

Aeromechanics in aeroecology: flight biology in the aerosphere

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Synopsis The physical environment of the aerosphere is both complex and dynamic, and poses many challenges to the locomotor systems of the three extant evolutionary lineages of flying animals. Many features of the aerosphere, operating over spatial and temporal scales of many orders of magnitude, have the potential to be important influences on animal flight, and much as marine ecologists have studied the relationship between physical oceanography and swimming locomotion, a subfield of aeroecology can focus attention on the ways the biology of flight is influenced by these characteristics. Airflows are altered and modulated by motion over and around natural and human-engineered structures, and both vortical flow structures and turbulence are introduced to the aerial environment by technologies such as aircraft and wind farms. Diverse aspects of the biology of flight may be better understood with reference to an aeroecological approach, particularly the mechanics and energetics of flight, the sensing of aerial flows, and the motor control of flight. Moreover, not only does the abiotic world influence the aerospheric conditions in which animals fly, but flying animals also, in turn, change the flow environment in their immediate vicinity, which can include the air through which other animals fly, particularly when animals fly in groups. Flight biologists can offer considerable insight into the ecology of the aerial world, and an aeroecological approach holds great promise for stimulating and enriching the study of the biology of flight.

Introduction

Ecology is a large and thriving field by any standards, with thousands of professional practitioners, dozens of scientific societies and journals, and subject matter taught within biological curricula at every level. Within contemporary ecology, specialists join together around numerous foci, such as particular disciplinary approaches (i.e., chemical ecology, behavioral ecology, and ecological economics), groups of organisms (insect ecology and microbial ecology), or climates (tropical ecology and arctic ecology). Marine and terrestrial ecology are both longstanding, distinct subfields, with their own scientific organizations, textbooks, and conferences but, to date, no such subject has coalesced around the aerial realm, despite decades of behavioral, physiological, and even ecological study by biologists, as well as diverse meteorological, climatic, and engineering studies by others. One explanation may be that biological and physical research in the complex, dynamic conditions of the thin shell of the troposphere closest to the earth presents considerable technical and logistical challenges, but advances over the last 20 years in instrumentation and technology

are making this world truly accessible to study. This symposium marks a pioneering effort to bring together biologists engaged in research on organisms that move through and inhabit the aerosphere, and to share perspectives and research progress with each other and with atmospheric scientists. In the process, the symposium will promote the advancement of an interdisciplinary field of aeroecology. Here, we explore how the crystallization of aeroecology as a field might influence and be influenced by the biology of flight.

One goal of explicit definition and recognition of a field of aeroecology is to facilitate a more integrative view of the ways different kinds of animals locomote through the aerosphere. How might such an integrative perspective change our understanding of the biology of flight? We propose that several new kinds of insights might be gained. First, students of the biology of flight may be motivated to better identify physiological, morphological, and behavioral similarities, and differences among the many lineages of flying and gliding taxa. Second, more attention will be brought to bear upon the relationships among animals moving through aerial environments

From the symposium "Aeroecology: Probing and Modeling the Aerosphere—The Next Frontier" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 2–6, 2008, San Antonio, Texas.

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Integrative and Comparative Biology, volume 48, number 1, pp. 85–98
doi:10.1093/icb/icn054

Advanced Access publication June 18, 2008

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and the variable physical nature of these environments, with attention to the full diversity of relevant temporal and spatial scales. Third, the role of flight performance in the broader ecology of flying species and their communities, studied in real or realistic aerial environments, will begin to be clarified. In this article, we explore how a field of aeroecology might benefit from studies of the mechanics, aerodynamics, and energetics of diverse kinds of animal flight, and from knowledge of the structural and physiological bases of flight performance. We discuss how an aeroecological perspective will stimulate researchers to define and address novel issues, and both consider ways that students of animal flight might adapt research programs to increase the relevance of their studies to the evolving field of aeroecology, and discuss the kinds of aeroecological investigations and approaches that can influence research on the physiology and mechanics of flight. Microbes, parts of plants, particularly pollen and seeds, and small invertebrates also move through the aerosphere. Following Isard and Gage (2001), we distinguish these movements of organisms through the air from the flapping flight of insects, birds, and bats, and from controlled gliding flight. These two classes of movement differ fundamentally in the degree to which the organism is able to actively determine and control its trajectories. In part due to active promotion of this research area by AFAR, the Alliance for Aerobiological Research, passive movement of biological materials and organisms in the atmosphere has received much attention (Pedgley 1982; Cox 1987; Rainey 1989; Lighthart and Mohr 1994; Madden and Hughes 1995; Isard and Gage 2001). Our discussion here will focus primarily on animals, although some issues raised here will ultimately prove vital to a full understanding of atmospheric biological movement other than animal flight.

