et al. 2014a). Activity began somewhat earlier in the wingbeat cycle at higher speed, which suggests

that activity of intramembranous muscles is likely flight speed dependent. This study also found that multiple muscles activate synchronously, consistent with a model that hypothesized that simultaneous activity in all or nearly all plagiopatagialis muscle fibers may be required to significantly influence tension induced in wing membrane skin by aerodynamic forces (Cheney et al. 2014a). Changes in the stiffness of wing skin or wing camber accompanying muscle activation have yet to be documented but this first demonstration of activation of musculature embedded in the skin of a wing opens the possibility of greater understanding of the muscular modulation of compliant membrane aerodynamics in bats.

Sensory structures

During flight, bats, like insects and birds, traverse many body lengths per second, and rapid integration of multiple streams of sensory information is crucial to their ability, like that of other fliers, to respond effectively to environmental stimuli (Bilo 1991; Schulte and Necker 1998; Fayyazuddin and Dickinson 1999; Frye and Dickinson 2004). Chiropteran flight, like that of all other animal groups, depends strongly on sensory input, and during flight, bats receive auditory, vestibular, visual, olfactory, and magnetosensory information that is informative in determining flight dynamics on various time scales (e.g. Laska 1990; Schnitzler et al. 2003; Horowitz et al. 2004; Ghose and Moss 2006; Wang et al. 2007; Ulanovsky and Moss 2008; Holland et al. 2010; Boonman et al. 2013). Bat taxa vary substantially in their sensory capacities; auditory and visual inputs available to guide flight differ between echolocating and non-echolocating species, in particular, and bat echolocation has been a highly active area of research for more than seventy years. In addition, the somatosensory system of the wing provides information that has potential to directly mediate control of the flight apparatus (Zook and

Fowler 1986), and has recently received increased attention (Zook 2007; Chadha et al. 2011; Sterbing-D'Angelo et al. 2011; Sterbing-D'Angelo and Moss 2014; Marshall et al. 2015).

As characterization of bat wings as organs that serve as sensors as well as propulsors improves, it is perhaps not surprising to find that wings are indeed exquisitely sensitive. Tests of the tactile response of wing skin in big brown bats, *Eptesicus fuscus* (Beauvois, 1796), show very low thresholds on the full extent of the dorsal and ventral surface of the wing, including the tail membrane. Average sensitivity of wing membrane skin proved greater than or equal to that of human finger tips, with particularly high sensitivity in the handwing, the trailing edge region of the armwing, and the thumb (Chadha et al. 2011). In addition, the skin of bat wings is supplied by specialized sensory hairs that project from the wing surfaces, usually a fraction of a millimeter (Zook 2007; Sterbing-D'Angelo et al. 2011). (Figure 5). Modeling suggests that the specific geometry and dimensions of bat wing sensory hairs is well suited to detect changes in boundary layer air velocity profiles (Dickinson 2010). In finely controlled experiments, airflow over the hairs produces activity in the primary somatosensory cortex (S1), also in *Eptesicus fuscus* (Beauvois, 1796), with notable directional sensitivity: the neural response to airflow deflection of each hair was 50 to 100% stronger along its preferred direction than in any other (Sterbing-D'Angelo et al. 2011). Directional dependence appears to be wing region-dependent, with a tendency for increased sensitivity to airflow directed in the proximal direction (from the wingtip toward the body) in the propatagium or leading edge region, heightened sensitivity to flow from the leading toward the trailing edge in the handwing, and flow directed from the trailing edge toward the leading edge or obliquely toward the head in the armwing or plagiopatagium (Sterbing-D'Angelo et al. 2011).

The basis of the expanded functional capacity of wing skin, compared to skin of arms and hands of other mammals, is now under further exploration thanks to contemporary neurophysiological and neuroanatomical approaches. Immunohistochemical studies demonstrate that the bases of wing skin sensory hairs are surrounded by complexes of Merkel or “touch” cells (Marshall et al. 2015). These touch-sensitive cells are now understood to transduce mechanical stimuli from skin to sensory neurons (specifically, slowly adapting type I afferents) (Woo et al. 2015). Merkel cells are typically found in highly sensitive regions of vertebrate skin, such as fingertips, lips, and around follicles of whiskers, although at relatively low densities. Bat wing skin has an unusually high density of Merkel cells (1 to over 3 cells per mm²), juxtaposed to almost half of wing follicles, particularly near the wing’s leading edge, the ends of digits IV and V, around the carpus, and most remarkably, an increase in Merkel cell density of over 100-fold at the interphalangeal joints and distal region of the distal phalanges of digits IV and V (Marshall et al. 2015). Like other mammal skin, bat wing skin also possesses diffuse receptors with free nerve endings, known to function in perception of temperature and pain in humans and rodents; in addition, wing skin contains neurons with distinctive structures somewhat reminiscent of endings observed in some neurons that may be sensitive to high forces (Munger and Ide 1988; Marshall et al. 2015). Like sensory hairs and Merkel cells, the receptors with diffuse endings are not distributed uniformly over the wing surface. Here, receptors are concentrated in the dactylopatagium, in the regions least populated by hair-receptors and Merkel cells (Marshall et al. 2015).

