Aeroecology: probing and modeling the aerosphere

Thomas H. Kunz,[1,*] Sidney A. Gauthreaux Jr,[†] Nickolay I. Hristov,[*,#] Jason W. Horn,[*] Gareth Jones,[‡] Elisabeth K. V. Kalko,[§] Ronald P. Larkin,[¶] Gary F. McCracken,[‖] Sharon M. Swartz,[#] Robert B. Srygley,[**] Robert Dudley,[††] John K. Westbrook[‡‡] and Martin Wikelski[§§]

[*]Center for Ecology and Conservation Biology, Department of Biology, Boston University, Boston, MA 02215, USA; [†]Department of Biological Sciences, Clemson University, Clemson, SC 29634, USA; [‡]School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK; [§]Department of Experimental Ecology, University of Ulm, Albert-Einstein-Allee 11, 89069, Ulm, Germany; [¶]Illinois Natural History Survey, 607 East Peabody Drive, Champaign, IL 61820, USA; [‖]Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996-1610, USA; [#]Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912, USA; [**]USDA-ARS, 1500 N. Central Avenue, Sidney, MT 59270, USA; [††]Department of Integrative Biology, University of California, Berkeley, CA 94720, USA; [‡‡]USDA-ARS, 2771 F&B Road, College Station, TX 77845, USA and [§§]Department of Ecology and Evolutionary Biology, Princeton University, Princeton NJ 08544, USA

Synopsis Aeroecology is a discipline that embraces and integrates the domains of atmospheric science, ecology, earth science, geography, computer science, computational biology, and engineering. The unifying concept that underlies this emerging discipline is its focus on the planetary boundary layer, or aerosphere, and the myriad of organisms that, in large part, depend upon this environment for their existence. The aerosphere influences both daily and seasonal movements of organisms, and its effects have both short- and long-term consequences for species that use this environment. The biotic interactions and physical conditions in the aerosphere represent important selection pressures that influence traits such as size and shape of organisms, which in turn facilitate both passive and active displacements. The aerosphere also influences the evolution of behavioral, sensory, metabolic, and respiratory functions of organisms in a myriad of ways. In contrast to organisms that depend strictly on terrestrial or aquatic existence, those that routinely use the aerosphere are almost immediately influenced by changing atmospheric conditions (e.g., winds, air density, precipitation, air temperature), sunlight, polarized light, moon light, and geomagnetic and gravitational forces. The aerosphere has direct and indirect effects on organisms, which often are more strongly influenced than those that spend significant amounts of time on land or in water. Future advances in aeroecology will be made when research conducted by biologists is more fully integrated across temporal and spatial scales in concert with advances made by atmospheric scientists and mathematical modelers. Ultimately, understanding how organisms such as arthropods, birds, and bats aloft are influenced by a dynamic aerosphere will be of importance for assessing, and maintaining ecosystem health, human health, and biodiversity.

Introduction

The biosphere has been traditionally viewed as being composed of the lithosphere, hydrosphere and atmosphere, each of which interact dynamically with the other. In an ecological context, the Earth's lower atmosphere or troposphere has long been considered an important functional component of the biosphere through the exchange of nutrients, water, and gases in the form of local, regional, and global climate variation and biogeochemical cycles. However, to our knowledge, the aerosphere—the relatively thin substratum of the troposphere closest to the Earth's surface that supports life–has rarely been considered beyond studies of meteorological conditions and functional ecosystem relationships, such as nutrient cycling and gas exchanges in the atmosphere (Oke 1987, Sorbjan 1989, National Research Council 1997). Until quite recently, ecologists with interests in organisms that depend on the aerosphere as a fluid medium for movement (e.g., dispersal, foraging, and migration), a source of food and nutrients, and ever-changing physical conditions (e.g., weather and air pollution), have worked more or less independently of atmospheric scientists. Research goals of organismal biologists who study airborne organisms have mostly focused on the behavior, ecology, and evolution of specific taxonomic groups (e.g., microbes, arthropods,

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, at San Antonio, Texas.
[1]E-mail: kunz@bu.edu
Integrative and Comparative Biology, volume 48, number 1, pp. 1–11
doi:10.1093/icb/icn037
Advanced Access publication May 21, 2008

birds, and bats), or specific physiological or behavioral functions such as thermoregulation, water balance, respiration, or flight. In contrast, research goals of atmospheric scientists and engineers have largely emphasized how severe weather and climate can affect human well-being, and thus have focused on the efficacy and efficiency of human developments, including building construction (e.g., skyscrapers), modes of transportation (e.g., sail boats, aircraft, spacecraft), design and installation of communication infrastructure (e.g., tall towers and transmission lines), and power generation (e.g., utility and residential scale wind energy facilities). Achieving these two sets of goals in large measure depends upon understanding the dynamic properties of wind and associated meteorological conditions at local, regional, or global scales, and understanding how these conditions affect movements of organisms.

To our knowledge, no organism spends its entire life in the aerosphere, yet many species spend a significant portion of their lives in this environment (Wilcove 2008). Species that spend significant amounts of time in terrestrial and aquatic ecosystems also may depend on the aerosphere for daily and seasonal locomotion, and sometimes for courtship and mating. Important selection pressures accordingly influence the biology of flight, including the size and shape of structures that comprise the flight apparatus, and sensory modalities that provide information about the aerosphere, and the active and passive systems that control locomotor movements.

On both temporal and spatial scales, the aerosphere is more variable and dynamic than the lithosphere or hydrosphere. Relative to strictly terrestrial and aquatic organisms, species that regularly occupy the aerosphere are almost immediately influenced by changing atmospheric conditions (e.g., pressure, wind, air density, precipitation, temperature), and other physical factors (e.g., solar radiation, polarized light, moon light, and geomagnetic and gravitational forces). Organisms that use the aerosphere for foraging, dispersal, and seasonal movements have evolved unique body forms and shapes, but also specific physiological traits (e.g., increased production of hemoglobin at high altitudes), thermoregulatory and respiratory responses, and the like, in response to different selection pressures. The aerosphere and the organisms that compose it not only are strongly influenced by predictable atmospheric conditions, but also by a myriad of anthropogenic conditions (e.g., lighted towns and cities, skyscrapers, air pollution, aircraft, radio and television towers, and more recently from the proliferation of wind turbines and communication towers) that increasingly have adverse effects on such essential activities such as feeding, dispersal, migration, and courtship (Kunz et al. 2007a, 2007b; National Research Council 2007; Arnett et al. 2008; Horn et al. 2008; Fig. 1). Similarly, human-altered landscapes (e.g., forest fragmentation, agriculture, and urbanization) are rapidly and irreversibly transforming the quantity and quality of available habitats for organisms that use the aerosphere, conditions that also can affect the structure and function of terrestrial and aquatic ecosystems and the assemblages of organisms therein. Prevailing climate change and its expected effects on global circulation of the atmosphere and resultant changes on local, regional, and weather conditions may have profound effects on the historic migratory patterns of animals that use the aerosphere (Wilcove 2008).