Understanding the ecology of the aerial realm requires understanding the physiology of getting to and from, as well as living in, the aerosphere. Physiological topics of particular importance in this context include thermoregulation, water balance, and respiration, as well as many others, and certainly must include diverse aspects of gliding and flying behavior. Numerous studies over many decades have documented the morphological and physiological specializations of muscle, bone, and connective tissue associated with the flight apparatus of animals (e.g., Vaughan 1970a, 1970b; Pennycuik 1972, 1975; Norberg 1990; Unwin and Bakhurina 1994; Dudley 2000a; Alexander 2002), and a somewhat smaller number have focused on neural control (Dial et al. 1987; Goslow et al. 1990; Hermanson et al.

1993; Dickinson et al. 1998; Warrick and Dial 1998; Marder and Bucher 2001; Taylor 2001), energetics (Thomas and Suthers, 1972; Casey, 1981; Carpenter 1986; Hedenstrom et al. 2001; Bishop et al. 2002), respiration (Suarez et al. 1999; Harrison and Roberts 2000; Maina 2000, 2006; Duncan and Byrne 2005), and circulation (Bevan and Butler 1992; MathieuCostello et al. 1996; Wasserthal, 1996; Pass 2000). This body of literature provides the starting points for determining how the physical demands of aerial locomotion have influenced the evolution of organismal structure and function. Recent studies of the mechanistic basis of flight, however, have advanced and, in some cases, substantially altered our understanding of how animals generate aerodynamic forces (Dudley 2000b; Birch and Dickinson 2001; Taylor 2001; Ramamurti and Sandberg 2002; Dial 2003; Sane 2003; Spedding et al. 2003; Hedrick et al. 2004; Altshuler et al. 2005; Lehmann et al. 2005; Swartz et al. 2005; Hedenström et al. 2007; Tobalske 2007) and an expanding field of aeroecology may demand new examinations of the diversity of morphology and physiology associated with flight that incorporates these new insights. An integrative aeroecological view of animal flight also requires analysis of the specializations of flight from an explicitly phylogenetic perspective. By more rigorously accounting for evolutionary history, including both origins and diversification of gliding and flying behaviors, it will be possible for the first time to distinguish the roles of the ecology of the aerosphere, physical constraints, and evolutionary history in shaping the machinery of animal flight.

Aeromechanics research in aeroecology

Where might efforts to analyze the characteristics associated with the evolution of specialization for flight best focus? We suggest that the clearest pictures will likely emerge from efforts that begin with consideration of the ways that different extant groups traverse and exploit the aerosphere. Documenting the kinematics of flight with considerable temporal and spatial resolution has become far easier in the era of digital videography, and kinematics might serve as a key starting point, given its direct connections to both behavior and mechanics. Because the technical capacity to readily document and describe flight kinematics is relatively new, there is surprisingly little information of this kind available at the present. Some recent efforts have focused on a handful of bird, bat, and insect species carrying out a limited range of flight behaviors (Swartz et al. 2005; Bomphrey 2006; Tian 2006; Gundry and

Ellington 2007; Hedrick and Biewener 2007; Ribak and Swallow 2007; Tobalske et al. 2007; Berg and Biewener 2008; Wang et al. 2008). It is likely that many flying and gliding animals modulate their locomotion depending on context. However, it is likely that we have only scratched the surface of the diversity of kinematic patterns employed in flight, and it is clear that kinematic patterns are altered to produce specific flight behaviors such as maneuvering, accelerating, take-off, and landing. Even less information is available concerning more directly ecological contexts; for example, there is considerable room to explore differences between commuting flight, primarily geared toward moving in a direct fashion from one point in space to another, and more specialized flight behaviors, including foraging and feeding, escape, communication, and courtship. We have reached a time when it is possible to begin to document the diverse kinematic repertoires that underlie the motions of animals in the aerosphere, and this information can be employed to better understand the specializations of the musculoskeletal, neural, respiratory, and circulatory systems that enable and support flight. Without much better information concerning the range and frequency of the many possible kinds of flight behavior in a diversity of taxa, we face the risk of focusing lab-based mechanistic study on aspects of flight that are not among the most important in the natural ecology of flying animals.

Field-based studies provide clear advantages in terms of ecological relevance and realism, but pose greater technical challenges, and may require sacrifices in temporal and spatial resolution, while laboratory-based research is much better able to “escape flatland,” that is, to document the true three-dimensionality of the wing motions and flight trajectories during diverse behaviors (Tytell et al. 2008). We propose that although approaches that combine field and laboratory research are challenging, they have great potential to advance flight studies in meaningful ways. For example, detailed field observations can document the range of wingbeat frequencies and forward velocities used by migrating birds; combining this information with higher-resolution laboratory-based studies of the mechanics, aerodynamics, and energetics of bird flight at the observed frequencies and velocities can supplement field observations with information of direct relevance to understanding the ecology of migration.