Together, the multiple somatosensory receptors found in the wing comprise a unique suite of structures that have not previously been observed in this combination or density in skin of other vertebrates. It has been proposed that this atypical organization directly enhances motor

control of flight (Chadha et al. 2011; Sterbing-D'Angelo et al. 2011; Sterbing-D'Angelo and Moss 2014; Marshall et al. 2015). Deflection of specialized vibrissal hairs can be informative in many contexts in mammals, (e.g. Brecht et al. 1997; Mitchinson et al. 2011; Diamond and Arabzadeh 2013), but in lineages that adopt aquatic or aerial locomotion, the basal adaptation to detecting sensory hair deflection can be co-opted for flow sensing; vibrissae of both harbor seals and California sea lions function as highly sensitive hydrodynamic receptor systems (Hanken et al. 1997; Miersch et al. 2011). In bat wings, hair sensors may provide information about flow intensity and orientation across the entire wing surface, including the capacity to compare flow conditions on the dorsal and ventral surface of the wing at a given anatomical location. And, although flight is clearly a key driver of wing structure, wings remain multifunctional organs in bats, which continue to carry out many primitive functions of mammalian forelimbs, such as food manipulation, climbing, suspension, and terrestrial propulsion, albeit in a modified manner (e.g. Schutt et al. 1997; Riskin and Fenton 2001; Vondoros and Dumont 2004; Riskin and Hermanson 2005; Riskin and Racey 2010; Zucca et al. 2010). Thus, the distinctive distribution of Merkel cells around distal phalanges may reflect specialization for functions that have been retained in altered form from a period in the evolutionary history of bats during which flight capabilities were more limited. This cell population may contribute inputs concerning interactions of the wing with the environment, particularly direct contact of the wing with surfaces, such as occurs during maternal/pup interactions, climbing, handling large food items, etc. (Marshall et al. 2015).

Future Directions

As a consequence of the research carried out over the past twenty years, studies of the structure of the bat flight apparatus can advance rapidly in coming years. Contemporary

comparative, phylogenetic approaches have rarely been applied to the fascinating variation in muscle, skeletal, skin, sensory, or even overall wing structure of bats, unlike recent evolutionary analyses of the bat feeding apparatus (e.g. Dumont et al. 2012; Dumont et al. 2014). Rigorous, explicitly phylogenetic analyses of the variation among bats in muscle morphology, key aspects of skeletal structure, and/or somatosensory apparatus could shed much light on how wings have evolved within Chiroptera. Moreover, very little research has delved into any structure of wings beyond the wrist. We predict that as this poorly studied area of the wing is investigated, much insight may be gained.

Kinematics of flight

The movements of bat wings during diverse flight behaviors are three-dimensionally complex because of their many joints and compliant skin. Detailed studies of bat flight kinematics employed cine films or stroboscopic multiple-exposure still pictures (Norberg 1976a; 1976b; Aldridge 1986) until the advent of relatively low cost high speed (≥ 250 images per second), high resolution digital imaging began to revolutionize studies of musculoskeletal function (Lauder and Madden 2008). Although videography is intrinsically limited in resolution in comparison to film, newer digital video cameras, some of which possess at least megapixel (1024 x 1024) resolution and can record at well over 2000 Hz, have facilitated kinematic studies by permitting researchers to view motion capture data in real time instead of days after data collection, when exposed film has processed. Videography is generally much less expensive and labor-intensive than high speed cinematography, and it is thus now feasible to carry out kinematic studies with two or three, or even more, cameras. Moreover, digital video can be acquired by post-event triggering of data collection to a continually refreshing digital buffer. It is

thus feasible to wait until the event of interest has occurred, and only then activate data collection. This specific capacity has greatly expanded investigators' ability to quantify behaviors that occur less frequently (Lauder and Madden 2008). The full complexity of the motion of bat wings during even steady forward flight, not to mention more acrobatic maneuvers such as rapid turns or landings, remains a challenge to describe and understand, however. The amplitude of wing movements is large, and the contribution of motion at multiple joints within the wing leads to extremely complicated patterns of folding and thus to anatomical markers being covered or otherwise obscured (Figure 2, Figure 6). Designing flight arenas or eliciting stable, stationary flight within a wind tunnel are daunting challenges in many cases. As a consequence, even with optimal camera positioning, it can remain difficult to follow a given anatomical landmark for multiple entire wingbeat cycles, particularly during turns and maneuvers.

As investigators have delved increasingly into the world of bat wing motions, details of kinematics of bat flight obtained from recent work have, in some cases, confirmed patterns first described in classic studies (e.g. Norberg 1976b; Aldridge 1986). Wingbeat frequency tends to decrease with increasing forward speed in bats of diverse flight ecology, phylogenetic affinity, and body size, and in almost all bats studied, the stroke plane angle, the angle at which the wingtip is swept relative to the horizontal, increases with speed (Norberg and Winter 2006; Riskin et al. 2010; Wolf et al. 2010; Hubel et al. 2012; von Busse et al. 2012). The exception to the observed pattern of stroke plane angle change with speed is *Tadarida brasiliensis* (Geoffroy, 1824), the Brazilian free-tailed bat, in which the stroke plane angle remains high (nearly vertical) at all flight speeds studied (Hubel et al. 2012) (Figure 6). In other studies, it has been possible to explore aspects of wing shape that were more difficult to describe from single camera studies