Challenges of probing and modeling the aerosphere

Ecologists who study species that use the aerosphere face three important challenges: (1) to discover how best to detect the presence, taxonomic identity, diversity, and activity of organisms that use this space, (2) to identify ways to quantify relevant environmental variables at different temporal and spatial scales, and (3) to determine how best to understand and interpret responses of organisms in the context of complex meteorological events and patterns within both natural and anthropogenically altered environments. Efforts to address these challenges require the collaboration of scientists from diverse disciplines who have expertise and instruments needed to probe the aerosphere whether by day or night, in arid and humid conditions, at low and high altitudes, in strong and weak magnetic fields, in cold and warm climates, and during calm and windy conditions. Increasingly available tools, some originally designed for military purposes, space exploration, climate modelling, and security applications, include remote sensing and imaging devices such as radar, lidar, aircraft surveillance, weather satellites, night vision, and thermal infrared imaging cameras. Other instruments designed specifically for the study of animal movements, include radio-telemetry networks of ground-based stations and satellites, devices that detect audible and ultrasounds of birds and bats, stable isotope and DNA markers for assessing migration, which can be particularly valuable when used in combination with remotely sensed atmospheric, oceanic, and landscape conditions. Availability of these tools and methods provides rich opportunities for addressing emerging questions in ecology and environmental sciences with an emphasis on the aerosphere.

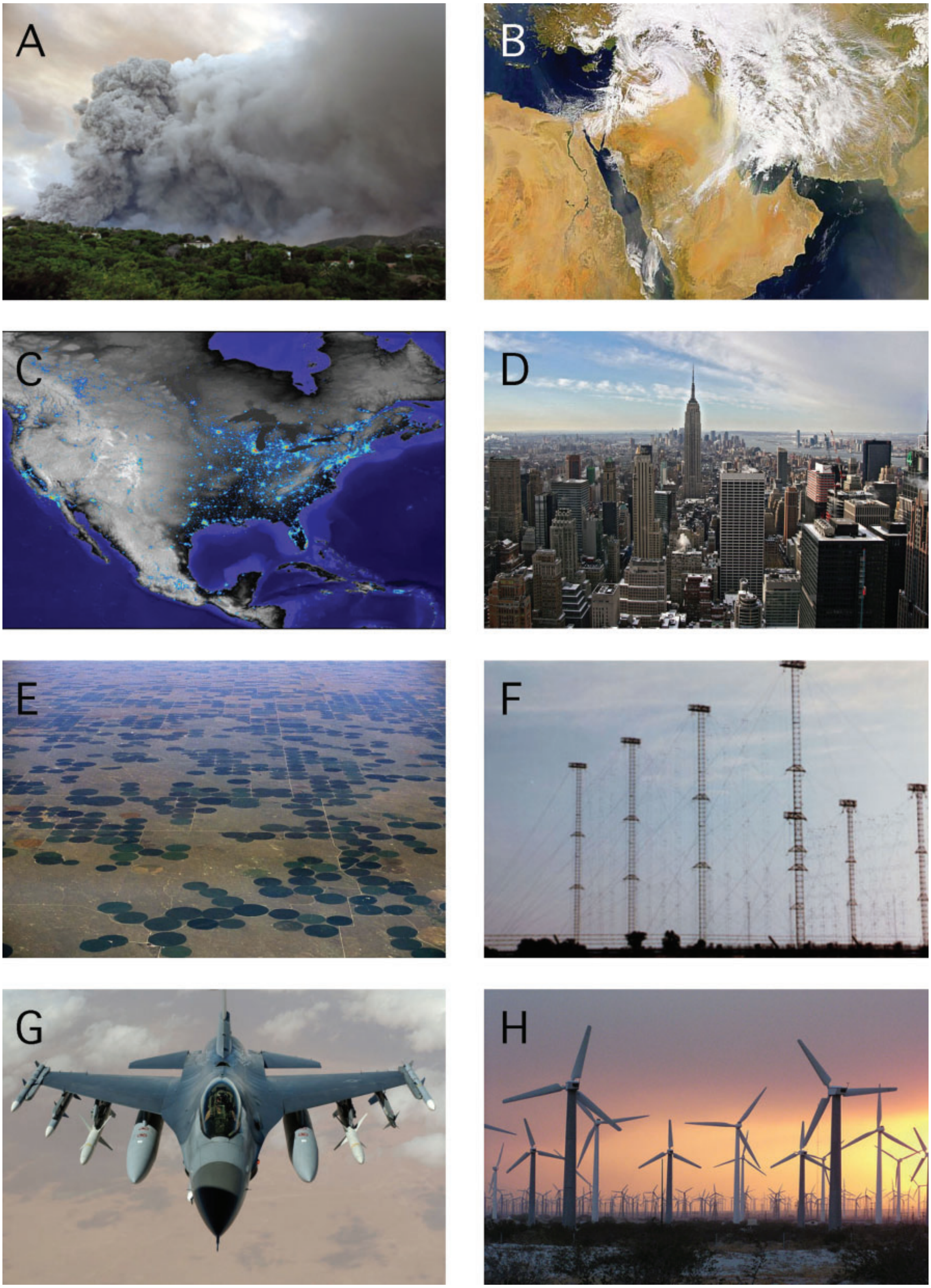

Fig. 1 The aerosphere is influenced by both natural phenomena and anthropogenic factors. (**A**) Aerospheric view of a volcanic eruption on the island of Montserrat (news.nationalgeographic.com); (**B**) Counter-clockwise swirl of clouds as a cyclone passed over Iraq, and dust being transported within the warm sector of the system (ucsu.colorado.edu/~drewsc/sandstorm/); (**C**) Aerial view of the North American landscape at night, showing lighted cites and towns (www.usgcrp.gov/usgcrp/images/ocp2003/8.1b-HCR); (**D**) Aerospheric view of skyscrapers New York City (www.justinlagace.com); (**E**) Aerial view of an agricultural landscape, showing the influence of center pivot irrigation in an arid region of Colorado (www.discoverlife.org/IM/EL_DP/0010/mx); (**F**) Aerospheric view of land-based communication towers (hawkins.pair.com/voadelano/voa_delano03.jpg); (**G**) Aerospheric view of a modern U.S. Air Force F-16 Fighting Falcon aircraft (galleries.fototagger.com/image/f-16_fighting_); (**H**) Aerospheric view of a modern, utility-scale wind energy facility in Palm Springs, California (www.planetscience.org/revisiontime/wind2.jpg).