For greatest benefit to a field of aeroecology, studies of the kinematics of flight behaviors should be coupled with research that focuses on the mechanistic basis for the generation and modulation of

flight forces, and to detailed analyses of the energetics of flight. Kinematics alone rarely, if ever, tells the whole story of how an animal employs the flight apparatus to carry out flight behavior. It is the interactions of animals’ bodies and wings with the fluid surroundings that give rise to aerodynamic forces, and flight energetics are dictated both by the metabolic costs of powering the motions of the flight apparatus and the energetic cost of generating lift and thrust.

If we are to attempt to move beyond relatively simple idealizations of flying animals and flight behavior to understand realistically the 3D flight of 3D animals in the parts of the aerosphere that they use and traverse, it will also be necessary to begin to incorporate questions concerning the features of the structure and motion of the aerosphere itself into our research programs. To date, virtually all experimental studies of animal flight begin with the creation of flow environments that are completely still or extremely orderly, such as laminar, steady, and uniform-velocity flows. These choices do not imply that the biologists and engineers studying animal flight in carefully controlled conditions believe that these conditions mimic the real world, but instead derive from the notion that minimizing flow disturbances allows investigators to carry out experiments in the simplest manner possible and to obtain results that can be interpreted clearly. Such research clearly recognizes that still air or steady laminar flows represent simplifications of the nature of the real aerosphere in which flying animals live, but assumes, explicitly or implicitly, that conclusions based on highly controlled lab conditions can be extrapolated directly to more realistic settings. However, we rarely ask much about the nature of this kind of simplification, and a key first step in moving toward greater realism and studies of animal flight is to begin to better understand the real diversity of flow conditions that flying animals encounter.

Micrometeorology and animal flight

The nature of the human sensory system leaves us with poor intuition regarding environmental flows. Typically, we are aware of only extreme wind conditions, and we are most attuned to the state of the flows around us when the air is “seeded” with visible entities, such as rain, snow, or even falling leaves. Clearly, there is considerable variation in typical mean airspeeds across habitats, with seasons, and with daily weather conditions. This variation is present in both mean airflow, defined in the meteorological literature as air velocity averaged over at least

1 h and 1 km, and in the deviations from those mean velocities, the unsteadiness and turbulence in the airstream.

An important starting point for any discussion of interactions between flying and gliding animals and the natural physical characteristics of the fluid that surrounds them is attention to issues of scale. The relative importance and precise nature of the effects of ambient flow conditions on animal fliers is highly scale dependent. Flying animals occur over a considerable range of body sizes, from the smallest flying insects, with wingspans under half a millimeter and body mass <0.05 mg, to the largest living flier, the wandering albatross, *Diomedea exulans*, a 12 kg bird with a 3–4 m wingspan; if one includes extinct animals, the largest known pterosaur, *Quetzalcoatlus*, possessed a wingspan of nearly 40 m. The speeds at which animals move through the aerosphere range from hovering, with net forward speed of zero, through the world record-holding flapping flight of the white-throated needletail, *Hirundapus caudacutus*, at almost 40 m/s, and the even faster stoops of the peregrine falcon, *Falco peregrinus*, clocked to 130 m/s. As a consequence, the Reynolds numbers of flying animals range from approximately one to a few million, six orders of magnitude. At the lowest end of this range, viscous forces are of such importance that a flying animal will be affected very little by changes in ambient flow; at this size range, small disturbances in the flow more than a wing length away will be damped out and will have little impact on the flight of the animal (Miller and Peskin 2004, 2005). Similarly, any wake generated by flight on this scale will extend only a small distance beyond the animal, and will persist for a very short time (Purcell 1977). On the other hand, the aerodynamic forces generated by the animal's flapping flight will play a relatively small role in determining its overall trajectory through the aerosphere in comparison to passive advection by ambient flow (Koehl 1996).

At the other end of the scale, very large or fast-flying birds, and perhaps bats, with Reynolds numbers into the hundreds of thousands to low millions, will themselves create considerable unsteadiness and turbulence as they fly, and will leave trailing wakes that extend behind them for many times their own wingspan and that can persist for the duration of tens of wingbeats. The mechanisms of generating aerodynamic forces relevant at the scales of bats, large insects, and birds can be readily influenced by a diversity of environmental and atmospheric phenomena on spatial scales both substantially smaller and larger than the animal's body or wings, and that can act over temporal scales ranging from fractions of

Table 1 Aerial and atmospheric phenomena produce vortical structures at sizes ranging over many orders of magnitude.