using cinematography, such as wing profile geometry through the hip and ankle (Cheney et al. 2014b), three dimensional folding and unfolding of the wing in relation to dynamically changing wing inertia (Riskin et al. 2012) or simultaneous measurement of geometric angle of attack and stroke plane angle (Hubel et al. 2012). Investigators have quantified flight speed-dependence of movements of joints in the handwing that control wing surface area (Riskin et al. 2008; Wolf et al. 2010; Hubel et al. 2012; von Busse et al. 2012). Aerodynamic force is a function of wing surface, and lift is proportional to airspeed squared; as one would predict from this fundamental relationship, during the downstroke, the portion of the wingbeat cycle when the majority of lift and thrust are produced, elbow, wrist, and digit movements are altered to produce smaller wing area in several species of fruit- and nectar-feeding bats, and, to a lesser extent, in the insectivorous *T. brasiliensis* (Geoffroy, 1824) as flight speed increases (Hubel et al. 2010; Riskin et al. 2010; Wolf et al. 2010; Hubel et al. 2012; von Busse et al. 2012). Some other aspects of 3D wing form that relate directly to aerodynamic force production can be assessed through kinematic analysis, particularly camber, the curvature of the airfoil or wing surface in the direction of the relative movement of the wing and the airstream, and angle of attack, the inclination of the wing relative to the oncoming air. For a thin compliant wing in an airflow of a particular speed, increasing either camber or angle of attack increases lift, and both are expected to decrease with increasing flight speed. Camber is higher at very low speeds than at moderate or higher speeds in the closely related hovering specialists, *Glossophaga soricina* (Pallas, 1766) and *Leptonycteris yerbabuenae* (Martínez & Villa-R, 1940), but shows no pattern of speed-related change in pteropodid bats or *T. brasiliensis* (Geoffroy, 1824); angle of attack appears to vary with speed in a more consistent manner, decreasing with flight speed in all species assessed to date (Riskin et al. 2010; Wolf et al. 2010; Hubel et al. 2012; von Busse et al. 2012).

Greater temporal and spatial resolution permit new insights into wing function during upstroke, while confirming that the wing is folded to varying degrees as it is moved dorsally and posteriorly, as suggested by previous work (Vaughan 1959; Vaughan 1970a; Norberg 1976a; Norberg 1976b; Riskin et al. 2008; Riskin et al. 2010; Wolf et al. 2010; Riskin et al. 2012; von Busse et al. 2012). At low forward flight speeds, in some species, the tip of the wing can be observed to move backward relative not only to the body, but even to the still air, in what has been termed a “tip-reversal upstroke”, long believed to be a mechanism to provide additional thrust in slow flight (Aldridge 1987). Detailed analysis of the movements of the wings, combined with modeling of the distribution of mass throughout the bat’s wings and body, show that in lesser short-nosed fruit bats, *Cynopterus brachyotis* (Müller, 1838), tip-reversal upstrokes lead to movements of the animal’s center of mass, but not to generation of net thrust (Iriarte-Díaz et al. 2011). This phenomenon arises from the relatively massive nature of bat wings; the wings, if one considers the wing to begin at the humeral head, comprise approximately 20% of body mass, hence large wing motions, in and of themselves, displace the body’s center of mass. Kinematics of the wing during upstroke thus affect flight through their inertial dynamics as well as by aerodynamic effects. Finely resolved kinematics, again coupled to modeling the motion of the distribution of wing mass, indicates that wing folding, compared to outstretched wing posture, reduces inertial power approximately 35% (Riskin et al. 2012). Lastly, bats must maneuver in a precise and acrobatic manner during landing, and once more, employ inertial mechanics to achieve functional performance not observed in other flying animals. Uniquely for bats, the posture attained at the end of virtually all flights requires a major reorientation of the body (from head forward and feet behind but similar in altitude, to ‘head-under-heels’ and wings folded). This is accompanied by a simultaneous need to ascend to reach landing sites at the same time as

the animal reduces speed and therefore incurs declining lift. As a consequence, bats must execute high precision aerial rotations to reorient the body as they slow in preparation for grasping a landing target with the hindlimbs, or hindlimbs and wings (Riskin et al. 2009, Bergou et al. in press). Indeed, some species are able to control landing maneuvers with such a high degree of precision that the magnitude of impact when landing with the hindlimb alone is only approximately 0.8 body weights (Riskin et al. 2009), lower than impact force in human walking (Nilsson and Thorstensson 1989). To accomplish this kind of maneuver is particularly challenging aerodynamically, given very low flight speeds just prior to landing. A combination of kinematic analysis, and inertial plus aerodynamic modeling shows that at least two bat species, *Carollia perspicillata* (L. 1758) and *Cynopterus brachyotis* (Müller, 1838), reposition wing and body segments to accomplish landing maneuvers by inertial dynamics, and during the last two to three wingbeats of landing, aerodynamics has only a minimal effect on flight path or wing movements (Bergou et al. in press).

The capacity to exert fine-scale control of flight may be a critically important aspect of the natural history of flight performance in bats, and the ability to cope with changing body mass, to rapidly accelerate and decelerate, and to effectively alter flight direction may be instrumental to ecological success for many species. These traits must contribute to bats' proficiency in successfully navigating three-dimensionally complex environments during foraging, predator evasion, and in-flight interactions with conspecifics. Although technologies for studying animal flight have matured rapidly during the past twenty years, studies of behaviors other than steady forward flight remains far more challenging than more controlled but less ecologically relevant activities. As a consequence, understanding of turning, accelerating or

ascending flight, and other, more acrobatic maneuvers remains very limited to date (but see (Iriarte-Díaz and Swartz 2008; MacAyeal et al. 2011)).

Future studies

To date, detailed analyses of kinematics that track mass distribution and hence inertial dynamics through the wingbeat cycle have been carried out on only two species, and never on insectivorous bats, in part because of technical challenges. Indeed, most of bat diversity remains to be explored. Data reduction from motion capture has been laborious and time consuming, but methods continue to improve, and recent interest in streamlining the “motion to data” pipeline for animal movement studies will likely lead to substantial decreases in the time required, opening possibilities for broader comparisons. Such enabling advances can liberate investigators to broaden not only the range of taxa to which kinematic analysis can be applied, but the range of flight behaviors. Similarly, as cameras increase in sophistication and become less expensive, it is increasingly feasible to obtain high quality video of many kinds of flight behavior, even in the rugged conditions of the field-laboratory or in completely natural settings. It is now practical, in at least some circumstances, to employ two or more video cameras with moderate temporal and spatial resolution in field settings, and combined with creative design of flight enclosures, we anticipate that the next decades will see a great increase in basic knowledge of how bats fly.

