# Chapter 8 Aeroecology

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**Abstract** Aeroecology is an emerging scientific discipline that seeks to broaden understanding about the ecological function and biological importance of the aerosphere. The unifying concept of this interdisciplinary field is a focus on the aerosphere itself and the myriad airborne organisms that inhabit and depend upon this environment for their existence. In this chapter, we discuss the conceptual framework of aeroecology and underscore the technological advances that support for an interdisciplinary approach to studying the aerosphere.

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#### 8.1 Introduction

When we think about habitat for bats or other creatures, we often think about the vegetation communities associated with where an animal forages or the physical landscape features that an animal uses for periods of rest (e.g., caves). For volant animals like bats, the air through which they fly is also arguably a habitat. Air is a fluid medium utilized by bats and birds along with their prey for critical activities such as foraging, dispersal, and migration. The aerosphere—the relatively thin substratum of the troposphere closest to the Earth's surface that supports life—has long been studied in the context of meteorological conditions and functional ecosystem relationships, such as nutrient cycling and gas exchanges, but it has not been recognized as a separate ecosystem until relatively recently (Kunz et al. 2008).

Aeroecology is an emerging scientific discipline that seeks to broaden understanding about the ecological function and biological importance of the aerosphere (Kunz et al. 2008). The unifying concept underlying this new interdisciplinary field of study is a focus on the aerosphere itself and the myriad airborne organisms that inhabit and depend upon this environment for their existence. Biologists that study animals that use the aerosphere have typically focused on behavior, ecology, and evolution of specific taxonomic groups (e.g., vertebrates, arthropods) or specific physiological or behavioral functions, such as thermoregulation, water balance, respiration, or flight. The aerosphere has been studied extensively by atmospheric scientists and meteorologists with the goal of expanding our understanding of meteorology and ability to predict weather. Aeroecology provides a unifying framework for investigating how dynamic properties of meteorological conditions at local, regional, and global scales affect organisms that depend on air for foraging and movement (Fig. 8.1).

Marine biology has long been recognized as a stand-alone discipline that unites a diversity of scientists, including oceanographers, ecologists, and organismal biologists. The unifying theme in marine biology is the aqueous fluid of the oceans and the interactions of animals with that habitat. Similarly, aeroecology unites scientists that study the physical aerosphere with ecologists and organismal biologists that study species that use this medium as habitat. By connecting scientists across existing disciplines into a common framework, aeroecology advances collaborative science and addresses both fundamental scientific questions as well as applied research topics important for conservation.

Unlike aquatic ecosystems, no animal spends its entire life in the aerosphere. Yet many species spend a significant portion of their lives in this environment (Wilcove 2008). The aerosphere is a critical connective habitat for species that spend time in terrestrial or semiaquatic ecosystems but depend on the aerosphere for daily or seasonal movements. Because of their ability to move over large spatial extents, volant organisms such as birds, bats, and insects contribute to the ecological integrity of multiple ecosystems that span geopolitical boundaries linked by migration or dispersal through the aerosphere. Aeroecology provides a framework for understanding the effects of global phenomena such as climate change and anthropogenic alteration of diverse landscapes on biodiversity, global health, and ecological integrity



**Fig. 8.1** Conceptual diagram of the spatial and temporal scales of common meteorological phenomena and movement behaviors of bats in the aerosphere. Areas of *overlap* indicate the scales at which movements of bats in the aerosphere can be influenced by prevailing meteorological conditions (copied with permission from BAMS)

(Kunz et al. 2008). Many of the questions addressed by aeroecology require the use of advanced technological tools because of the logistical challenges of studying animals in the aerosphere.

## 8.2 Important Questions in Aeroecology

Kunz et al. (2008) laid out a vision for aeroecology that incorporated both technological solutions for studying animals that use the aerosphere as well as outlining some of the key questions that unite aeroecology. Here we outline some of the cutting-edge work currently being conducted in aeroecology and discuss current advances in integrative approaches that hold promise for future endeavors in this arena.

#### 8.2.1 Climate/Weather and Aerial Behavior of Bats

Predicting impacts of climate change on animal populations requires understanding how animals respond to variation in climate and weather patterns. Recent studies have shown that changes in seasonal climate, specifically drought, can have negative impacts on fitness in some bat species, including reproductive rates (Adams 2010) and annual survival (Frick et al. 2010b). Studies that address how both climate and weather conditions influence movement and foraging behavior of bats in the aerosphere will add to understanding how long-term shifts in climate may influence bat populations.

Anthropogenic climate change has caused shifts in phenology, such as spring arrival, emergence, and reproduction of many temperate species (Both and Visser 2005). Aeroecological investigations in phenology and migratory behavior should provide new information about phenology and whether bats are at risk from decoupling of resource-consumer interactions, as has been shown for some migratory passerines (Visser et al. 2005). Long-term monitoring of phenological patterns, such as arrival and departure from colonial roosts, can determine how bat populations respond to shifts in climate. Emergence counts and arrival/departure times from colonies can be done with traditional approaches of visual inspection on the ground or through remote-sensing technologies, such as radar, for species that fly at sufficient altitudes to be detectable (e.g., *Tadarida brasiliensis*) (Frick et al. 2012). Following bats during migration has thus far not been logistically feasible, except for very large-bodied bats outfitted with global positioning system (GPS) or satellite telemetry (Smith et al. 2011; Tsoar et al. 2011). Answering questions about longdistance migratory patterns will require technological advances in individual tracking devices that are currently in development coupled with integration of various remote-sensing instruments such as networked radars.