Spatial scale	Temporal scale	Flow phenomena
0.001 m	Fractions of second	Smallest turbulent eddies
0.001–0.1 m	Seconds	Vortices generated by flying insects Vortices generated behind leaves
1–10 m	Minutes	Dust whorls on the street dust devils
100–1000 m	Hours	Vortex rings in volcanic eruptions Convection clouds
100–2000 km	Days	Hurricanes High- and low-pressure systems
2000–5000 km	Weeks months	Ocean circulations General circulation of the atmosphere

Left column gives relevant size scale, right column some representative vortical structures. Adapted from Lugt 1983; Benniston 1998.

second through days to weeks. At a variety of relevant scales, the transfer of momentum, energy, and mass implicit in the motions of the air involved will produce varying levels of turbulent flow. In many cases, these complex air movements create eddies and vortices, coherent fluid structures with rotational character, whose dynamic behavior is complex and only partly predictable (Table 1). Flow phenomena on a wide range of size scales, from nearly microscopic to global, are potentially important for animal flight. Moreover, interactions among these processes and scales can be complex and nonlinear. Because of nonlinearities, small-scale processes, for example, lead to fluid features that interact in ways that can grow and propagate, and ultimately initiate much larger-scale patterns (Nathan et al. 2007). Hence, not only do flying animals themselves generate flows of a wide range of scale and dynamic complexity, flying animals will interact with the even larger range of atmospheric flows, leading to a vast spectrum of flow interactions of possible biological importance.

Taking advantage of the gains made in the field of micrometeorology over the past decade (Westbrook and Isard 1999; Aylor et al. 2003; Turnipseed et al. 2003; Cescatti and Marcolli 2004; Finnigan and Belcher 2004; Ross and Vosper 2005; Shamoun-Baranes et al. 2006; Yang et al. 2006; Reynolds et al. 2007), we can begin to identify some of the topographic features of animal habitats that have the potential to produce characteristic structure in the overlying aerosphere through which animals fly. For example, the nature of the aerosphere over relatively flat, smooth landscapes differs from that over landscapes of rougher texture, such as those that include



Fig. 1 Although flow structures in the air are usually difficult to visualize, they can be large, powerful, and long lasting, and have tremendous potential to influence the mechanics and aerodynamics of animal flight. **(A)** The air flow from the wing of this agricultural plane is made visible by a technique that uses colored smoke rising from the ground. The swirl at the wingtip traces the aircraft's wake vortex, which exerts a powerful influence on the flow field behind the plane. Photograph courtesy of NASA. **(B)** Wingtip vortices persist for many hundreds of times the distance from the leading to trailing edges, the chord length, of an airfoil, and can be perturbed by local air conditions such as small scale turbulence, as illustrated in this photograph of a landing Boeing 757 at London's Gatwick Airport. Photograph used with permission from AirTeamImages.com.

natural features like hills, mountains, valleys, and forests (Isard and Gage 2001). In addition, however, human habitation has introduced many novel environmental features that influence the structure of flow over the landscape at many scales. Even rural habitation influences the overlying aerosphere, and the large-scale topography of large urban areas has even greater effects (Isard and Gage 2001).

Human-engineered aircraft and their wakes modify the air near their flight paths in profound ways, depending, in part, on the size and speed of the aircraft (Fig. 1). The strongest vortices are generated by heavy aircraft at slow speeds, such as those generated during takeoff and landing, and flows within these vortices can exceed 70 m/s in rotational velocity and be detectable at distances of as much as 30 km for the largest jetliners (Spalart 1998; NASA 2007). These vortices can be powerful enough to cause structural damage to some airplanes, or to even flip small aircraft upside down. Significant vorticity is common 10–20 km downstream from large aircraft, and can persist for several minutes.

The scope of the human-built environment only continues to increase; large buildings, silos, etc. generate vortical structures in their wakes. Wind farms, not only influence the aerosphere via their very topography and presence in the landscape, but also significantly alter the flows in the aerosphere during operation. Wakes of wind turbines typically persist for 10–15 rotor diameters downstream of the structure, depending on ambient wind speed and turbulence, and the number and spatial placement

of turbines in an array. Modern wind turbines may have rotor disks as large as 70 m, and their influence can therefore be felt at a distance of over a kilometer from the blades. Indeed, wind turbines impose significant risks of injury and death to flying vertebrates (Barrios and Rodriguez 2004; Cryan and Brown 2007; Smallwood 2007; Arnett et al. 2008), and it is possible that disruption of airflow in the vicinity of rotating blades may contribute to bird and bat morbidity and mortality. All of these influences on flow structure are further modulated by changes in weather. Daily variation in temperature has an effect on the structure of the aerosphere, as do seasonality, periodic storms, and the nature of local prevailing winds. In all, a multitude of factors combine to create the conditions through which animals fly, and the diverse aerospheric conditions they encounter differ fundamentally from those presently taken as the standard in both experimental and computational studies of animal flight.