Aerodynamics of Bat Flight

As a lifting surface moves through a fluid and generates fluid dynamic force, it leaves a wake behind it. It is the lift experienced by the airfoil, reflected in the exertion of an equal and opposite force on the air that is directly reflected in the size and structure of the wake. The structure of a wake and the details of the patterns of flow within it therefore reveal much about

fluid dynamic forces, and over the last few decades, experimental fluid dynamicists have made increasingly sophisticated use of this phenomenon to extract information about aerodynamic occurrences from the structure and behavior of wakes (see Adrian 2005; Raffel et al. 2013). The wingtips of fixed wing aircraft create large wakes that persist for long periods of time, but bats, too, generate wakes that embody their aerodynamic force production, although they extend only for meters and persist for seconds to minutes. Vortex theory has proven a powerful approach for understanding the mechanics of lift and thrust generation by bats and other animals, (Rayner 1979; Daniel 1984; Dickinson 1996), and most contemporary research in animal aerodynamics adopts this perspective. The application of approaches from experimental fluid dynamics, especially particle image velocimetry (PIV) is now providing insight into biological as well as many other aerodynamic subjects (Bomphrey 2012). This method quantifies airflow generated, as in the case of bat flight, an aerodynamic surface directs air in a net downward direction in the process of generating lift and the resulting downwash interacts with the surrounding air to create a vortex wake. In PIV, a volume of fluid to be studied is seeded with small particles of some kind, usually a solid that is close to neutrally buoyant, which moves freely with the fluid at it flows (see Adrian 2005; Raffel et al. 2013). In most applications, a sheet of laser light is projected through the fluid in the wake, and illuminates the particles in a manner that allows their motion and hence velocity to be precisely quantified. By knowing particle 2D velocity vector fields with sufficient temporal resolution, it is feasible to accurately reconstruct many aspects of wake structure, and stereoscopic PIV gives the third component of the fluid velocity vector, further enriching the conclusions that can be drawn from analysis of the wake footprint. Adapting this method to bat flight has involved creative problem solving (such as methods to discourage interactions of bats and lasers), but PIV of bat wakes is essentially similar to other

PIV applications. PIV studies have been particularly valuable for understanding bat and bird flight because our ability to predict aerodynamic mechanisms for flapping flight at animal size is poor; bats and birds are too small and fly too slowly for analyses to assume that viscosity plays only a small role, as it does in airplane aerodynamics, but too large and fast for flows to remain laminar and well-organized in virtually all conditions, as for microorganisms (Spedding et al. 2003).

PIV has been applied to only a handful of bat species; although the strengths of the method include its non-invasive nature, potential for high temporal and spatial resolution, and applicability to any flight speed the animal will adopt, the method requires the subject to fly in place for multiple wingbeats in a wind tunnel, and can sample only a limited spatial volume. It is not, for example, presently feasible to apply PIV to bats with wingspans over 40 cm. To date, wakes of four primarily fruit- and nectar-feeding species from two families (Phyllostomidae: *Glossophaga soricina* (Pallas, 1766), *Leptonycteris yerbabuenae* Martínez & Villa-R., 1940, *Carollia perspicillata* (L. 1758); Pteropodidae: *Cynopterus brachyotis* (Müller, 1838)) have been studied, as well as one insectivorous member of the Molossidae (*Tadarida brasiliensis* (Geoffroy, 1824)) (Hedenström et al. 2007; Johansson et al. 2008; Muijres et al. 2008; Hubel et al. 2009; Hubel et al. 2010; Muijres et al. 2011; Hubel et al. 2012; von Busse et al. 2012; von Busse et al. 2014). In all species, the most prominent feature of bat wakes is a pair of wingtip vortices, shed throughout the wingbeat cycle at or near the flapping wingtip (Figure 7). These vortices reflect the majority of lift generation, and are strongest during the latter half of downstroke and the early part of upstroke, but they continue throughout the entire wingbeat, including the upstroke. The proximal wing, near the origin of the armwing at the body wall, sheds a second pair of vortices that rotate in the opposite direction; the persistence of this vortex

pair is species- and flight speed-dependent, appearing transiently in some bats, but forming a prominent wake feature in others (Hedenström et al. 2009; Hubel et al. 2009; Hubel et al. 2010; Muijres et al. 2011; Hubel et al. 2012). As the wing completes the upstroke, approaches the upper reversal point, and begins the downstroke, an additional pair of counter-rotating vortices is shed (the ‘distal vortex pair’ or ‘reverse vortex loop’). This structure is associated with local upwash and a small amount of negative lift (Hedenström et al. 2007; Johansson et al. 2008; Hubel et al. 2009; Hubel et al. 2010; Muijres et al. 2011; Hubel et al. 2012; von Busse et al. 2014), and is even more variable among taxa. Perhaps as a consequence, the functional interpretation of the distal vortex pair is, at present, somewhat ambiguous. These vortices are present at low and high speed in dog-faced fruit bats, and based on the close interrelationship between the appearance of the structure and kinematic details, it has been suggested that it may arise from the structure or motion of the fifth digit (Hubel et al. 2010). In the hovering-specialist glossophagines, *G. soricina* (Pallas, 1766) and *L. yerbabuena* Martínez & Villa-R., 1940, this vortex structure is observed at mid- to higher speeds (Muijres et al. 2011), but in the stiffer-winged molossid *T. brasiliensis* (Geoffroy, 1824), a contrasting pattern is observed: at higher flight speeds, neither the distal vortex pair nor the wing root vortex are observed, and the only wake structure present in the wake is the primary wingtip vortex (Hubel et al. 2012). PIV analyses have also identified instances in which weight support in bats is aided by leading edge vortices or LEVs (Muijres et al. 2008; Muijres et al. 2014), a phenomenon that has recently been observed in small, relatively slowly flying birds (Warrick et al. 2009; Muijres et al. 2012; Wolf et al. 2013), and is long known from insects (e.g. Ellington et al. 1996; Srygley and Thomas 2002; Bomphrey et al. 2005). Because lift is a function of the relative motion of the air and the wing, at low or zero forward speed, generating adequate lift to provide body weight support is

challenging, and kinematics employed at these speeds, with exceptionally high angles of attack, would tend to lead to stall in for typical human-engineered airfoils. In glossophagine bats, however, a stable vortex forms at the thin leading edge of the wing, and this region of consistent low pressure contributes disproportionately to net lift, producing up to 40% of total aerodynamic force during hovering and slow flight (Muijres et al. 2008; Muijres et al. 2014).