We still know relatively little about the scale of movements in most bat species. Numerous studies over the past several decades using small radio-tracking transmitters on bats have advanced knowledge considerably about selection of roost types and local foraging movements (Amelon et al. 2009). Given the relatively short life span of these types of devices (usually 1–2 weeks) and the labor necessary for tracking nightly foraging movements, there is still a considerable gap in knowledge about both seasonal movements of bats and how factors such as weather and prey availability influence foraging behavior. Technological advances in both individual tracking devices and remote-sensing systems such as radar offer promising opportunities toward breaking some of the logistical barriers to empirically investigating these questions.

#### 8.2.2 Population Monitoring

Although estimating population sizes and determining population trends is not exclusive to aeroecology, there is some exciting work being done on censusing bats at large colonies and tracking changes in colony size using thermal infrared imaging, near-infrared video, and radar technologies under the umbrella of aeroecology. Monitoring bat populations is important for determining impacts of natural and anthropogenic stressors on populations and developing effective conservation strategies (Hayes et al. 2009; O'Shea et al. 2003). Counting bats at hibernacula has been a traditional method of monitoring bat populations for species that hibernate in known hibernacula (Kurta and Kennedy 2002). This technique is highly valuable and has been pivotal in estimating impacts of white-nose syndrome (WNS) on bats in eastern North America (Frick et al. 2010a; Langwig et al. 2012). For species that do not hibernate, however, estimating bat population sizes and trends through time remains challenging (O'Shea and Bogan 2003).

In particular, accurately estimating colony sizes for large colonies of bats, such as Brazilian free-tailed bats, has been a long-standing challenge. The development of thermal infrared video provides a reliable method for censusing bat colonies and has been used successfully for estimating colony sizes (Kunz et al. 2009), including very large aggregations of Brazilian free-tailed bats (Betke et al. 2008; Hristov et al. 2010). Betke et al. (2008) developed computer vision algorithms for counting individual bats in a field of view with thermal infrared imagery. These methods have led to insights about population trends (Betke et al. 2008) and daily and seasonal fluctuations in colony size (Hristov et al. 2010).

Radar provides a potential alternative means of estimating bat populations for certain species. There are two basic approaches to using radar for estimating colony sizes of bats. Small, portable radars capable of fine spatial resolution can be positioned near a bat colony and used to observe and count individuals as they depart. This method is akin to the thermal infrared imagery technique. Conversely, larger and more powerful radars that exist as part of weather radar networks can detect bats and other aerial organisms as they scan the aerosphere in the vicinity of a particular colony site. In this case, the number of individuals is inferred from the strength of the received radio wave signal scattered by a bat or collection of bats. Using radar for estimating numbers of bats is a developing method and needs further validation, for example, through the use of complementary observations from thermal infrared video. As we discuss in more detail below, both of these radar approaches are associated with various strengths and limitations.

### 8.2.3 Aeroecology for Conservation

The aerosphere is affected by human activities and conditions such as air pollution, artificial light sources, and anthropogenic structures (e.g., skyscrapers, communication towers, and wind turbines) that may cause direct mortality or disruption of activities such as feeding, dispersal, migration, and courtship (Kunz et al. 2008). Habitat destruction and modification can also alter migratory or foraging activities in the aerosphere. Effective conservation policies will depend on understanding how bats are affected by these myriad threats in the aerosphere.

Mortality of bats from collisions with wind turbines at wind energy facilities has caused considerable concern for bat conservation (Kunz et al. 2007a, b; Arnett et al. 2008). Studies have shown that fatalities at wind turbine facilities are predictable based on seasonal periods (fall migration) as well as daily meteorological conditions, such as wind conditions (Arnett et al. 2011, Chap. 20). Determining migratory patterns of bats and how migratory movements are influenced by meteorological conditions will help identify high-risk areas for siting wind facilities. Remotesensing technologies such as radar and thermal infrared video, especially when coupled with tracking devices, are valuable resources for studies on fatalities associated with wind energy facilities. A better understanding of migratory routes and relationships between weather and bat movements will be key for developing effective conservation for species affected by wind energy development.

#### 8.3 Tools Used in Aeroecology

Investigating the behavior and movements of bats in the aerosphere has always been and will remain logistically challenging. Aeroecology addresses this challenge head on through an approach that focuses on technological advances and integration across multiple technologies and scientific disciplines. We discuss some of the key technological tools in an aeroecologists' toolbox with attention to how they can be used now or in the near future for advancing aeroecology. This is not meant to be an exhaustive list, but rather highlights certain tools we feel are particularly helpful or promising. Although acoustic recording devices are an important and rapidly evolving technology for aeroecological studies, we reference readers to chapters in this volume and elsewhere (Parsons and Szewczak 2009) dedicated to this topic.

#### 8.3.1 Radar Aeroecology

Remote-sensing tools offer opportunities for investigating ecological processes at spatial and temporal scales that have traditionally thwarted authoritative understanding of ecological dynamics in the aerosphere. The capacity of radars to detect biological scatterers in the aerosphere has been known for over 60 years (Lack and Varley 1945), and much has been learned about the aerial behavior of birds, bats, and flying arthropods through the assistance of this technology. For the most part, these studies have been conducted using small radars that were specifically adapted for observations of volant species (e.g., Bruderer et al. 1999; Chapman et al. 2011; Harmata et al. 2003). Since these studies have largely been taxa dependent, some investigators have self-classified their work as belonging to either radar ornithology or radar entomology. Here, we adopt a taxonomically broader and more integrative approach under the name of radar aeroecology (Chilson et al. 2012b). Several overview papers have been written that discuss the utility of radar for biological studies (Diehl and Larkin 2002; Chilson et al. 2012b; Gauthreaux and Belser 2003). A considerable boon to biological studies using radar and one that has helped lead to the advancement of radar aeroecology as an integrative discipline has been the development of operational networks of radars for the observation of weather. Gauthreaux began using weather radars in the USA for biological research not long after these facilities were established in 1959 (Gauthreaux and Livingston 2006). In the interim, many others have followed suit using networked weather radars across several countries (Buler and Moore 2011; Diehl et al. 2003; Dokter et al. 2011; Horn and Kunz 2008; Kelly et al. 2012; van Gasteren et al. 2008). As one example, we consider how the network of weather radars within the USA are being exploited for aeroecological studies.