The appropriate integration of diverse tools, technologies, and multiple databases promises to inform important ecological concerns and concepts, ranging from spread of invasive species, changes in biodiversity, and local- and global-scale animal movements in response to altered terrestrial, aquatic, and aerial environments. To date, ecologists have been hampered by a lack of technological awareness, inconsistent vocabularies, and challenges of working across different disciplinary platforms, including the complexities of establishing meaningful collaborations with atmospheric and computer scientists. Similarly, ecologists interested in proximate and evolutionary responses of airborne fauna to climate change and other anthropogenic perturbations have yet to optimally use the rich databases on landscapes assembled by earth scientists and geographers using remote sensing tools [e.g., American MODIS (Moderate Resolution Imaging Spectroradiometer), the European MERIS (Medium Resolution Imaging Spectrometer), and the Indian IRS-P6 (Indian Remote Sensing Satellite)].

Goals of the aeroecology symposium

The papers presented in this symposium address some of the limitations and challenges highlighted above, and highlight opportunities for gaining new insights that could arise from overcoming these challenges. To accomplish these goals, each of the authors considered several ecological questions that require analyses that embrace ecological and environmental sciences relevant to the aerosphere. Specifically, questions relate to animal displacements, and atmospheric and biological factors that may affect daily and seasonal patterns of prey density, foraging behavior, and migration. In addition to developing and promoting new tools and technologies to support research in aeroecology, it is important to integrate knowledge from different disciplines by encouraging the participation of scientists from varied backgrounds to develop a broader understanding of complex processes and the responses of organisms to a dynamic aerosphere. To achieve these goals, the authors share ideas with respect to novel tools, emphasize tangible and specific scientific questions, and adopt novel research paradigms. To this end, we have identified instrumentation and software tools, and discuss their applications to improve our collective understanding of the aerosphere and the interactions of airborne organisms with the hydrosphere and lithosphere. Several research areas were not included in this symposium because time was limited. Notwithstanding, we include brief comment on these and other emerging disciplines relevant to understanding the ecology of organisms that use the aerosphere.

Historical and current research on aeroecology

Weather radar historically has been used for detecting groups of migrating birds (Able 1970; Bruderer and Steidinger 1972). Since the early 1990s, weather surveillance, NEXRAD (NEXt Generation RADar) Doppler radar has been used at various temporal scales to quantify movements of birds (Diehl et al. 2003; Diehl and Larkin 2005; Larkin 2005; Gauthreaux and Belser 2003, 2005; Gauthreaux et al. 2003, 2006; Kunz 2004), although it has become increasingly clear that many targets also include bats and insects (Westbrook et al. 1998; Kunz 2004; Cleveland et al. 2006; Cryan and Diehl in press). Similarly, tracking radar is being used to investigate foraging, dispersal, and migratory movements of flying arthropods, birds, and bats (Bruderer and Boldt 2001; Bruderer and Popa-Lisseanu 2005; Larkin 2005). Additionally, use of vertical profiler radar promises to provide new insight into the distribution and movement of air masses, and of arthropods, birds, and bats in the aerosphere (Smith et al. 1993; Eaton et al. 1995; McLaughlin 2003; Kunz et al. 2007b; T.A. Kelly, personal communication).

Advances in radio-telemetry (e.g., miniature radio transmitters for insects, small birds and bats, and satellite tracking with GPS for larger species), have advanced our knowledge of movements at smaller spatial and temporal scales than can be provided by radar. Recent developments of integrated arrays of receiving antennae and satellite tracking of small birds and bats (Cochran and Wikelski 2005; Smith et al. 2005; Wikelski et al. 2007), in addition to advanced canopy-netting techniques (Hodgkison et al. 2002), are beginning to yield new insights on animal movements, pollination of flowers by nectarivores, and dispersal of seeds by frugivores (Hodgksion et al. 2003; Thies and Kalko 2004; Croxall et al. 2005; Nathan et al. 2005; Thies et al. 2006)—research that also is relevant to the conservation of biodiversity (Trakhtenbrot et al. 2005) and for understanding the transmission and mitigation of emerging diseases (Chivian 2003; Epstein et al. 2003).

Radio transmitters, together with other visualization methods, also are enabling researchers to quantify energy expenditure, wingbeat patterns, respiration, and flight altitudes of small, free-ranging animals (e.g., Lord et al. 1962; Dudley 2000; Altshuler et al. 2004; Bowlin et al. 2005). Use of wind tunnels and computer-aided visualization techniques (Srygley and Thomas 2002; Altshuler and Dudley 2003; Pivkin et al. 2005; Swartz et al. 2006; Hedenström et al. 2007; Henningsson et al. 2008; Muijres et al. 2008) also are helping to inform field ecologists in how flow dynamics and atmospheric conditions influence flight behavior of bats, birds, and insects (e.g., Dillon et al. 2006).

Measuring physiological traits of foraging and migrating animals, under different atmospheric conditions (Greenstone 1990, 1991), also has begun to advance our knowledge of how animals respond to different aerospheric conditions. Moreover, novel efforts are being made to understand how insects, birds, and bats navigate during migration (Holland et al. 2006a, 2006b). Experimental manipulations have included alteration of magnetic fields to understand how animals navigate over long distances (e.g., Cochran et al. 2004; Srygley et al. 2006; Holland et al. 2006b; Wang et al. 2007). A recent initiative to employ radio technology on a near-earth satellite to track small animals around the globe holds considerable promise for understanding migratory movements of free-ranging animals (Wikelski et al. 2007). A recent global initiative, known as the International Cooperation for Animal Research Using Space (ICARUS; www.icarusinitiative.org), also has been formed to help achieve this goal. Other initiatives, including NEON (National Ecological Observatory Network [http://www.neoninc.org/]), and related Research Coordination Networks, such as MIGRATE (Migration Interest Group: Research Applied toward Education [www.migrate.ou.edu]), both funded by the National Science Foundation, have been formed to help answer important questions such as the influence behavioral plasticity of migrants, drivers of population dynamics of migratory animals, determinants of individual fitness, and impacts of environmental change on migratory life-histories (JF Kelly, personal communication).