Future studies

Although applying PIV to bat flight is technically demanding, there remains much to learn, and thoughtfully constructed studies can provide new insight going forward. To date, species have been selected for study based primarily on ready availability, convenience, suitability to experimental setups, etc. Although wake studies can not match the sample sizes of most exemplary comparative biomechanical analyses (e.g. Irschick and Losos 1998; Anderson et al. 2014), increased species sampling can improve understanding of the relationships among wing form, kinematics, and aerodynamic force production. Bats share aerodynamic traits, but distinct species also differ in details of wake architecture, as they differ in wing morphology and kinematics. For example, among species studied to date, patterns of wake dynamics in *T. brasiliensis* (Geoffroy, 1824) differ notably from those of observed in other bat species, but resemble those of commons swifts (*Apus apus* (L. 1758)), a bird with similar flight ecology, wing form, and wingbeat kinematics (Hubel et al. 2012). Fuller sampling with an eye to phylogeny as well as form and function could facilitate clearer insights into wing design and evolution (see also Bompfrey et al. 2012). Moreover, as PIV methods continue to mature, they increase in flexibility and power, and the latest developments, such as tomographic or volumetric PIV, are beginning to allow fuller reconstruction of 3D wakes by employing additional cameras (at least four) and capturing data at very high rates (one kHz); at present, however, such methods

are only suitable for small volumes of air ($60 \times 80 \times 4 \text{ mm}^3$ width $\times$ height $\times$ depth in a recent application) (Bomphrey et al. 2012, but see Henningsson et al. 2015), appropriate to the study of insects, but not large enough for bat wakes.

Energetic Cost of Bat Flight

Locomotion often comprises the largest part of the energy budget of an animal, particularly for flying animals, and understanding the energetics of flight is a major goal of flight biology. Multiple factors influence the energetic cost of flight. Body mass plays a dominant role in all aspects of metabolism, including bat flight energetics (e.g. Voigt and Winter 1999; Voigt 2000; von Busse et al. 2013), but kinematics, wing shape, and mechanical properties of wing tissues influence aerodynamic power, the energy required aerodynamic force production, as well as the magnitude and orientation of these forces (e.g. Bahlman et al. 2014; von Busse et al. 2014). Muscle efficiency may not remain constant with flight speed for a variety of reasons, particularly changes in muscle physiology with temperature (Nelson et al. 1977; Lancaster et al. 1997; Choi et al. 1998), hence the relationship between metabolic power, the energetic “input” to flight, and aerodynamic power, its “output” may change with velocity. Moreover, in natural ecological context, bats can alter flight behavior in relation to specific patterns of local wind conditions (Sapir et al. 2014). As a consequence, the energetic cost of a particular flight for a given bat may vary tremendously depending on many details. Over the past fifteen years, new techniques and approaches have increased our understanding of the energetics of bat flight many-fold.

The most important methodological innovation influencing recent understanding of energetic cost of flight for bats has been the labeled sodium-bicarbonate technique (reviewed in

588 Hambly and Voigt 2011). In this technique, ^{14}C or ^{13}C -labelled sodium-bicarbonate solution is
589 administered to an animal or human subject, and allowed to come into equilibrium with the body
590 bicarbonate pool. Following equilibration, a constant fraction of expired CO_2 is labeled with the
591 heavy isotope; less than 2% of the label is lost in urinary excretion (Hambly and Voigt 2011).
592 Researchers are able to assess CO_2 production by accurate assessment of the amount of isotope
593 in exhaled breath, and observe the steady, linear decline in isotopic fraction in exhaled breath
594 with time since injection. The slope of the regression of isotopic enrichment (δ) vs. time
595 since injection is directly proportional to basal metabolic rate. If metabolic activity, and hence
596 VCO_2 , increase – as during flight – the rate of decline of isotopic enrichment increases (the
597 regression slope is steeper) in proportion to the increase in rate of metabolism. When elevated
598 metabolic activity ceases – as when a flying animal lands – the rate of isotope decline slows
599 down once more. Although application of the technique requires access to labeled isotopes and
600 instrumentation for assessment of the amount of labeled isotope in exhaled breath, this method is
601 a valuable addition to other approaches for quantifying metabolism because it operates
602 accurately on a much shorter time scale than the doubly-labeled water method (Speakman 1997),
603 and it less cumbersome logistically than respirometry, requiring neither masks nor tubing
604 connecting the subject to a gas analyzer during the activity of interest. From the perspective of
605 flight biology, the sodium-bicarbonate method is revolutionary, allowing measurement of
606 metabolic rates for flights lasting as little as a minute, by animals unencumbered by any
607 instrumentation, wiring, or cables.