Flight specialization and the dynamic structure of the aerosphere

In what ways can the conditions of flow encountered by flying animals in nature influence the biology of flight? We propose that there are at least four major aspects of flight biology that can serve as research foci in the next decade, and in which aerospheric conditions are likely to figure in critical ways: (1) mechanics and aerodynamics of flight; (2) energetics of flight; (3) sensory detection of status

of the aerosphere; and (4) motor control of flight in relation to aerospheric conditions. This list is by no means exhaustive, but represents, we believe, aspects of flight biology in which an aeroecological perspective may have a profound influence, and in which investment of research effort is likely to produce novel insights, even over a relatively short time.

Aerospheric flow and flight mechanics

All flying animals generate lift and thrust through interactions between parts of the body, typically wings, and the surrounding air. Just as marine ecology has begun to probe the ways in which swimming animals are influenced by the flows they encounter (Cozar and Echevarria 2005; Coombs et al. 2007; Dabiri et al. 2007; Koehl et al. 2007; Plew et al. 2007; Strickler and Balazsi 2007), aeroecology should attend to the interactions between animal flight and flow conditions of the aerosphere. Indeed, an elegant alternative to complex, intricate descriptions of highly unsteady motions of extremely complicated, dynamically changing anatomical configurations is the description of an animal's flight as the motions of its musculoskeletal structures in a manner that creates a specific pattern of wake vorticity (Spedding 2003). This approach has greatly improved our understanding of the mechanistic basis of the flight of insects, birds, and bats (Spedding 1986; Spedding et al. 2003; Warrick et al. 2005; Hedenstrom et al. 2006; Tian 2006). The interactions among vortex structures can, however, be quite complex (Cantwell and Coles 1983; Boratav et al. 1992; Saffman 1992; Zabusky et al. 1995), and all studies of animal flight from the perspective of wake dynamics have operated from the perspective that the air surrounding the animal is either still or experiencing steady, uniform, laminar flow. However, it is by no means clear that a particular kinematic motion that gives rise to a given vortex structure in a clean flow will generate similar aerodynamic forces in a perturbed or highly unsteady flow.

To what extent do the interactions between fliers and environmental conditions influence animal flight mechanics? Are animals able to modulate kinematics to accommodate variable atmospheric conditions? The answers to these questions are not likely to be simple. Issues of scale are central; phenomena important for very small insects are not likely to apply to large raptors. To date, the best, and for some issues, the only information about the interplay between conditions in the aerosphere and flight mechanics comes from studies of flight during migratory behaviors (Liechti 2006; Thorup et al. 2006; Wikelski et al. 2006; Akesson and Hedenstrom 2007;

Budick et al. 2007). For example, large birds, such as geese and ducks, which are capable of powerful active flight, exhibit small-scale changes in their direction of flight during migratory flight that probably result from turbulent fluctuations in wind direction (Desholm 2003).

Although gaining insight into these processes will be technically demanding, and likely require a carefully crafted combination of field, laboratory, and computational studies, it is ultimately crucial for those who seek to understand animal flight to document the nature of the flows encountered during all kinds of animal flight, and to analyze the ways they interact with the animals' flight apparatus.

Aerosphere flow and the energetics of flight

Aerospheric characteristics have the potential to be a dominant factor in the energetics of an animal's flight by influencing its flight speed, the distance it travels, and the need for and cost of thermal regulation (Voigt and Winter 1999; Harrison and Roberts 2000; Suarez 2000; Ward et al. 2004; Lehmann and Heymann 2006). Moreover, at a fundamental level, the metabolic power required for flight depends in part on aerodynamic power, which, in turn, depends on flight speed for a given structure of any given form that generates aerodynamic forces in flow (Rayner 2001; Spedding and Pennycuik 2001; Tobalske et al. 2003). We can therefore predict that realistic estimates of the metabolic cost of locomotion for flying animals will depend in part on the kinds of flow regimes that they encounter. Laboratory-based estimates may either underestimate or overestimate natural costs of flight, depending on wind direction, speed, and level of turbulence. At present, we know so little about the ways flying animals cope with turbulence that it is not yet possible to make quantitative predictions relating energetics to the intensity of turbulence. However, studies of interactions between the vortical structures shed by swimming fish and environmental vortices encountered during swimming demonstrate the clear possibility that locomotor energetics can be substantially influenced by fluid dynamics (Liao et al. 2003a, 2003b; Liao 2004).