Recent developments in audible and ultrasonic acoustic detection and analysis, coupled to high-speed infrared and thermal images now make it possible to quantify three-dimensional flight trajectories of bats as they pursue airborne arthropods (Schnitzler and Kalko 2001; Holderied et al. 2005; Holderied and Jones in press; Hristov et al. 2008), and to unambiguously identify the mix of free-ranging bat species in both temperate and tropical assemblages (Parsons and Jones 2000; Brigham et al. 2004; Szewczak 2004; Parsons and Szewczak in press). This technology now makes it possible to characterize species richness and activity patterns that previously been difficult to quantify or record species have gone completely undetected, such as many aerial insectivorous bats, especially in tropical regions (Jung et al. 2007). Night vision devices and thermal infrared cameras have become increasingly used to observe birds, bats, and insects aloft, not only for assessing foraging behaviors (Simmons 2005; Betke et al. 2007; Horn et al. 2008; Hristov et al. 2008), but also for censusing animals during nightly emergence flights (Sabol and Hudson 1995; Frank et al. 2003; Betke et al. 2007, 2008; Hristov et al. 2008). When used simultaneously with tracking radar, night vision devices and thermal infrared cameras also make it possible to distinguish between birds and bats as they respond to anthropogenic structures such as wind turbines (Gauthreaux and Livingston 2006; Kunz et al. 2007a; 2007b).

Many important aspects of the behavior of flying organisms in the aerosphere occur in groups, sometimes of immense sizes. Many collective behaviors are influenced by the three-dimensional geometry of the environment, and by the cognitive abilities of animals that interact with prevailing atmospheric conditions. Understanding the behavior of individuals in isolation does not necessarily provide information about the properties of individuals within groups (Couzin and Krause 2003). Increased focus on empirical studies, self-organization theory, and mathematical modelling of group and collective behavior of insects, birds, and other organisms promises to help advance knowledge about daily flocking behavior at the population level and group dynamics during migration (Couzin 2006a, 2006b).

Use of stable isotopes of carbon and nitrogen as dietary tracers also can provide valuable insights into trophic relationships of airborne predators and their prey (Ibáñez et al. 2001; Sullivan et al. 2006: Popa-Lisseanu et al. 2007), and isotopes of hydrogen can additionally be used for discerning geographic origins of nocturnal migrants (Hobson and Wassenaar 2001; Cryan et al. 2004; Kelly et al. 2002, 2005; Hobson et al. 2006).

Collaborations of biologists with atmospheric scientists and aerospace engineers are needed to help advance understanding of animal behavior in the aerosphere. In turn, these collaborations can help advance the technical design and function of small, unmanned aerial vehicles, as inspired by the ecology, behavior, physiology, and biomechanics of real organisms (Watts et al. 2001; Pivkin et al. 2005; Swartz et al. 2006).

The symposium

To the extent possible, each contribution from this symposium has posed several important questions and has reviewed existing and upcoming applications that inform new answers. Interdisciplinary approaches are emphasized, particularly those designed to optimally exploit the expertise of domain scientists in behavior, ecology, biomechanics, meteorology, computer science, and geography—approaches that are central to developing meaningful cross-disciplinary collaborations.

Using Doppler weather surveillance radar, Gauthreaux et al. (2008) discuss major challenges in understanding daily and seasonal movements of airborne fauna. Reflectivity data contain information on the quantity of organisms aloft, and data on velocity and winds aloft are needed to determine the different types of organisms that use the aerosphere. The latter is accomplished by examination of statistical distributions of the maximum ground speeds of airborne fauna in the aerosphere. Because migrating birds and bats have mean velocities greater than most insects and randomly foraging birds and bats in a sample volume of the aerosphere, these data can often be used to detect and discriminate specific targets aloft.

Horn and Kunz (2008) used NEXRAD databases to explore how Brazilian free-tailed bats disperse nightly into the aerosphere, and how this information can provide insight into local population dynamics. NEXRAD radar images are georeferenced and compiled in a GIS along with colony locations and landscape features. In temporal sequences of NEXRAD images, identification of individual bat colonies is accomplished by assessing reflectivity from bats aloft using computer vision algorithms. These measurements are used to compute relative colony size and mean direction of travel and to compare variation in emergence behavior both within and among colonies. Analyses using circular statistics suggest that multiple factors play a role in the nightly flight and dispersal behavior of bats, and demonstrate that NEXRAD data can be a valuable resource for monitoring the nightly behavior of large bat colonies, and larger-scale seasonal and inter-annual changes in abundance of local populations.

Larkin and Szafoni (2008) discuss how tracking radar data can be used to investigate nocturnal aggregations of birds. Statistical analyses of detailed flight paths support the hypothesis that individual birds that fly together (closer than 200–300 m) move in the same direction and at the same speed more often than those that are widely dispersed. Evidence from tracking radar suggests that birds flying together also may have similar wing beat frequencies than can be expected by chance.

Hristov et al. (2008) provide an overview of recent applications of thermal infrared imaging in ecological research and discuss how this technology has revolutionized our ability to observe and document the behavior of free-ranging organisms in the dark. Unlike traditional imaging that requires visible light, thermal infrared imaging relies on the emission of heat energy from objects in the environment. Temperature-sensitive cameras and computer vision algorithms are used to detect differences in thermal values in their fields of view and to depict information visually as different brightness (temperature) values. As noted in this article, successful applications of thermal infrared imaging from ongoing studies of bat ecology and behavior also are relevant for the study other organisms.

Kalko et al. (2008) present results based on recordings and analysis of echolocation calls of Neotropical bats that, for the first time, permit explicit species identification as well as assessment of foraging activity in these species-rich tropical assemblages. Use of miniature radio transmitters also makes it possible to assess foraging strategies, range size, and differential habitat use of species that previously have been otherwise difficult to study. Given the high impact of bats as seed dispersers, pollinators, and predators on arthropods, the fine resolution of movements afforded by radio-telemetry provides a better understanding of the links between spatial use and resource distribution and abundance. In turn, this provides novel information needed to understand temporal dynamics, to help quantify the ecosystem services provided by bats, and to predict how anthropogenic changes may affect the abundance and distribution of their prey.