The NOAA National Weather Service (NWS) maintains and operates 159 Weather Surveillance Doppler Radar (WSR-88D) installations collectively known as NEXRAD. This network provides near-continuous coverage of the airspace corresponding to roughly the lowest 10 km for the conterminous continental USA. NEXRAD stations regularly detect scatter from airborne animals, including bats, birds, and insects (bioscatter) (Fig. 8.2). Data are updated every 5–10 min and the entire data archive, which goes back to the early 1990s, is now publicly available through the National Climatic Data Center (NCDC). The benefits and uses of NEXRAD for weather monitoring and forecasting are well demonstrated; however, the use of this radar network for aeroecological studies focused on bats remains limited (Frick et al. 2012; Horn and Kunz 2008).

Weather radars probe the surrounding airspace using a particular volume coverage pattern (VCP) suitable for prevailing meteorological conditions. Data are reported and stored in spherical coordinates with observations binned into discrete units of azimuth angle, elevation angle, and range with the origin of the coordinate system located at the radar installation. For each bin, three conventional radar products are reported: radar reflectivity factor (*Z*), radial velocity ( $v_r$ ), and spectrum width ( $\sigma_w$ ). The measure of backscattered intensity, radar reflectivity factor (*Z*), can be directly related to the number of aerial organisms occupying the aerosphere (Chilson et al. 2012c) and therefore is the appropriate measure for identifying aggregations of animals for phenological studies (Kelly et al. 2012) or estimating aerial densities (Chilson et al. 2012c). Radial velocity ( $v_r$ ) can be used to detect patterns in migration by looking at flight directions and speeds of bioscatterers (Gauthreaux and Belser 1998).

A recent and key innovation for increasing the utility of NEXRAD data for ecological studies is the visualization of NEXRAD data in real time in a Cartesian grid that mosaics across different radar installations (Fig. 8.2). Radar data from NEXRAD are fused with observations from other meteorological instruments into one collective data product provided by the National Atmospheric and Oceanic Administration (NOAA) National Severe Storms Laboratory (NSSL). This database is known as the National Mosaic and Multi-Sensor Quantitative Precipitation Estimation (NMQ) system (nmq.ou.edu). Within this framework, NEXRAD data are ingested, controlled for quality, and combined to form a three-dimensional map of *Z*, which is projected onto a Cartesian grid (Zhang et al. 2004, 2011). The horizontal resolution of the NMQ output is 1 km with 31 vertical levels and a temporal resolution of



**Fig. 8.2** Diagram showing how multiple-instrument sampling is being used to develop quantitative tools for aeroecology. Radar measurements of single animals are conducted in an anechoic chamber (*top right*) and are used in conjunction with both portable radars (*bottom left*) and individual fixed radar installations (*bottom right*) to calibrate and interpret received radar signals from bioscatter. Radar data from networked fixed stations are mosaicked and mapped into a Cartesian grid system (*top right*) that shows continental-scale patterns of bioscatter activity. These maps can be viewed in near real time to watch biological phenomena such as emergences of Brazilian free-tailed bats (*Tadarida brasiliensis*) in south-central Texas (*center*). Emergences are identifiable as distinct clouds of radar reflectivity associated with known cave locations

5 min. Data are displayed as two-dimensional map of composite maximum reflectivity values across the conterminous continental USA. Currently, there is a biologically oriented companion website supported by NSSL called SOAR—Surveillance of the Aerosphere—using Weather Radar that displays the composite reflectivity (CREF) before bioscatter signal has been filtered out for improving meteorological predictions (http://soar.ou.edu).

The advantage of the NMQ/SOAR system is that it allows ecologists to view in real time (and from their desk chair) the behavior of organisms in the aerosphere at unprecedented spatial scales (Fig. 8.2). For example, it is possible to view emergences of Brazilian free-tailed bats from cave and bridge roosts in south-central Texas (Fig. 8.2) and determine patterns of daily timing of emergences as well as seasonal arrival/departures. Novel foraging behaviors of bats in the aerosphere are also being revealed. For example, Fig. 8.3 shows radar reflectivity patterns that suggest that Brazilian free-tailed bats emerged from Frio Cave and foraged for insects aggregated by outflowing winds produced by storm systems. These types of



**Fig. 8.3** Radar visualization from the SOAR website (soar.ou.edu) showing insects aggregated along a storm-generated gust front and Brazilian free-tailed bats (*Tadarida brasiliensis*) emerging from cave roosts and foraging along the insect buffet

visualizations and observations can help generate hypotheses about behavior of bats in the aerosphere and how meteorological conditions can drive predator-prey interactions in the aerosphere.