Studies of migratory flight, primarily in birds, but also in insects, do provide some glimpses of the dependence of flight energetics on the conditions of ambient flow (Butler et al. 2000; Weimerskirch et al. 2000; Gannes 2001; Bowlin et al. 2005; Altshuler and Dudley 2006). For example, the nature of the winds encountered along migration routes can influence flight speed and the precise paths followed by birds, and these variations in flight path can increase the

total time of migration by >10% (Desholm 2003). Effects of this kind will clearly change the energetic cost of a migratory flight, but because metabolic cost of flight per unit distance depends on flight speed, quite detailed information on flight metabolism is required for realistic energetic accounting (Bowlín et al. 2005).

Aerospheric flow and sensing

In locomotor modes that rely on the interaction of flexible propulsors with the surrounding fluid instead of exerting force via rigid limbs encountering rigid substrates, the physical nature of the surrounding air or water, including variation in mean speed of flow and degree and nature of turbulence, become critically important for producing and controlling locomotor force. The characteristics of the aerosphere, moreover, are only rarely discernable by the visual system, a primary determinant of motor output in vertebrates and arthropods. Marine animals employ many sensory modalities to discern relevant aspects of the flows through which they swim (Domenici et al. 2007; Liao 2007). Flying animals use the visual system to provide information regarding body posture and movement through the air, as epitomized by the ability of both insects and vertebrates to sense optic flow, the apparent motion of images within the visual field as an animal's body translates or rotates in the environment. However, vision primarily provides information regarding displacement of the individual with respect to the terrestrial, solid surroundings, and not in relation to the motions of the fluid medium itself, because air motion is only detectable by the visual system indirectly through its effects on solid objects. Aspects of ambient flows can, nonetheless, be sensed by at least some flying animals in a manner that allows them to modulate flight behavior effectively. For example, adult frigate-birds searching for food high in the boundary layer are able to detect and employ small-scale turbulent updrafts to achieve altitude with minimal expenditure of energy (Weimerskirch et al. 2003). This ability may vary with age or experience; in strong crosswinds, migrating adult raptors are able to compensate three times more effectively than can juveniles (Thorup et al. 2003).

To date, relatively little is known about the abilities of flying animals to sense surrounding fields of flow during flight. Insects possess a diverse array of mechanosensory structures, some of which, particularly hair sensillae and antennae, are clearly capable of sensing flows near the body and wings (French 1988). Although feathers are not themselves sensory

organs, mechanoreceptors on, or near, follicles of feathers appear to be able to provide information about airflow over the wing (Brown and Fedde 1993). The surfaces of the wings of bats possess sensory hairs whose morphology and distribution suggests a role in sensing the characteristics of airflow (Zook and Fowler 1986; Zook 2007). Even the basic neurophysiology of these sensors is poorly understood, but the comparative biology of the sensing of flow by animals, although as yet in its infancy, can play an important role in delimiting the kinds of aerospheric conditions a particular group of animals will be able to detect and to which they respond.

Diverse sensory modalities can be useful to animals navigating through a fluid environment, in addition to the specific ability to sense the magnitude and/or direction of local flow conditions. Some species of flying and swimming animals are able to sense magnetic fields, infrasound, or gradients of temperature or odorants (Murlis et al. 1992; Walcott 1996; Thies et al. 1998; Wiltshko and Wiltshko 1999; Luschi et al. 2001; Srygley 2001; Budick and Dickinson 2006; Koehl 2006; Srygley et al. 2006; Hodgkison et al. 2007; Lohmann 2007).

Aerospheric flow and motor control in flight

After receiving sensory input regarding the physical state of the air through which it flies, a flying animal is presented with numerous complex challenges vis-à-vis control of the locomotor systems and its interactions with the environment. Clearly, navigation through a fully 3D environment is more demanding than moving across even the most complex terrestrial landscape.

Consideration of the inherent challenges of three-dimensional navigation also calls attention to the ways in which the mechanical properties of both animals and their physical environments can provide dynamic adaptation of animals to environmental conditions. For example, the variation in air density associated with altitudinal gradients influences the amount of lift generated for a particular animal moving its wings in a particular kinematic pattern (Chai and Dudley 1995; Altshuler et al. 2004; Roberts et al. 2004; Altshuler 2006). At least as importantly, portions of the musculoskeletal constituents of the flight apparatus store elastic strain energy during parts of the wingbeat cycle and return at least a portion of that energy to the animal later in the cycle, contributing significantly to the energetic budget for flight (Jensen and Weis-Fogh 1962). These kinds of mechanisms, sometimes termed "preflexes" (Dickinson et al. 2000), have far-reaching