Jones and Holderied (2008) discuss how echolocation is used by bats to detect, localize, and classify airborne targets at night. As obstacles or prey species are approached, it has become increasingly clear that the call structure of echolocating bats changes in predictable ways: calls become shorter to reduce overlap between pulse and echo, and calls change in shape so that localization errors in the detection of insect prey can be minimized. Echolocation behavior and flight performance of bats are closely synchronized by monitoring both features simultaneously using stereo photo- and videogrammetry, and by acoustic tracking of their flight paths. These approaches make it possible to quantify the intensity of signals used by free-ranging bats, and thus demonstrate systematic changes in signal design in relation to the proximity of obstacles (e.g., moving insect prey and stationary objects) in the aerosphere.

Westbrook (2008) discusses long-distance migration of important agricultural pests, such as adult corn earworm moths (*Helicoverpa zea*), also called cotton bollworm moths, and several other noctuid moth species upon which bats and birds sometimes feed. These seasonal geographic expansions of pest populations and the consequent increased infestations of agricultural crops are documented on a continental scale in North America. Observed patterns of migratory flight by these insect pests are largely associated with vertical profiles of temperature and wind direction and are concentrated in the atmospheric boundary layer. Collective patterns of moth migrations generally are related to wind direction, but often at significant angular deviations. Preliminary analyses suggest that moth distributions in the aerosphere can be estimated from discrete moth counts using X-band radar and bulk reflectivity data from NEXRAD Doppler radar.

McCracken et al. (2008) discuss bat echolocation calls recorded using radio microphones suspended in the aerosphere from kites and tethered helium balloons. These data mostly include calls of Brazilian free-tailed bats from ground-level up to 1118 m above ground level (AGL). Altitudinal profiles show significantly different levels of bat echolocation call activity at different levels AGL in the aerosphere. Bat activity was greatest at ground level and 400–600 m AGL, coincident with the atmospheric boundary layer and the highest densities of moths as described in the paper by Westbrook (2008). Feeding buzzes, indicating attacks on aerial prey, were most abundant near ground level and at 400–600 m AGL, although some were detected at altitudes up to 1 km AGL.

Srygley and Dudley (2008) review data on insects in the atmospheric boundary layer by tracking individuals as they migrate across the Caribbean Sea and the Panama Canal. Data presented on dragonflies of the genus *Pantala* show that migration occurs in October and is associated with frontal systems. Butterflies and dragonflies are capable of directed movement towards a preferred compass direction in variable winds, whereas moths of the genus *Urania* migrate from Central to South America and drift with winds over water. Butterflies navigating in the aerosphere appear to use both global and local cues. In support of optimal migration theory, butterflies and dragonflies appear to adjust their flight speeds to maximize migratory distance per unit energy, whereas moths do not.

Swartz et al. (2008) examine the biomechanics and physiology of flight of bats in the laboratory, and explore how this knowledge can help advance understanding of foraging, dispersal, and migration of free-ranging animals. Laboratory studies of animal flight in wind tunnels provide valuable information for improving and understanding of airflow dynamics. Emphasis is placed on flow characteristics of distinct aerial environments as a critical first step toward understanding the ecology of free-ranging animals aloft. The dynamics of natural airflow, characterized by air speeds, variability, intensity, and turbulence, will likely influence many aspects of an animal's behavior in the aerosphere. A combination of field- and laboratory-based research also is needed to delineate conditions under which flight mechanics and energetics are influenced by turbulence created by other animals.

Cochran et al. (2008) discuss the advanced use of miniaturized radio-transmitters that allow for the continuous monitoring of behavioral and physiological variables of small, free-ranging animals that use the aerosphere. Monitoring of nocturnal migratory flights of three species of neotropical thrushes in the mid-western US has revealed variations in wing beat frequencies, flight speeds and body accelerations that may reflect ascending and descending movements of individuals during flights. Individual thrushes also pause (in wingbeat) more often than expected during their migratory flights, likely to save energy. The high variation in wingbeat frequencies also cautions against categorizing radar echoes as particular types of birds.

Future directions

To further advance the emerging discipline of aeroecology, studies are needed that integrate the research discoveries of atmospheric scientists, engineers, and computer scientists with those of ecologists, physiologists, and functional morphologists, to more fully understand the activity and movements of organisms in the aerosphere. Research that incorporates laboratory and field studies on biomechanics, physiology, behavior, and ecology also promises to provide new insights into how, where, when, and why organisms interact with anthropogenic features in the aerosphere. To this end, studies are needed to assess: (1) physiological and behavioral responses of airborne organisms to climate change, (2) behavioral and ecological responses of organisms to structures that extend into the aerosphere (e.g., communication towers, tall buildings, and wind turbines), (3) how landscape fragmentation and land use change affects movements, and (4) how the altered structure of aeroecological communities, through the invasion of exotics, may affect species distributions and abundance (Lindenmayer and Fischer 2006; National Research Council 2007; Kunz et al. 2007a; Lian 2007; Wilcove 2008). Use of stable isotopes to investigate trophic relationships between insects, birds, bats, and their prey also promises to yield valuable insight into how the myriad of organisms interact in the aerosphere. Ultimately, understanding the ecosystem services provided by arthropods, birds, and bats that use the aerosphere is important for maintaining ecosystem health, human health, and biodiversity on the planet (Daily et al. 1997; Cleveland et al. 2006; Chivian and Burnstein 2008).

Acknowledgments

We wish to thank the Society for Integrative and Comparative Biology (SICB) Program Committee, its program director, Linda Walters, the chairs of the divisions of Vertebrate Zoology, Comparative Biomechanics, and Ecology and Evolution for supporting the 'Symposium on Aeroecology.' We also thank Sue Burk, SICB meeting director for making the logistical arrangements to convene our symposium. We are grateful to Paul Cryan, Mark Friedl, Jeff Kelly, and Ana Popa-Lisseanu for their valuable suggestions on an earlier draft of this manuscript. We are especially grateful to Johnny Evers and Willard Larkin for their encouragement and support in convening this symposium. We wish to thank the Air Force Office of Scientific Research, through a grant to Boston University (FA9550-7-1-0449 to THK), for providing partial travel support for each of the speakers to present their papers as part of the 'Symposium on Aeroecology,' and the SICB for waiving registration fees for symposium speakers.

References

Able KP. 1970. A radar study of passerine migration. Bird Band 41:282–90.

Altshuler DL, Dudley R. 2003. Kinematics of hummingbird hovering flight along simulated and natural elevational gradients. J Exp Biol 206:3139–47.

Altshuler DL, Stiles FG, Dudley R. 2004. Of hummingbirds and helicopters: hovering costs, competitive ability and foraging strategies. Am Nat 163:16–25.

Arnett EA, et al. 2008. Patterns of bat fatalities at wind energy facilities in North America. J Wildlife Manage 72:61–78.