Although many insights regarding behavior and distributions of animals in the aerosphere can be made by investigating visualizations of NEXRAD radar imagery, more quantitative interpretations of radar data are needed. Persistent and significant limitations remain in using existing operational systems such as NEXRAD for biological monitoring and aeroecological research. In part, these problems stem from (1) lack of a robust biological nexus within the radar community and conversely a lack of familiarity of radar products among ecologists, (2) absence of radar product outputs focused on bioscatter, and (3) the manner in which radar output data are filtered prior to release to the public (Chilson et al. 2012b). A workshop on radar aeroecology was convened in 2012 at the National Weather Center in Norman, Oklahoma, to address these and other issues (Chilson et al. 2012a). Realizing the full potential of radar aeroecology will require advances in (1) validation studies based on theory and experiments in the laboratory to evaluate reflectivity measurements provided by radars, (2) multi-instrument sampling in the field

that can validate approaches across different radar platforms, and (3) development of tools and techniques for mining radar data in concert with field observations and other remotely sensed data.

Meteorologists have long used multiple-instrument sampling techniques for ground-truthing observations and integrating information across sampling domains to quantify characteristics and behavior of weather phenomena (Chilson et al. 2012b; National Resource Council 2009). This same technique of using mobile radars in conjunction with NEXRAD installations is also being employed in the field of radar aeroecology with the aim of using radar data for quantifying densities of animals in the aerosphere. Figure 8.2 depicts a multi-instrument sampling approach that aims to use measurements of individual animals in the laboratory to permit quantitatively interpretations of large-scale observations of bioscatter over continental scales. Reflectivity of individual animals can be measured in the laboratory to determine the backscattering radar cross section (RCS) of an individual animal (e.g., bat). These RCS measurements are necessary for estimating aerial densities of a species from radar reflectivity values (Chilson et al. 2012c). Some smaller portable radars can count discrete echoes which can be used to calibrate reflectivity values from NEXRAD and other large radars, and this method has been successful in estimating bird densities aloft (e.g., Diehl et al. 2003; Dokter et al. 2011). Small portable radars are also useful for helping scale from individuals to groups of bioscatterers (e.g., bats) by having finer spatial resolution than large radars typical of NEXRAD. These portable radars can also be oriented toward biological aggregations of interest (e.g., a bat roost). Radars in the NEXRAD network are at fixed locations, but the data are continuously collected and archived, which offers considerable advantages for long-term monitoring. The ultimate goal is to enable use of NEXRAD data for estimating population sizes so that long-term monitoring of bat species such as Brazilian free-tailed bats can be accomplished through current remote-sensing efforts. Use of the NEXRAD data network for population monitoring would permit retrospective analyses going back through the life of the archive (20 years) as well as continuous monitoring into the future.

Estimating population densities at ground-truthed point localities such as known bat roosts appears quite promising. However, use of this technology for estimating densities during migration is currently limited by the inability to discriminate taxonomic origin of received signals. However, many weather radar installations are now capable of supporting polarimetric operation, which should greatly enhance abilities to discriminate among types of biological scatterers. Whereas conventional weather radars transmit and receive radio waves with a single polarization, polarimetric weather radars use two orthogonally aligned radio waves (Fig. 8.3). Information related to size, shape, and orientation of a scatterer can be extracted by comparing the amplitudes and phases recorded for the different polarizations (Chilson et al. 2012b; Mueller and Larkin 1985; Zrnić and Ryzhkov 1998). Consider, for example, a collection of bioscatterers sampled by a weather radar consisting of both moths and small bats (Fig. 8.4). If the sampled bioscatter predominantly results from one of the two species (either bats or insects), then the resulting polarimetric signature, which is unique to the type of animal in this case, can be used for taxonomic discrimination.



**Fig. 8.4** Depiction of a radar sampling volume containing moths and bats. Resulting bioscatter signal contains contributions from both species. Depending on the relative numbers of each species, the backscattered signal may be dominated by one species over the other. Also shown is an illustration of polarimetric radio waves propagating through the aerosphere before interacting with the bioscatterers contained within the sampling volume

Overall, radar aeroecology holds much potential for contributing to understanding of many aspects of bat ecology and conservation, including phenology, foraging behavior of bats in the aerosphere, and long-term population monitoring of targeted species. Certain bat species cannot be studied effectively with radar, particularly those that fly under forest canopies. The Brazilian free-tailed bat has been the classic model organism for radar aeroecology in the USA. Species that aggregate in large groups and fly in open habitats will be good candidates for studies in radar aeroecology that focus on phenology and population monitoring. The ability for dual polarization to help discriminate taxonomic groups in the aerosphere will help increase the utility of radar for migratory studies of bats.

#### 8.3.2 Thermal Imaging

Since the initial development of commercial handheld thermal infrared cameras in the 1980s, ecologists have used thermal cameras as an approach to understanding ecophysiology (e.g., Reichard et al. 2010). Many studies have shown that thermal infrared cameras can provide information about metabolic rates, thermal regulation, and water loss. While the studies are not usually considered aeroecology studies per se, when applied to volant animals, they can be quite revealing. There are very few

techniques available that can provide reliable information about the energetics of flight collected through noninvasive means.

Recent advancements in thermal infrared technology have led to wider applications for ecological studies (Hristov et al. 2008). Even the most basic models of thermal infrared cameras have the single most important advantage over visual light camera systems: the ability to see in the dark. This capability allows for imaging bats roosting or moving inside caves, emerging from roosts, commuting across the landscape, and foraging. These behaviors have typically been difficult to observe with other technologies. Thermal infrared video overcomes limitations of normal photography or videography in low light situations that cause blurring and narrow depth of field. There are also benefits to using thermal infrared cameras in daylight, such as obtaining high-contrast images that are valuable for computer vision analysis.

Thermal infrared videography has played an integral role developing aeroecology as an integrative discipline across fields. This collaborative integration has raised interest in how a single data stream can be used for multiple scientific lines of inquiry. For example, while biologists may be interested in understanding movements of individual bats and observing behaviors such as insect capture and obstacle avoidance, collaborators in more technical fields, such as computer science and engineering, may be interested in understanding the movements of large groups of entities in 3D space. Data acquisition and analysis for multiple purposes requires cross-disciplinary communication and understanding.