consequences. Not only do they affect mechanics and energetics, they also provide potential control mechanisms. A mechanical system that responds to perturbations in a graded fashion, in which the magnitude of the mechanical response is related to the magnitude of the perturbation, is stable (Dickinson et al. 2000). In some cases, this kind of structural design possesses self-correcting capabilities that arise from the ability to resist forces imposed by the external environment or arising within the locomotor system itself. In addition to passive self-stabilizing systems, which are likely to be far more common in flying animals than we yet realize, birds, bats, and insects can possess intrinsically adaptive morphological characteristics that serve as part of the control system for flight. Recent work has identified instances in which the architecture of the neuromuscular and/or musculoskeletal systems of swimming animals confers stability or control of posture or movement in aquatic environments (Biewener and Gillis 1999; Gillis and Biewener 2000; Nauwelaerts et al. 2001; Satterlie and Norekian 2001; Nauwelaerts and Aerts 2002, 2003; Pirtle and Satterlie 2004; Szymik and Satterlie 2005; Nishikawa et al. 2007). Although efforts to uncover similar mechanisms in flying animals are just beginning, this is a promising avenue of investigation. For example, at high angles of attack, the underwing covert feathers of steppe eagles, *Aquila nipalensis*, deflect automatically, behaving as a high-lift device to mediate the loss of lift at wing configurations that would otherwise produce stall; similarly, the early stages of deployment of the alula are initiated passively (Carruthers et al. 2007; Taylor et al. 2008). Other aeroelastic wing structures in the distinctive wings of diverse birds, bats, and insects may enhance flight performance by improving aerodynamic control when triggered by specific conditions of flow, particularly during unsteady maneuvers.

Clearly, many parts of flying animals do not possess self-stabilizing or self-modulating characteristics, or animals are able to actively override the passive mechanical behavior of these systems. Without stabilization, less force or energy are required to move an animal off course, a real advantage for enhancing maneuverability by facilitating steering maneuvers. Effects of scale play an important role in this regard, given that relative translational and rotational inertia increase allometrically with body size (Dudley 2002). The trade-offs between stability and maneuverability in the control of flight may be among the most important characteristics of the flight system in determining ecology within the aerosphere, influencing how animals forage, escape predators, mate, and seek and find shelter.

Do flying animals influence their own flight behavior and the mechanics of flight?

As we have discussed in this article, a variety of physical structures and wind conditions clearly influence the flow conditions of flying animals. Although marine biologists have long recognized that a swimming individual modifies the dynamics of the surrounding fluid (Weihs 1973; Webb 1993; Fish 1999; Liao 2007), much less attention has been paid to the idea that flying animals also influence the surrounding air, creating structured wakes as they generate aerodynamic forces. Although the wakes created by flying animals are much smaller and weaker than those of human-engineered aircraft, they are present nonetheless, and have the potential to influence the mechanics of flight. Indeed, flying insects are known to employ controlled wake–wake and wing–wake interactions as important mechanisms in flight dynamics (Sane and Dickinson 2001; Srygley and Thomas 2002; Birch and Dickinson 2003; Lehmann et al. 2005; Bomphrey et al. 2006). In addition to interactions of an individual flying animal with its own wakes, it is possible for animals flying in groups to interact with one another's wakes, and some have proposed that migrating birds and insects, in particular, can benefit energetically from their interactions with the wakes of conspecifics flying with them (Kutsch et al. 1994; Hummel 1995; Rayner 1995). These hypotheses are difficult or impossible to rigorously test, given the technical challenges of both assessing energetics 'on the wing' and of visualizing flow structures created by flying animals. As aeroecology matures, we propose that it will be possible to combine laboratory studies, such as controlled studies of the interactions of flying animals with models that generate known wakes, or studies of multiple flying animals in wind tunnels, with fieldwork documenting variation in interanimal spacing and its relationship to the energetics of flight, to gain new insight into these questions.

Computational methods and aeroecology

As a result of the rapid advances in computational sciences over the past several decades, we expect numerical methods to play a particularly prominent role in many aspects of aeroecology that involve the biomechanics of animal flight. Computational methods are now routinely used for the design and analysis of aircraft (Drela 1989, 1999; Anderson 1995; Katz and Plotkin 2001), and biologists will be increasingly able to take advantage of methods developed for the

aviation industry. Although significant challenges exist, computational methods permit controlled studies of the fundamental flow phenomena of the aerosphere. High-fidelity simulations of the flow can act as virtual wind tunnels, providing opportunities to visualize flow physics. This approach is particularly powerful in providing insight into the interactions among parts of the animal flight apparatus and flow components. One advantage of computational methods rests in the ability to prescribe specific aerosphere conditions that may not be easily found or reproduced in nature, in order to gain a deeper understanding of the flow-fields of interest in the aerosphere. There is presently a large diversity of computational methods for studying fluid flows and solid–fluid interactions, ranging from the most detailed, finest-scaled methods requiring many hours of supercomputing power to resolve, to those that make simplifying assumptions but can be solved in mere minutes on a desktop. Each simulation method is suitable for specific conditions, but careful selection of the appropriate level of physical fidelity can lead simulation approaches that represent reasonable compromises between speed of solution and precision of computation for phenomena at particular physical scales. However, considerable challenges arise with attempts to simulate the flight of animals in general, and in realistic models of the aerosphere in particular, hence novel approaches will be necessary to attain the potential of these methodologies.