Betke M, Hirsh DE, Bagchi A, Hristov NI, Makris NC, Kunz TH. 2007. Tracking large variable numbers of objects in clutter. Minneapolis, MN: Proceedings of the IEEE Computer Society Conference on Computer Vision and Pattern Recognition.

Betke M, et al. 2008. Thermal imaging reveals significantly smaller Brazilian free-tailed bat colonies than previously estimated. J Mammal 89:18–24.

Bowlin MS, Cochran WW, Wikelski M. 2005. Biotelemetry of New World thrushes during migration: physiology, energetics and orientation in the wild. Integr Comp Biol 45:295–304.

Brigham RM, Kalko EKV, Jones G, Parsons S, Limpens HJGA, editors. 2004. Bat echolocation research: tools, techniques, and analysis. Austin, TX: Bat Conservation International.

Bruderer B, Steidinger P. 1972. Methods of quantitative and qualitative analysis of bird migration with a tracking radar. In: Galler SR, Schmidt-Koenig K, Jacobs GJ, Belleville RE, editors. Animal orientation and navigation. Special Publication 262. Washington, DC: National Aeronautics and Space Administration. p. 151–67.

Bruderer B, Boldt A. 2001. Flight characteristics of birds I: radar measurements of speeds. Ibis 143:178–204.

Bruderer B, Popa-Lisseanu AG. 2005. Radar data on wingbeat frequencies and flight speeds of two bat species. Acta Chirop 7:73–82.

Chivian E, Burnstein E, editors. 2008. Sustaining life: how human health depends on biodiversity. New York, NY: Oxford University Press.

Cleveland CJ, et al. 2006. Economic value of the pest control service provided by Brazilian free-tailed bat in south-central Texas. Front Ecol Environ 4:238–43.

Cochran WW, Wikelski M. 2005. Individual migratory tactics of New World *Catharus* thrushes: current knowledge and future tracking options from space. In: Greenberg R, Marra P, editors. The ecology and evolution of migration. Baltimore, MD: Johns Hopkins University Press. p. 274–9.

Cochran WW, Mouritsen H, Wikelski M. 2004. Migrating songbirds recalibrate their magnetic compass daily from twilight cues. Science 304:405–8.

Cochran WW, Bowlin MS, Wikelski M. 2008. Wingbeat frequency and flap-pause ratio during natural migratory flight in thrushes. Integr Comp Biol. doi: 10.1093/icb/icn044.

Couzin ID. 2006a. Behavioral ecology: social organization in fission-fusion societies. Curr Biol 16:169–71.

Couzin ID. 2006b. Effective leadership and decision making in animal groups on the move. Nature 433:513–6.

Couzin ID, Krause J. 2003. Self-organization and collective behavior of vertebrates. Adv Study Behav 32:1–75.

Croxall JP, Silk RD, Phillips RA, Afanasyev V, Briggs DR. 2005. Global circumnavigations: tracking year-round ranges of nonbreeding albatrosses. Science 307:249–50.

Cryan P, Diehl R. Analyzing bat migration. In: Kunz TH, Parsons S, editors. Ecological and behavioral methods for the study of bats. Baltimore, MD: Johns Hopkins University Press. (in press).

Cryan P, Bogan MA, Rye RO, Landis GP, Kester CL. 2004. Stable hydrogen isotope analysis of bat hair as evidence of seasonal molt and long-distance migration. J Mammal 86:995–1001.

Daily GC, et al. 1997. Ecosystem services: benefits supplied to human societies by natural ecosystems. Issues Ecol

1:1–18 (Available from http://www.ecology.org/biod/value/EcosystemServices.html).

Diehl RH, Larkin RP. 2005. Introduction to the WSR-88D (NEXRAD) for ornithological research. In: Ralph CJ, Rich TD, editors. Bird conservation implementation and integration in the Americas. Proceedings of the Third International Partners in Flight Conference. March 20–24, 2002, Asilomar (CA), Vol. 2. General Technical Report PSW-GTR-191. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture. p. 876–88.

Diehl RH, Larkin RP, Black JE. 2003. Bird migration around the Great Lakes on Doppler radar: implications for habitat conservation. Auk 120:278–90.

Dillon M, Frazier MR, Dudley R. 2006. Into thin air: physiology and evolution of alpine insects. Integr Comp Biol 46:49–61.

Dudley R. 2000. The biomechanics of insect flight: form, function, evolution. Princeton, NJ: Princeton University Press.

Eaton FD, McLaughlin SA, Hines JR. 1995. A new frequency-modulated continuous wave radar for studying planetary boundary layer morphology. Radio Sci 30:75–88.

Epstein PR, Chivian E, Frith K. 2003. Emerging diseases threaten conservation. Environ Health Perspect 111:A506–7.

Frank JD, Kunz TH, Horn J, Cleveland C, Petronio S. 2003. Advanced infrared detection and image processing for automated bat censusing. Infrared Technol Appl XXIX. Proc SPIE 5074:261–71.

Gauthreaux SA Jr, Belser CG. 2003. Overview: radar ornithology and biological conservation. Auk 120:266–77.

Gauthreaux SA Jr, Belser CG. 2005. Radar ornithology and the conservation of migratory birds. In: Bird Conservation Implementation and Integration in the Americas: Proceedings of the Third International Partners in Flight Conference. March 20–24, 2002, Asilomar (CA), Vol. 2. General Technical Report PSW-GTR-191. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture. p. 871–5.

Gauthreaux SA Jr, Livingston JW. 2006. Monitoring bird migration with a fixed beam radar and a thermal imaging camera. J Field Ornithol 77:319–28.

Gauthreaux SA Jr, Belser CG, Van Blaricom D. 2003. Using a network of WSR 88-D weather surveillance radars to define patterns of bird migration at large spatial scales. In: Berthold P, Gwinner E, Sonnenschein E, editors. Avian migration. Berlin: Springer-Verlag. p. 335–46.

Gauthreaux SA Jr, Belser CG, Welch CM. 2006. Atmospheric trajectories and spring bird migration across the Gulf of Mexico. J Ornithol 147:317–25.

Gauthreaux SA, Livingston JW, Belser CG. 2008. Detection and discrimination of fauna in the aerosphere using Doppler weather surveillance radar. Integr Comp Biol. doi: 10.1093/icb/icn021.

Greenstone MH. 1990. Meteorological determinants of spider ballooning: the roles of thermals vs. the vertical windspeed gradient in becoming airborne. Oecologia 84:164–8.