A very recent and successful contribution of thermal infrared cameras to aeroecology has been their use in censusing large colonies of bats, specifically Brazilian free-tailed bats (Betke et al. 2008; Hristov et al. 2010). It has long been the goal of many ecologists to estimate abundances and understand the ecological role of bats (Kunz et al. 2009). In particular, the large colonies of Brazilian free-tailed bats that form in caves and under overpass bridges in Texas have long fascinated ecologists as they constitute some of the largest aggregations of mammals in the world. Earlier estimates of numbers of bats were based on error-prone methods of counting and led to unreliable estimates of colony size (Betke et al. 2008). A reliable method of estimating colony size was necessary for tracking population trends through time and determining the ecosystem services of these bats to the agricultural industry in Texas (Cleveland et al. 2006).

By taking advantage of a strong collaborative effort between computer science and biology, Betke et al. (2008) developed several tracking and counting algorithms to be used with thermal infrared video of emerging Brazilian free-tailed bats. To collect these videos, a FLIR Merlin system (including a camera and associated computer station) was deployed perpendicular to the flow of bats, usually with a backdrop of sky, which allowed for the highest degree of contrast, and video was recorded throughout emergence (Fig. 8.5). These videos were then processed using standard computer vision techniques, such as background subtraction, to locate moving heat signatures that were identified as likely to be bats. These bats were then tracked from frame to frame using recursive Bayesian filtering and counted as they left the



**Fig. 8.5** Thermal imaging can be used to produce high-contrast, high-resolution imagery that can be used by a variety of researchers. (a) A visual light image of *Tadarida brasiliensis* emerging from Frio Cave. Thermal cameras are arranged such that their field of view includes the bats with a backdrop of the sky. (b) The resulting images provide unprecedented detail of bat flight and group behavior (photo credit N.W. Fuller)

frame of view. When compared to hand-annotated videos of emerging bats, the automated census system was extremely effective and reliable in its final counts (Betke et al. 2008).

Thermal infrared imaging is also being used to describe the movements of organisms in three-dimensional space as they fly through the aerosphere and interact with various types of clutter, including self-clutter (i.e., other bats), stationary obstacles (e.g., trees), and moving obstacles (e.g., predators). Information such as angle of approach, turning radius, 3D wing position, angular velocity, proximity of approach, 3D group structure, and group behavior can be determined using multiple calibrated camera views, each focused on an overlapping frame of view. Understanding the mechanics of three-dimensional flight of animal groups can provide general insights about group structure and individual behavior (Parrish and Hamner 1997). Threedimensional data from thermal imaging can also be combined with other technologies to better understand the way forest structure influences movement and flight of bats. Research has shown that forest structure plays an important role in bat flight (Lacki et al. 2007). Recent advances in under-canopy LiDAR systems have allowed for even greater resolution of animal flight within forests. For example, data gathered through these analyses has the potential to provide novel research directions and valuable insight into the biomechanics and mastery of flight.

#### 8.3.3 Tracking Individuals

A full understanding of the aggregate phenomena observable by radar and thermal imaging must take into account the motivation and constraints that influence the behavior of individual animals. We must, therefore, give some attention to the activities of the individual to understand the mechanisms that give rise to the emergent properties of groups and populations. Tracking the movements of individual bats is particularly challenging due to the fact that bats are small yet move rapidly over great distances. The majority of bat species weigh less than 20 g (Smith et al. 2003), which severely limits the types of tracking devices that can be attached to bats without unduly affecting their behavior (Bridge et al. 2011). For large bat species, the possibilities for tracking individuals are more expansive. There have been numerous successful efforts to employ satellite tracking to studies of bats, and there are even published guidelines for what equipment is most appropriate for different species (Smith et al. 2011). The smallest signal-transmitting devices capable of functioning on a global scale are satellite transmitters that weigh on the order of 5 g, which is far too large for most bats. Although we can expect increasing miniaturization of complex electronics, a significant decrease in the mass of traditional satellite transmitters is unlikely due to fundamental constraints on the energy requirements of long-distance transmission and the chemical nature of batteries. Unless there is a breakthrough in battery technology, traditional satellite tracking will not be possible for small bats.

Geolocation dataloggers weighing less than 1 g have provided some of the first renderings of migrations by small birds (Bächler et al. 2010; Stutchbury et al. 2009), but these devices rely on determining the precise times of sunrise and sunset, which limits their use on many bat species due to their roosting habits. Moreover, these tracking devices rely on recapturing tagged individuals to obtain data, and such a scenario may be unlikely for many bat species. Nevertheless, there may be some potential for geolocation dataloggers to provide insights into the long-distance movements of some species, particularly tree-roosting bats (Holland and Wikelski 2009).

The future is much more promising with regard to short-range tracking. The requirements for battery power limit the degree of miniaturization possible for radio transmitters. Nevertheless, one can now find transmitters as small as 0.11 g (MacCurdy et al. 2011). The range and longevity of such small transmitters are quite limited (on the order of 2 weeks and 4 km depending on the design), but this high degree of miniaturization enables tracking individuals of even very small bat species. Radio transmitters are not only getting smaller, but radio telemetry systems are becoming more sophisticated. Traditionally, tracking movements of individuals with radio transmitters relied on labor-intensive methods, such as following individuals across the landscape with a portable receiver and antenna, or crude location estimates based on triangulation from multiple directional antennas. In addition, the number of tags that could be monitored at once was usually limited because each tag had to operate at its own frequency. Emerging technologies have automated tracking endeavors and increase the accuracy of location estimates. Moreover, signals from radio tags can be coded such that multiple tags can operate on the same frequency. For example, MacCurdy et al. (2009) have demonstrated a tag location system, in which specialized receivers can discern differences in the arrival time of transmitter signals such that the system can determine the relative distances between an individual tag and several known locations. Once implemented, this sort of "reverse GPS" system can automatically generate locations for an individual every few seconds.