608 This approach has been applied to several important questions in bat flight energetics.
609 Comparison of relatively short flights by the neotropical fruit bat *Carollia perspicillata* (L. 1758)
610 in daylight versus dark shows that metabolic costs of flight rise more than 15% in sunny

conditions, while core body temperature changes only 2°C, an approximately 5% change (Voigt and Lewanzik 2011). These findings are the first robust, direct evidence supporting a long-held hypothesis that bats are constrained to primarily nocturnal activity because wing membrane skin, with its lack of insulation and dark pigmentation, would absorb high levels of visible light during daylight, leading to harmful or lethal rise in body temperature, particularly at lower latitudes (Thomas and Suthers 1972; Speakman and Hays 1992; Speakman et al. 1994). The ^{13}C -labelled sodium-bicarbonate was also employed to explore the energetic dimension of the notable avoidance of flight by bats during rain (Belwood and Fullard 1984). It has been proposed that rain can impair bats' sensory performance, particularly for echolocating species (Griffin 1971), but it is also possible that bats fly less frequently during rain for other reasons. This method of assessing flight metabolism demonstrates, using *Carollia sowelli* (Baker, Solari & Hoffmann, 2002) as the study species, that flight metabolism nearly doubles when bats fly with wet wings and fur, with or without rain (Voigt et al. 2011). The amount of water added to the bats' body mass by the wetting treatments was far too small to account for the substantial increase in energetic cost of flight, but evidence obtained to date cannot distinguish between elevated metabolism due to increased thermoregulatory costs because of an evaporative cooling effect, altered aerodynamics due to changes in wing membrane skin dynamics when wet or related effects, or both. However, this finding demonstrates that flight energetics should be considered in analysis of bat foraging strategies in rain: foraging in wet conditions will result in net energetic benefit only when potential energetic gain can offset the elevated cost of flight in wet conditions (Voigt et al. 2011).

Efforts have also been made to employ the sodium-bicarbonate method to better understand the relative importance of wing shape, phylogenetic affinity, and flight mode in

determining the metabolic cost of flight in insectivorous, narrow winged (high aspect ratio) molossids (Gervais, 1856) in comparison to sympatric, broader-winged (lower aspect ratio) frugivorous phyllostomids (*Carollia sowelli* Baker, Solari & Hoffmann, 2002) (Voigt and Holderied 2012). This research illustrates how challenging it can be to interpret comparative data from a limited number of taxa. The metabolic cost of flight is significantly higher in *M. currentium* (Thomas, 1901) than predicted from body mass alone, but overlaps with that of similar-sized *C. sowelli* (Baker, Solari & Hoffmann, 2002. Flight cost in *M. sinaloae* (Allen, 1906 is higher, but not significantly, than predicted from body size. The higher rate of flight metabolism in the molossids than in the broad-winged phyllostomid at flight speeds of 5 to 7 m/s is consistent with the idea that this speed range could represent slow flight for the narrow-winged species, and that the incremental metabolic cost of slow flight with a high fraction of maneuvers could be high enough for these bats to make energy cost a significant driver of dietary preference (Voigt and Holderied 2012). In this view, molossids tend to forage in open space, flying rapidly along relatively linear trajectories, and maneuvering relatively little, because the energetic penalty for maneuvering flight at rather low speed, which would be required to obtain food in cluttered environments, may be too costly for species with high aspect ratio wings. However, there are multiple factors at play. The species sample size is small, and the two narrow-winged species are close relatives whose similarities in metabolism may arise from shared evolutionary history and not specifically from wing form. Maneuvering flights in large flight cages may consist of many bouts of deceleration and acceleration in addition to turning, and acceleration could well be more energetically costly than steady forward flight. If the comparisons are made among flights that differ in proportion of accelerating vs. steady flight, interpretation of results will be more challenging.

Some additional insight into energetics of steady forward flight has also come from application of the sodium-bicarbonate method. Over a moderate range of flight speeds, five of seven *C. perspicillata* (L. 1758) showed a U-shaped flight power curve; flight was more metabolically expensive at very low speeds, where wing movements must generate aerodynamic power, and at higher flight speeds where wing and body surfaces incur relatively high drag penalties, than at intermediate speeds (von Busse et al. 2013). However, not all individuals showed identical patterns of speed-dependent energetics, and in some bats, metabolic cost of flight changed little from 1 to $>7 \text{ ms}^{-2}$. Bringing physiological and aerodynamic energetics together, these measurements of the changing expenditure of metabolic energy of with flight speed have recently been compared with the speed-dependent modulation of aerodynamic power, measured using PIV from the energy shed into the wake (von Busse et al. 2014). Unlike metabolic power, at least in *C. perspicillata* (L. 1758), aerodynamic power remains consistent with increasing flight speed. As a consequence, mechanical efficiency, η , changes with speed, from a low of less than 6% to a high of nearly 10%, overlapping with estimates for hovering glossophagine bats and hummingbirds, and falling at the low end of the range for flying animals (Voigt and Winter 1999).

Conclusion

Our view of the bat flight apparatus and its remarkable capabilities has expanded tremendously over the last twenty years. Multiple kinds of factors have contributed to shifts in our knowledge. The arsenal of techniques available to students of animal structure and function has vastly increased. Today, it is possible to probe the mechanical nature of the tissues that comprise wings on many scales, or to employ immunofluorescence to trace neurons of the

somatosensory system. We can capture the full intricacy of flight trajectories of bats and the movements of their wings with multi-camera high speed videography, and leverage experimental fluid dynamics to make wake footprints visible and amenable to quantitative analysis. The continually growing toolbox of animal physiology is bringing direct assessment of flight energetics within reach not only in the lab but also in natural settings. But advancing understanding of bat flight, like that of flight in other groups of animals, has also arisen from integration of across disciplines. Concepts, as well as methods, in this field are shaped by diverse disciplines in the physical and mathematical sciences, including solid mechanics, fluid dynamics, material science, and applied mathematics. On the biological side as well, a broad range of subfields impact flight studies, including comparative morphology, biomechanics, and physiology, but also neuroscience, ecology, evolutionary biology, paleontology, phylogenetics, and others.