Greenstone MH. 1991. Aerial dispersal of arthropod natural enemies: altitudinal differences in taxonomic distribution of dispersers. In: Tenth Conference on Biometeorology and Aerobiology and the Special Session on Hydrometeorology. Boston, MA: American Meteorological Society. p. 104–6.

Hedenström A, Johansson LC, Wolf M, von Busse R, Winter Y, Spedding GR. 2007. Bat flight generates complex aerodynamic tracks. Science 316:894–7.

Henningsson P, Spedding GR, Hedenström A. 2008. Vortex wake and flight kinematics of a swift in cruising flight in a wind tunnel. J Exp Biol 211:717–30.

Hobson KA, Wassenaar LI. 2001. Isotope dilineation of North American migratory wildlife populations: loggerhead shrikes. Ecol Appl 11:1545–53.

Hobson KA, Van Wilgenburg S, Wassenaar LI, Hands H, Johnson WP, O'Meilia M, Taylor P. 2006. Using stable isotope analysis of feathers to delineate origins of harvested sandhill cranes in the central flyway of North America. Waterbirds 29:137–47.

Hodgkison R, Ahmad D, Balding S, Kingston T, Zubaid A, Kunz TH. 2002. Capturing bats (Chiroptera) in tropical forest canopies. In: Mitchell TAW, Secoy K, Jackson T, editors. The global canopy programme handbook: techniques of access and study in the forest roof. Oxford, UK: Global Canopy Programme. p. 160–7.

Hodgkison R, Balding ST, Zubaid A, Kunz TH. 2003. Fruit bats (Chiroptera: Pteropodidae) as seed dispersers and pollinators in a lowland Malaysian rain forest. Biotropica 35:491–502.

Holderied MW, Corine C, Fenton MB, Parsons S, Robson S, Jones G. 2005. Echolocation call design and intensity in the aerial hawking bat *Eptesicus bottae* (Vespertilionidae) studied using stereo videogrammetry. J Exp Biol 208:1321–7.

Holderied MW, Baker CJ, Vespe M, Jones G. 2008. Understanding signal design during the pursuit of aerial insects by echolocating bats: tools and applications. Integr Comp Biol. doi: 10.1093/icb/icn035.

Holderied MW, Jones G. Flight dynamics of bats. In: Kunz TH, Parsons S, editors. Ecological and behavioral methods for the study of bats. 2nd edn. Baltimore, MD: Johns Hopkins University Press. (in press).

Holland RA, Wikelski M, Wilcove DS. 2006a. How and why do insects migrate? Science 313:794–6.

Holland RA, Thorup K, Vonhof MJ, Cochran WW, Wikelski M. 2006b. Bat orientation using Earth's magnetic field. Nature 444:702.

Horn JW, Arnett EB, Kunz TH. 2008. Interactions of bats with wind turbines based on thermal infrared imaging. J Wildlife Manage 72:123–32.

Horn JW, Kunz TH. 2008. Analyzing NEXRAD Doppler radar images to assess nightly dispersal patterns and population trends in Brazilian free-tailed bats (*Tadarida brasiliensis*). Integr Comp Biol. doi: 10.1093/icb/icn037.

Hristov NI, Betke M, Kunz TH. 2008. Applications of thermal infrared imaging for research in aeroecology. Integr Comp Biol. doi: 10.1093/icb/icn053.

Ibáñez C, Juste J, Garcia-Mudarra JL, Arirre-Mendi PT. 2001. Bat predation on nocturnally migrating birds. Proc Natl Acad Sci USA 98:9700–2.

Jung K, Kalko EKV, Helverson VO. 2007. Echolocation calls in Central American emballonurid bats: signal design and call frequency alternation. J Zool Lond 272:1125–37.

Kalko EKV, Villegas SE, Schmidt M, Meyer CFJ, Wegmann M. 2008. Flying high-assessing the use of the aerosphere by bats. Integr Comp Biol. doi: 10.1093/icb/icn030.

Kelly JF, Atudorei V, Sharp ZD, Finch DM. 2002. Insights into Wilson's warbler migration from analyses of hydrogen stable-isotope ratios. Oecologia 130:216–21.

Kelly JF, Ruegg KC, Smith TB. 2005. Combining isotope and genetic markers to identify breeding origins of migrant birds. Ecol Appl 15:1487–94.

Kunz TH. 2004. Foraging habits of North American bats. In: Brigham RM, Kalko EKV, Jones G, Parsons S, Limpens HJGA, editors. Bat echolocation research: tools, techniques, and analysis. Austin, TX: Bat Conservation International. p. 13–25.

Kunz TH, Arnett RB, Erickson WP, Hoar AR, Johnson GD, Larkin RP, Strickland MD, Thresher RW, Tuttle MD. 2007a. Ecological impacts of wind energy development on bats: questions, research needs, and hypotheses. Front Ecol Environ 5:315–24.

Kunz TH, Arnett EB, Cooper BM, Erickson WP, Larkin RP, Mabee T, Morrison ML, Strickland MD, Szewczak JM. 2007b. Assessing impacts of wind energy development on nocturnally active birds and bats: a guidance document. J Wildlife Manage 71:2449–86.

Larkin RP. 2005. Radar techniques for wildlife biology. In: Braun CE, editor. Techniques for wildlife investigations and management. 6th edn. Bethesda, MD: The Wildlife Society. p. 448–64.

Larkin RP, Szafoni RE. 2008. Evidence for widely dispersed birds migrating together at night. Integr Comp Biol. doi: 10.1093/icb/icn038.

Lian PK. 2007. Impacts of land use change on south-east Asian forest butterflies: a review. J Appl Ecol 44:703–13.

Lindenmayer DB, Fischer J. 2006. Habitat fragmentation and landscape change. Washington, DC: Island Press.

Lord RD, Bellrose FC, Cochran WW. 1962. Radio telemetry of the respiration of a flying duck. Science 137:39–40.

McCracken GF, Gillam EH, Westbrook JK, Lee YF, Jensen ML, Balsley BB. 2008. Brazilian free-tailed bats (*Tadarida brasiliensis*: Molossidae, Chiroptera) at high altitude: links to migratory insect populations. Integr Comp Biol. doi: 10.1093/icb/icn033.

McLaughlin SA. 2003. A new data acquisition system for the U.S. Army FM-CW radar: still a great way to see half-meter resolution. P1.20 (Extended Abstract, 5 pp.) in Program, 12th Symposium on Meteorological Observations and Instrumentation, American Meteorological Society Annual Meeting, February 9–13, 2003, Long Beach (CA). Boston, MA: American Meteorological Society. Available from http://ams.confex.com/ams/annual2003/techprogram/paper_58607.htm.