The holy grail of radio tagging—global coverage via a unified set of space-based receivers—is the goal of the International Cooperation for Animal Research Using Space or ICARUS. This system proposes to use devices very similar to traditional radio transmitters in conjunction with highly sophisticated receivers in space to track individual animals. Tests of the system have been carried out using airplanes, and plans have begun for deployment of the first space-based receivers. If the system works as anticipated, ICARUS could provide global coverage for transmitters weighing on the order of 1 g.

Radio-frequency identification (RFID) is another promising technological field that has great potential for tracking individual bats. RFID generally refers to shortdistance wireless communication on the order of a few meters to a few centimeters between a small, passive tag and a powered interrogator or reader. The reader emits a carrier wave that powers a transmission from the tag such that the tag does not need a battery. There are forms of RFID communication that use powered tags and that can function over relatively large distances (tens of meters), but most RFID systems have passive tags and limited read range. Passive Integrated Transponders or PIT tags are now familiar to most biologists. These RFID tags are commonly used in animal studies and can weigh less the 0.1 g. Because they do not require a battery, their service life is typically longer than the life span of a bat, and they have already been used to monitor the behaviors of individual bats (e.g., Kerth et al. 2011).

The primary limitation to RFID systems is that their extremely limited read ranges generally restrict their use to situations in which one is monitoring a very localized resource or area (e.g., a small cave entrance). Typical low power systems, such as those that use PIT tags, cannot really track individual movement paths. However, high-frequency systems are in development that can locate individual tags by employing a network of power nodes connected to reading units. Systems of this sort would be able to track individual movements among the network of power nodes, which would typically be an area equivalent to a large room or gymnasium.

In some situations, geographic information can be inferred from intrinsic biomarkers, such as stable isotopes and DNA, which are, of course, free of any size constraints (Cryan et al. 2004; Robinson et al. 2010). Detailed movement paths are beyond the reach of these tools, but if adequate background data are available, they can provide coarse estimates of breeding or wintering locations and/or link groups of individuals to regional populations (Hobson and Wassenaar 2008). Combining the inference from these techniques to generate probability landscapes has led to surprisingly precise geographic assignments in a limited number of bird species (T. Smith and M. Wunder, personal communication), and there is potential for this technique to yield insights into connectivity and movement of bat populations as well.

Not only does tracking individuals have scientific value, but it also provides a means of educating and engaging the public. People identify with individuals, and describing a life cycle from the perspective of an individual bat is appealing to communicate about bats to the general public. Tracking individuals will undoubtedly provide key insights into important issues affecting bats and humans today,

including disease transmission, mortality at wind turbines, and consumption of insect pests, and perhaps the narratives revealed by tracking technology will help raise public awareness to these important issues.

#### 8.4 Conclusions

By focusing on integrating across a diversity of disciplines and technological innovations, aeroecology is furthering scientific investigations in a diversity of research arenas. For example, aeroecology is at the forefront of research on topics such as daily and nightly dispersal, migratory patterns, foraging behavior, distribution and quantification of aerial biomass, aerial biodiversity, phenological patterns related to climate change, and impacts of land-use policy. In addition to basic scientific research, aeroecology has the potential to make significant contributions to human society by providing information on issues ranging from aviation safety, agricultural productivity, and siting of wind energy facilities.

A pressing need exists for scientists to identify and use creative technological and analytical solutions for understanding biological phenomena at broad spatial and temporal scales in the aerosphere, given global threats to biodiversity, emerging infectious diseases, and the need to sustain ecological integrity (Kunz et al. 2008). By developing new analytical and interpretive tools from existing and emerging technologies, aeroecology encourages scientists and citizens from a diverse set of disciplines to tackle contemporary conservation and ecological questions in unprecedented ways.

#### References

- Adams RA (2010) Bat reproduction declines when conditions mimic climate change projections for western North America. Ecology 91:2437–2445
- Amelon SK, Dalton D, Millspaugh JJ, Wolf S (2009) Radiotelemetry: techniques and analysis. In: Kunz TH, Parsons S (eds) Ecological and behavioral methods for the study of bats. The John Hopkins University Press, Baltimore, MD
- Arnett EB, Brown WK, Erickson WP, Fiedler JK, Hamilton BL, Henry TH, Jain A, Johnson GD, Kerns J, Koford RR, Nicholson CP, O'Connell TJ, Piorkowski MD, Tankersley RD (2008) Patterns of bat fatalities at wind energy facilities in North America. J Wildl Manag 72:61–78
- Arnett EB, Huso MMP, Schirmacher MR, Hayes JP (2011) Altering turbine speed reduces bat mortality at wind-energy facilities. Front Ecol Environ 9:209–214
- Bächler E, Hahn S, Schaub M, Arlettaz R, Jenni L, Fox JW, Afanasyev V, Liechti F (2010) Yearround tracking of small trans-saharan migrants using light-level geolocators. PLoS One 5:3
- Betke M, Hirsh DE, Makris NC, McCracken GF, Procopio M, Hristov NI, Tang S, Bagchi A, Reichard JD, Horn JW, Crampton S, Cleveland CJ, Kunz TH (2008) Thermal imaging reveals significantly smaller Brazilian free-tailed bat colonies than previously estimated. J Mammal 89:18–24
- Both C, Visser ME (2005) Review Shifts in phenology due to global climate change: the need for a yardstick. Proc R Soc B272:2561–2569