Interdisciplinary approaches have helped to highlight promising subjects for ongoing study. We have greater understanding of morphological and mechanical aspects of specializations of skin, muscle, bone in the wing, as well as the wing's unique complement of sensors, today than at any previous time. We suggest that it will be possible to explore how these multiple elements are integrated to function as coordinated units during flight. With better knowledge of the wing's somatosensory system, it will be possible to look to identify those aspects of flight conditions transmitted to the musculoskeletal effectors of the wing as cues for specific flight responses. Students of locomotion continue to discover that elastic mechanisms play crucial roles in a broad diversity of animals; do some wing tendons act to amplify or attenuate power, or to conserve energy (Patek et al. 2011; Roberts and Azizi 2011)? The combination of recent advances in technology and conceptual developments will also facilitate

moving flight biology from the lab into the field (Swartz et al. 2008; O'Mara et al. 2014; Sapir et al. 2014; Cvikel et al. 2015) as researchers adopt more sophisticated techniques for tracking flight behavior of bats in their natural environments, and are able to relate specific flight behaviors to environmental conditions, behavioral cues from predators or conspecifics, etc. We can also expect an ongoing expansion of studies relating to flight physiology, broadly construed, into several relevant arenas. For example, motivated by the impressive but as yet rather poorly understood physiological capacities of migratory bats, recent work is already beginning to unravel the nature of bat migration and its underlying mechanistic basis (Fraser et al. 2012; McGuire and Boyle 2013). Finally, no clear consensus concerning the evolutionary origins and diversification of bat flight has emerged. We propose that greater knowledge of phylogenetic patterns in morphological, physiological, aerodynamic, and behavioral aspects of bat flight can inform knowledge of the evolutionary history of bat flight.

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1113 Figure Captions

1114

1115 Figure 1. Aerodynamic surface of the wing in light shading in (A) insects, (B) birds, (C)
1116 pterosaurs and (D) bats; for vertebrates, the internal bony skeleton is depicted in dark shading.
1117 Circles indicate joints that may potentially be under active neuromuscular control. The numerous
1118 wing joints in bats can aid in dynamic control of wing motion three-dimensional geometry.

1119 Figure 2. Because bat wings possess many joints served by skeletal muscle, complemented by
1120 compliant skin, bats use neural control of muscles to manipulate three-dimensional shape of
1121 wings. (a) *Dermanura phaeotis* (Miller, 1902), Andersen's fruit-eating bat. Photograph by Neal
1122 Boyle; (b) *Rousettus aegyptiacus* (Geoffroy, 1810), Egyptian fruit bat. Photograph by Brock
1123 Fenton.

1124 Figure 3. Large connective tissue bundles run through the skin of the bat wing membrane, and
1125 dominate its material behavior. Each bundle is composed primarily of elastin, a soft and resilient
1126 protein, with a thin layer of much stiffer collagen on the perimeter. The skin is additionally
1127 invested with network of muscles that attach to the elastin-collagen network. Top panel:
1128 armwing, or plagiopatagium, of *Megaderma spasma* (L. 1758), the lesser false vampire bat,
1129 imaged in cross-polarized light, showing major groups of intramembranous muscles and elastin
1130 fibers. Bottom panel: Histological section of wing membrane skin of *Carollia perspicillata* (L.
1131 1758), Seba's short-tailed fruit bat, with plagiopatagialis muscle running vertically to insert into
1132 perpendicularly-oriented elastin bundle. Elastin (purple) is surrounded by a thin layer of collagen
1133 (pink) that is continuous with the collagenous perimysium surrounding the cells of the
1134 plagiopatagiales.

1135 Figure 4. Bat skin is characterized by prominent wrinkles, induced by mechanical buckling of the
1136 soft skin by the elastin network. In a ventral view of the elbow region of a Jamaican fruit bat,
1137 *Artibeus jamaicensis* (Leach, 1821), (a) relaxed wing membrane is wrinkled, with wrinkles
1138 running between the elastin fibres that extend from the elbow joint, at the left of the image,
1139 toward the fifth finger, at the right of the image ($\triangleleft$). When elastin fibers are removed by
1140 dissection, (b), wing skin becomes smooth and unwrinkled. Where elastin fibres are not dissected
1141 away (region around asterisk), wrinkles remain. (Adapted from Cheney et al. 2015). el, elbow;
1142 v, digit V. Scale bar, 5 mm.

1143 Figure 5. (a) Supports for sensory hairs are readily visible and widely distributed on the wing
1144 membrane in *Noctilio leporinus* (L. 1758), the greater bulldog bat, both on the elastin-collagen
1145 bundles (O) and overlying muscles, especially the plagiopatagiales ($\triangle$). r, radius; v, digit V.
1146 Scale bar: 20 mm. Photography by Kamiel Spoekstra, courtesy of Dina Dechman. (b) In a cross-
1147 section through wing membrane skin in *Artibeus lituratus* (Olfers, 1818), the great fruit eating
1148 bat, a sensory hair, in a follicle and surrounded by a sebaceous gland, immediately overlies an
1149 elastin bundle running longitudinally (horizontally); just to its left, an elastin bundle can be
1150 observed running perpendicular to the plane of section (cut in cross-section); modified
1151 Verhoeff's elastin & Van Gieson's stains. exs, elastin bundle in cross section; els, elastin bundle
1152 in longitudinal section; bw, blood vessel; sg, sebaceous gland; sgd, sebaceous gland duct; h,
1153 wing hair. Scale bar:
1154 100 μ m.