Muijres FT, Johjansson LC, Barfield R, Wolf M, Spedding GR, Hedenström A. 2008. Leading-edge vortex improves lift in slow-flying bats. Science 319:1250–3.

Nathan RN, et al. 2005. Long-distance biological transport processes through the air: can nature's complexity be unfolded *in silico*? Diversity Distrib 11:131–7.

National Research Council. 1997. Boundary layer dynamics. Washington, DC: The National Academies Press.

National Research Council. 2007. Environmental impacts of wind-energy projects. Washington, DC: The National Academies Press.

Oke TR. 1987. Boundary layer climates. 2nd edn. New York: Routledge.

Parsons S, Jones G. 2000. Acoustic identification of twelve species of echolocating bat by discriminant function analysis and artificial neural networks. J Exp Biol 203:2641–56.

Parsons S, Szewczak JM. Detecting, recording, and analyzing the vocalizations of bats. In: Kunz TH, Parsons S, editors. Ecological and behavioral methods for the study of bats. 2nd edn. Baltimore, MD: Johns Hopkins University Press. (in press).

Pivkin I, Hueso E, Weinstein R, Laidlaw DH, Swartz SM, Karniadakis GE. 2005. Simulation and visualization of air flow around bat wings during flight. In: Sunderam VS, et al. editor. Proceedings of the International Conference on Computer Science. Berlin: Springer-Verlag. p. 689–94.

Popa-Lisseanu AG, Delgado-Huertas A, Forero MG, Rodriguez A, Arletaz, R, Ibáñez C. 2007. Bats'conquest of a formidable foraging niche: the myriads of nocturnally migrating songbirds. PloSOne 2:e205. doi: 10.1371/journal.pone.0000205.

Sabol BM, Hudson MK. 1995. Technique using thermal infrared–imaging for estimating populations of gray bats. J Mammal 76:1242–8.

Schnitzler HU, Kalko EKV. 2001. Echolocation behavior of insect-eating bats. Bioscience 51:557–69.

Simmons JA. 2005. Big brown bats and June beetles: multiple pursuit strategies in a seasonal acoustics predator-prey system. Acoust Let Online. doi: 10.1121/1.1985959.

Sorbjan Z. 1989. Structure of the atmospheric boundary layer. New York: Prentice Hall.

Smith AD, Riley JR, Gregory RD. 1993. A method for routine monitoring of the aerial migration of insects by using a vertical-looking radar. Phil Trans R Soc Lond. B 340:393–404.

Smith C, Epstein JH, Rahman S, Field HE, Sharifah S, Daszak P. 2005. Use of satellite telemetry to study the movement of the Malayan flying fox (*Pteropus vampyrus*): implications for conservation and public health. In: Youl J, McClelland D, Young S, editors. Wildlife Health in a Shrinking World: Ecology, Managment and Conservation, Cairns, Australia: Proceedings of the International Wildlife Disease Association, June 2005. p. 168.

Srygley RB, Thomas ALR. 2002. Unconventional lift-generating mechanisms in free-flying butterflies. Nature 420:660–4.

Srygley RB, Dudley R. 2008. Optimal strategies for insects migrating in the flight boundary layer: mechanisms and consequences. Integr Comp Biol. doi: 10.1093/icb/icn011.

Srygley RB, Dudley R, Oliveira EG, Riveros AJ. 2006. Experimental evidence for magnetic sense in Neotropical migrating butterflies (Lepidoptera: Pieridae). Anim Behav 71:183–91.

Sullivan JC, Buscetta KJ, Michener RH, Whitaker JO Jr, Finnerty JR, Kunz TH. 2006. Models developed from ^{13}C and ^{15}N of skin tissue indicate non-specific habitat use by the big brown bat (*Eptesicus fuscus*). Ecoscience 13:11–22.

Swartz SM, Bishop K, Ismael-Aguirre MF. 2006. Dynamic complexity of wing form in bats: implications for flight performance. In: Zubaid A, McCracken GF, Kunz TH, editors. Functional and evolutionary ecology of bats. New York: Oxford University Press. p. 110–30.

Swartz SM, Breuer KS, Willis DJ. 2008. Aeromechanics in aeroecology – flight biology in the aerosphere. Proceedings of the Society for Integrative and Comparative Biology, January 2–6 in San Antonio, TX (http://www.sicb.org/meetings/2008/schedule).

Szewczak JM. 2004. Advanced analysis techniques for identifying bat species. In: Brigham RM, Kalko EKV, Jones G, Parsons S, Limpens HJGA, editors. Bat echolocation research: tools, techniques, and analysis. Austin (TX): Bat Conservation International. p. 121–6.

Thies W, Kalko EKV. 2004. Phenology of neotropical pepper plants (Piperaceae) and their association with their main dispersers, two short-tailed fruit bats, *Carollia perspicillata* and *C. castanea* (Phyllostomidae). Oikos 104:362–76.

Thies W, Kalko EKV, Schnitzler HU. 2006. Influence of environment and resource availability on activity patterns of *Carollia castanea* (Phyllostomidae) in Panama. J Mammal 87:231–8.

Trakhtenbrot A, Nathan R, Perry G, Richardson DM. 2005. The importance of long-distance dispersal in biodiversity conservation. Diversity Distrib 11:173–81.

Wang Y, Pan Y, Parsons S, Walker M, Zhang S. 2007. Bats respond to polarity of a magnetic field. Proc R Soc Lond B 274:2901–5.

Watts P, Mitchell EJ, Swartz SM. 2001. A computational model for estimating mechanics of horizontal flapping flight in bats: model description and comparison with experimental results. J Exp Biol 204:2873–98.

Westbrook JK. 2008. Noctuid migration in Texas within the nocturnal aeroecological boundary layer. Integr Comp Biol. doi: 10.1093/icb/icn040.

Westbrook JK, Esquivel JF, López JD Jr, Jones GD, Wolf WW, Raulston JR. 1998. Validation of bollworm migration across south-central Texas in 1994–96. Southwest Entomol 23:209–19.

Wikelski M, Kays RW, Kasdin J, Thorup J, Smith JA, Cochran WW, Swenson GW Jr. 2007. Going wild: what a global small-animal tracking system could do for experimental biologists. J Exp Biol 210:181–6.

Wilcove DS. 2008. No way home: the decline of the World's great animal migrations. Washington, DC: Island Press.