In low Reynolds number flight regimes (Reynolds number ~ 1 – 1000), the computational simulation of flow phenomena has slightly lower complexity due to the moderate ratio of inertial and viscous effects. In this Reynolds number regime, the flow remains laminar and boundary layers are sufficiently thick. At higher Reynolds number flight regimes (Reynolds number $\sim 10\,000$ – $1\,000\,000$) inertial effects dominate. Viscous effects are restricted to thin boundary layers, which possess complex laminar-turbulence transition characteristics making computational representations of these flows significantly more challenging. Due to the dominance of inertial effects in higher Reynolds number flows, linearization of the governing equations, by considering the flow to be inviscid, results in computational models which have a fraction of the cost of high fidelity simulations, and at the same time predict lift and induced drag, the inertial components of the flow, with high accuracy (Drela 1989, 1999; Anderson 1995; Hall and Hall 1996; Hall et al. 1998; Katz and Plotkin 2001; Willis et al. 2007). In this way, reduced-fidelity models can provide insight into interactions in the aerosphere at a

reasonable computational cost and are likely to play as significant a role as full fidelity simulations.

Future directions

The flow phenomena that are important for animal flight clearly encompass a broad spectrum of spatial and temporal scales, and influence diverse aspects of the biology of flight. An important early step in the development of aeroecology must be identification of the scale of the most relevant phenomena, and characterization of the aerosphere with respect to these important temporally-varying characteristics. This will help to “map” the physical medium through which flying animals move, which will, in turn, help to focus laboratory-based studies so that they can be carried out in biologically realistic, ecologically relevant contexts. The scales at which critical phenomena occur will likely prove to vary among the three living lineages of flying animals, among specific clades within these lineages, and with body size and flight characteristics, across phylogenetic boundaries. Documentation of flow in the habitats and microenvironments in which animals fly is no trivial task, but with the development of aeroecology, it is a timely one.

An aeroecological perspective also calls on those who study flight to broaden their attention to a fuller range of flight behaviors. Ornithologists have taken the lead here, and those interested in the ecology of flying insects and bats can benefit from their example, looking to better characterize the flight repertoires of diverse fliers, and to relate flight behaviors to their associated ecological contexts. Horizontal flight at constant speed is relative simple, and clearly it is necessary to understand a great deal about simple conditions to be able to move on to more complex phenomena, but we emphasize the value of beginning to think about realistic contexts and flight behaviors, even in early stages of flight study. The technologies available for studying animal flight in more naturalistic settings are improving rapidly (see Hristov and Kunz, 2008), and will continue to open new opportunities for understanding the mechanics, energetics, and control of flight. Two good examples come from recent advances in quantitative measurement of flow velocities as applied to biology.

Investigators of fish have begun to employ scanning particle image velocimetry (PIV) systems to describe flow fields around multiple (three to ten) swimming fish simultaneously, and will be able to use these results to test a variety of hypotheses concerning the hydrodynamic benefits of schooling behaviors (G.V. Lauder and W. Hanke,

personal communication). Other researchers have begun development of self-contained velocimetry suitable for field measurement (Katija and Dabiri 2008). Similar advances in techniques suitable for aerial environments may prove even more challenging than their extension underwater, but clearly technological innovations will ultimately follow the demands of researchers and a heightened interest in, and focus on, the aeromechanics of natural flight can help motivate new technologies.

Acknowledgments

We thank Linda Walters and the SICB Program Committee, and the Divisions of Vertebrate Morphology, Comparative Biomechanics, and Ecology and Evolution for sponsoring the "Symposium on Aeroecology," and Johnny Evers and Willard Larkin for their encouragement and support. This article has been improved by contributions from Hal Heatwole and two anonymous reviewers. We especially thank Tom Kunz for challenging us to imagine what a field of aeroecology might be like, and for bringing diverse approaches and perspectives together to promote this endeavor. We wish to thank the National Science Foundation and the Air Force Office of Scientific Research for their ongoing support of our research. Funding to pay the Open Access publication charges for this article was provided by the Air Force Office of Scientific Research.

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