- Bridge ES, Thorup K, Bowlin MS, Chilson PB, Diehl RH, Fléron RW, Hartl P, Kays R, Kelly JF, Robinson WD (2011) Technology on the move: recent and forthcoming innovations for tracking migratory birds. Bioscience 61:689–698
- Bruderer B, Peter D, Steuri T (1999) Behaviour of migrating birds exposed to X-band radar and a bright light beam. J Exp Biol 202:1015–1022
- Buler JJ, Moore FR (2011) Migrant-habitat relationships during stopover along an ecological barrier: extrinsic constraints and conservation implications. J Ornithol 152:101–112
- Chapman JW, Drake VA, Reynolds DR (2011) Recent insights from radar studies of insect flight. Annu Rev Entomol 56:337–356
- Chilson PB, Bridge E, Frick WF, Chapman JW, Kelly JF (2012a) Radar aeroecology: exploring the movements of aerial fauna through radio-wave remote sensing. Biol Lett 8:698–701
- Chilson PB, Frick WF, Kelly JF, Howard KW, Larkin RP, Diehl RH, Westbrook JK, Kelly TA, Kunz TH (2012b) Partly cloudy with a chance of migration. Bull Am Meteorol Soc 93:1–19
- Chilson PB, Frick WF, Stepanian PM, Shipley JR, Kunz TH, Kelly JF (2012c) Estimating animal densities in the aerosphere using weather radar: To Z or not to Z? Ecosphere 3:72
- Cleveland CJ, Betke M, Federico P, Frank JD, Hallam TG, Horn J, López JD Jr, McCracken GF, Medellín RA, Moreno-Valdez A, Sansome CG, Westbrook JK, Kunz TH (2006) Economic value of the pest control service provided by Brazilian free-tailed bats in south-central Texas. Front Ecol Environ 4:238–243
- Cryan PM, Bogan MA, Rye RO, Landis GP, Kester CL (2004) Stable hydrogen isotope analysis of bat hair as evidence for seasonal molt and long-distance migration. J Mammal 85:995–1001
- Diehl RH, Larkin RP (2002) Introduction to the WSR-88D (NEXRAD) for ornithological research. In: Ralph CJ, Rich TD (eds) Bird conservation implementation and integration in the Americas: proceedings of the third international partners in flight conference, 2002, Pacific Southwest Research Station, USDA Forest Service, Albany, CA
- Diehl RH, Larkin RP, Black JE, Moore F (2003) Radar observations of bird migration over the Great Lakes. The Auk 120:278–290
- Dokter AM, Liechti F, Stark H, Delobbe L, Tabary P, Holleman I (2011) Bird migration flight altitudes studied by a network of operational weather radars. J R Soc Interface 8:30–43
- Frick WF, Pollock JF, Hicks AC, Langwig KE, Reynolds DS, Turner GG, Butchkoski CM, Kunz TH (2010a) An emerging disease causes regional population collapse of a common North American bat species. Science 329:679
- Frick WF, Reynolds DS, Kunz TH (2010b) Influence of climate and reproductive timing on demography of little brown myotis *Myotis lucifugus*. J Anim Ecol 79:128–136
- Frick WF, Stepanian PM, Kelly JF, Howard KW, Kuster CM, Kunz TH, Chilson PB (2012) Climate and weather impact timing of emergence in bats. PLoS One 7:e42737
- Gauthreaux SA Jr, Belser CG (1998) Displays of bird movements on the WSR-88D: patterns and quantification. Weather Forecast 13:453–464
- Gauthreaux SA Jr, Belser CG (2003) Overview: radar ornithology and biological conservation. The Auk 120:266–277
- Gauthreaux SA Jr, Livingston JW (2006) Monitoring bird migration with a fixed-beam radar and a thermal-imaging camera. J Field Ornithol 77:319–328
- Harmata AR, Leighty GR, O'Neil EL (2003) A vehicle-mounted radar for dual-purpose monitoring of birds. Wildl Soc Bull 31:882–886
- Hayes JP, Ober HK, Sherwin RE (2009) Survey and monitoring of bats. In: Kunz TH, Parsons S (eds) Ecological and behavioral methods for the study of bats. The John Hopkins University Press, Baltimore, MD
- Hobson KA, Wassenaar LI (2008) Tracking animal migration with stable isotopes. Elsevier, New York
- Holland RA, Wikelski M (2009) Studying the migratory behavior of individual bats: current techniques and future directions. J Mammal 90:1324–1329
- 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 48:24