1155 Figure 6. Kinematics of horizontal flight in (a) *Tadarida brasiliensis* (Geoffroy, 1824), a fast-
1156 flying aerial insectivore with narrow, high aspect ratio wings and (b) *Cynopterus brachyotis*
1157 (Müller, 1838), a highly maneuverable fruit-eater with lower aspect ratio wings. Images from

1158 high-speed (500 fps) video trace the wingbeat cycle from beginning of downstroke to end of
1159 upstroke.

1160 Figure 7. The characteristic features of bat wakes are illustrated in an image created from particle
1161 image velocimetry (PIV) data are “stacked” to create a pseudo-volumetric wake from *Carollia*
1162 *perspicillata* (L. 1758) flying at 6 m s^{-1} ; the wingtip vortex is shed from the path of the wingtips
1163 during the wingbeat cycle, wing root vortices from near the junction of the wings and body, and
1164 reversed vortex pairs, shed at the end up upstroke, dorsal and lateral to the root vortices. end us:
1165 end of upstroke; beg ds: beginning of the downstroke; mid ds: mid down-stroke; end ds: end of
1166 downstroke; beg us: beginning of upstroke; mid us: mid upstroke. Vortex surfaces are colored
1167 local x vorticity or vortex strength. From von Busse et al., 2014.

Figure 1. Aerodynamic surface of the wing in light shading in (A) insects, (B) birds, (C) pterosaurs and (D) bats; for vertebrates, the internal bony skeleton is depicted in dark shading. Circles indicate joints that may potentially be under active neuromuscular control. The numerous wing joints in bats can aid in dynamic control of wing motion three-dimensional geometry.
70x139mm (300 x 300 DPI)

Figure 2. Because bat wings possess many joints served by skeletal muscle, complemented by compliant skin, bats use neural control of muscles to manipulate three-dimensional shape of wings. (a) *Dermanura phaeotis*, Andersen's fruit-eating bat. Photograph by Neal Boyle; (b) *Rousettus aegyptiacus*, Egyptian fruit bat. Photograph by Brock Fenton.
180x70mm (300 x 300 DPI)

Figure 3. Large connective tissue bundles run through the skin of the bat wing membrane, and dominate its material behavior. Each bundle is composed primarily of elastin, a soft and resilient protein, with a thin layer of much stiffer collagen on the perimeter. The skin is additionally invested with network of muscles that attach to the elastin-collagen network. Top panel: armwing, or plagiopatagium, of *Megaderma spasma*, the lesser false vampire bat, imaged in cross-polarized light, showing major groups of intramembranous muscles and elastin fibers. Bottom panel: Histological section of wing membrane skin of *Carollia perspicillata*, Seba's short-tailed fruit bat, with plagiopatagialis muscle running vertically to insert into perpendicularly-oriented elastin bundle. Elastin (purple) is surrounded by a thin layer of collagen (pink) that is continuous with the collagenous perimysium surrounding the cells of the plagiopatagiales.

85x190mm (300 x 300 DPI)

Figure 4. Bat skin is characterized by prominent wrinkles, induced by mechanical buckling of the soft skin by the elastin network. In a ventral view of the elbow region of a Jamaican fruit bat, *Artibeus jamaicensis*, (a) relaxed wing membrane is wrinkled, with wrinkles running between the elastin fibres that extend from the elbow joint, at the left of the image, toward the fifth finger, at the right of the image (ϖ). When elastin fibers are removed by dissection, (b), wing skin becomes smooth and unwrinkled. Where elastin fibres are not dissected away (region around asterisk), wrinkles remain. (Adapted from Cheney et al. 2015). el, elbow; v, digit V. Scale bar, 5 mm
86x65mm (300 x 300 DPI)

Figure 5. (a) Supports for sensory hairs are readily visible and widely distributed on the wing membrane in *Noctilio leporinus*, the greater bulldog bat, both on the elastin-collagen bundles (r) and overlying muscles, especially the plagiopatagiales (p). r, radius; v, digit V. Scale bar: 20 mm. Photography by Kamiel Spoekstra, courtesy of Dina Dechman. (b) In a cross-section through wing membrane skin in *Artibeus lituratus*, the great fruit eating bat, a sensory hair, in a follicle and surrounded by a sebaceous gland, immediately overlies an elastin bundle running longitudinally (horizontally); just to its left, an elastin bundle can be observed running perpendicular to the plane of section (cut in cross-section); modified Verhoeff's elastin & Van Gieson's stains. exs, elastin bundle in cross section; els, elastin bundle in longitudinal section; bw, blood vessel; sg, sebaceous gland; sgd, sebaceous gland duct; h, wing hair. Scale bar: 100 μ m.

86x113mm (300 x 300 DPI)

Figure 6. Kinematics of horizontal flight in (a) *Tadarida brasiliensis*, a fast-flying aerial insectivore with narrow, high aspect ratio wings and (b) *Cynopterus brachyotis*, a highly maneuverable fruit-eater with lower aspect ratio wings. Images from high-speed (500 fps) video trace the wingbeat cycle from beginning of downstroke to end of upstroke.
182x89mm (300 x 300 DPI)

Figure 7. The characteristic features of bat wakes are illustrated in an image created from particle image velocimetry (PIV) data are "stacked" to create a pseudo-volumetric wake from *Carollia perspicillata* flying at 6m s⁻¹; the wingtip vortex is shed from the path of the wingtips during the wingbeat cycle, wing root vortices from near the junction of the wings and body, and reversed vortex pairs, shed at the end up upstroke, dorsal and lateral to the root vortices. end us: end of upstroke; beg ds: beginning of the downstroke; mid ds: mid down-stroke; end ds: end of downstroke; beg us: beginning of upstroke; mid us: mid upstroke. Vortex surfaces are colored local x vorticity or vortex strength. From von Busse et al., 2014. 498x361mm (108 x 108 DPI)