- Hristov NI, Betke M, Kunz TH (2008) Applications of thermal infrared imaging for research in aeroecology. Integr Comp Biol 48:50–59
- Hristov NI, Betke M, Bagchi A, Theriault DEH, Kunz TH (2010) Seasonal variation in colony size of Brazilian free-tailed bats at Carlsbad Cavern based on thermal imaging. J Mammal 91:183–192
- Kelly JF, Shipley RJ, Chilson PB, Howard KW, Frick WF, Kunz TH (2012) Quantifying animal phenology in the aerosphere at a continental scale using NEXRAD weather radars. Ecosphere 3:16
- Kerth G, Perony N, Schweitzer F (2011) Bats are able to maintain long-term social relationships despite the high fission-fusion dynamics of their groups. Proc R Soc B 278:2761–2767
- Kunz TH, Arnett EB, Cooper BM, Erickson WP, Larkin RP, Mabee T, Morrison ML, Strickland MD, Szewczak JM (2007a) Assessing impacts of wind-energy development on nocturnally active birds and bats: a guidance document. J Wildl Manag 71:2449–2486
- Kunz TH, Arnett EB, Erickson WP, Hoar AR, Johnson GD, Larkin RP, Strickland MD, Thresher RW, Tuttle MD (2007b) Ecological impacts of wind energy development on bats: questions, research needs, and hypotheses. Front Ecol Environ 5:315–324
- Kunz TH, Gauthreaux SA Jr, Hristov NI, Horn JW, Jones G, Kalko EKV, Larkin RP, McCracken GF, Swartz SM, Srygley RB, Dudley R, Westbrook JK, Wikelski M (2008) Aeroecology: probing and modeling the aerosphere. Integr Comp Biol 48:1–11
- Kunz TH, Betke M, Hristov NI, Vonhof MJ (2009) Methods for assessing colony size, population size, and relative abundance of bats. In: Kunz TH, Parsons S (eds) Ecological and behavioral methods for the study of bats. The John Hopkins University Press, Baltimore, MD
- Kurta A, Kennedy J (2002) The Indiana bat: biology and management of an endangered species. Bat Conservation International, Austin, TX
- Lack D, Varley GC (1945) Detection of birds by radar. Nature 156:446
- Lacki MJ, Amelon SK, Baker MD (2007) Foraging ecology of bats in forests. In: Lacki MJ, Hayes JP, Kurta A (eds) Bats in forests: conservation and management. The John Hopkins University Press, Baltimore, MD
- Langwig KE, Frick WF, Bried J, Hicks AC, Kunz TH, Kilpatrick AM (2012) Sociality, densitydependence, and microclimates determine the persistence of populations suffering from a novel fungal disease, white-nose syndrome. Ecol Lett 15:1050–1057
- MacCurdy RB, Gabrielson RM, Spauldin E, Purgue A, Cortopassi KA, Fristup K (2009) Automatic animal tracking using matched filters and time difference of arrival. J Commun 4:489–495
- MacCurdy RB, Gabrielson RM, Cortopassi KA (2011) Automated wildlife radio tracking. In: Zekavat SE, Buehrer RM (eds) Handbook of position location. Wiley, New Jersey
- Mueller EA, Larkin RP (1985) Insects observed using dual-polarization radar. J Atmos Ocean Technol 2:49–54
- National Resource Council (2009) Observing weather and climate from the ground up: a nationwide network of networks. The National Academies Press, Washington, DC
- O'Shea TJ, Bogan MA (2003) Monitoring trends in bat populations of the United States and territories: problems and prospects US geological survey, biological resources discipline, information and technology report, USGS/BRD/ITR-(2003)-003
- O'Shea TJ, Bogan MA, Ellison LE (2003) Monitoring trends in bat populations of the United States and territories: status of the science and recommendations for the future. Wildl Soc Bull 31:16–29
- Parrish JK, Hamner WM (1997) Animal groups in three dimensions. Cambridge University Press, Cambridge
- Parsons S, Szewczak JM (2009) Detecting, recording, and analyzing the vocalizations of bats. In: Kunz TH, Parsons S (eds) Ecological and behavioral methods for the study of bats. The John Hopkins University Press, Baltimore, MD
- Reichard J, Fellows S, Frank A, Kunz TH (2010) Thermoregulation during flight: body temperature and sensible heat transfer in free-ranging Brazilian free-tailed bats (*Tadarida brasiliensis*). Physiol Biochem Zool 83:885–897

- Robinson WD, Bowlin MS, Bisson IA, Shamoun-Baranes J, Thorup K, Diehl RH, Kunz TH, Mabey SE, Winkler DW (2010) Integrating concepts and technologies to advance the study of bird migration. Front Ecol Environ 8:354–361
- Smith FA, Lyons SK, Ernest SKM, Jones KE, Kaufman DM, Dayan T, Marquet PA, Brown JH, Haskell JP (2003) Body mass of late quaternary mammals. Ecology 84:3403
- Smith CS, Epstein JH, Breed AC, Plowright RK, Olival KJ, de Jong C, Daszak P, Field HE (2011) Satellite telemetry and long-range bat movements. PLoS One 6:e14696
- Stutchbury BJM, Tarof AS, Done T, Gow E, Kramer PM, Tautin J, Fox JW, Afanasyev V (2009) Tracking long-distance songbird migration by using geolocators. Science 323:896–897
- Tsoar A, Nathan R, Bartan Y, Vyssotski A, Dell'Omo G, Ulanovsky N (2011) Large-scale navigational map in a mammal. Proc Natl Acad Sci USA 108:E718–E724
- van Gasteren H, Holleman I, Bouten W, van Loon E, Shamoun-Baranes J (2008) Extracting bird migration information from C-band Doppler weather radars. Ibis 150:674–686
- Visser ME, Holleman LJM, Gienapp P (2005) Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia 147:164–172
- Wilcove D (2008) No way home: the decline of the world's great animal migrations. Island Press, Washington, DC
- Zhang J, Howard KW, Langston C, Wang S, Qin Y (2004) Three-and four-dimensional highresolution national radar mosaic. ERAD Publ Ser 2:105–108
- Zhang J, Howard KW, Langston C, Vasiloff S, Kaney B, Arthur A, Van Cooten S, Kelleher K, Kitzmiller D, Ding F (2011) National Mosaic and Multi-Sensor QPE (NMQ) system: description, results, and future plans. Bull Am Meteorol Soc 92:1321–1338
- Zrnić DS, Ryzhkov AV (1998) Observations of insects and birds with polarimetric radar. IEEE Trans Geosci Remote Sens 36:661–668