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Analyzing Bat Migration

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THE MIGRATORY MOVEMENTS OF BATS have proven extremely difficult to determine. Despite extensive efforts during the past century to track the movements of bats across landscapes, efficient methods of following small- to medium-size volant animals (<240 g) for extended periods (>8 weeks) over long distances (>100 km) have not been developed. Important questions about bat migration remain unanswered: Which bats migrate? Where do they go? How far do they move? How high and fast do they fly? What are their habitat needs during migration? How do bats orient and navigate during migration? Addressing these apparently simple questions will be a considerable challenge to anyone interested in advancing the study of bat migration. In this chapter, we present direct and indirect methods used to study bat migration, as well as techniques that have worked for studying bird migration that could feasibly be adapted to the study of bats.

FOLLOWING MARKED INDIVIDUALS

As detailed in other chapters of this book, bats can be marked using a variety of methods. Herein we categorize such markings as either *passive* tags—those that must be relocated without guidance, or *active* tags—those that broadcast their whereabouts. Passive marking techniques that are appropriate for migration studies, such as banding (ringing) or implantation of passive integrated transponder (PIT) tags, are detailed elsewhere in this volume (see Kunz and Weise, this volume). These marking methods are relatively permanent and add little to the total mass of the bat (<0.2 g), an important consideration in behavioral studies. The major drawback of using passive tags for migration research is that marked bats are extremely difficult to relocate or recognize after they leave the tagging site.

Delays associated with relocating bats marked with passive tags typically preclude gathering information on the details (e.g., speed and route) of movement (Griffin, 1970; Dingle, 1996). Active tags, such as radio and satellite transmitters (see Amelon et al., this volume), are more easily relocated, but their use in migration research is currently limited by a combination of tag size, transmission distance, and/or battery life.

Passive Tagging

Much of what we currently know about bat migration is the result of mark-recapture studies conducted using wing bands (Strelkov, 1969; Griffin, 1970; Gunier, 1972; Humphrey and Cope, 1976; Tuttle, 1976; Baker, 1978; Glass, 1982). Although the details of applying bands to bats are covered in other chapters of this book, there are important considerations to make when marking bats with passive tags for migration studies. Foremost, it is essential that the tags are imprinted or encoded with sufficient information so that anyone who recovers them can report the recovery. At the least, bands should be imprinted with the name of the institution responsible for attachment and a unique identifier number. Many band manufacturers offer the option of custom characters at a modest cost. Whether banding efforts are for migration studies or not, researchers should consider including contact information on bat bands in case the bat is recovered at a distant location. For example, a female hoary bat (*Lasiurus cinereus*) was recently recovered in Wayne County, Nebraska, marked with a numbered plastic band typical of many studies. The absence of contact information on the band made it difficult to identify the bat's original banding location; in this case, the band matched the description of one applied to an animal marked for a study in Saskatchewan, Canada, nearly 1300 km from the recovery site (C. Willis, pers. comm.).

Although mostly used for studies of population dynamics, PIT tags may prove useful in tracking the long-distance movements of bats. PIT tags can only be detected at short range (a few cm), but offer several advantages over bands for migration studies: (1) they are persistent and not likely to influence the long-term survival of bats, (2) they can be detected without handling the animal and in situations where wing bands may not be visible (e.g., tight clusters of hibernating bats), and (3) they can be detected by remote systems at roost entrances. Detection of PIT tags in bat carcasses submitted to health department laboratories for rabies testing may also disclose migratory movements, particularly in regions where large numbers of bats have been marked for other studies. For example, several of the more than 4,000 big brown bats (*Eptesicus fuscus*) marked for a population study in Fort Collins, Colorado (O'Shea et al., 2004), subsequently turned up in samples of dead bats submitted to surrounding health departments (T. J. O'Shea, pers. comm.). Unlike bands, all PIT tags are encoded with unique identification numbers, thus providing a better means of tracking their source across political boundaries.

An important component of any migration study that employs passive tags is the establishment and maintenance of a data clearinghouse. Bats might be recovered long after completion of the study for which they were marked and the history of their marking should be archived and accessible. At present, efforts to coordinate the numbering and history of bat bands deployed at continental scales are uncommon (e.g., Australian Bird and Bat Banding Scheme). Where banding coordination programs exist, such as in numerous European countries, they typically function at only a national scale and are often driven by legislation or transnational agreements (e.g., Convention on the Conservation of Migratory Species of Wild Animals) for the protection of bats. Unlike migratory birds, there are currently neither transnational laws for the protection of migratory bats in the Americas (O'Shea and Bogan, 2003) nor numbering systems or information repositories for banded bats. In the United States, the Bat Banding Office (BBO) of the U.S. Fish and Wildlife Service at the National Museum of Natural History operated in the latter function from the 1930s through the mid-1970s (Peurach, 2004). During its operation, the BBO issued more than 2 million bat bands that included unique identifier numbers as well as contact information for reporting the recoveries. In addition, the BBO served as the data repository for information on banded bats. Although the BBO still accepts information on recovery of animals marked with bands it originally issued, it has not distributed new bands or archived new banding data since 1973 (Peurach, 2004) because of concerns that bands were harming bats (O'Shea et al., 2004). Considering the relatively long life spans of bats (Wilkinson and South, 2002) and the comparatively short durations of most research projects, it is important that records of permanently marked bats are somehow accessible into the future. Scientists that permanently mark bats should consider how their markings would be interpreted and made use of if the marked animal or its remains are recovered decades later. Adequate measures, such as including band or PIT tag numbers in the methods sections of publications or reports to permitting agencies, should always be taken to ensure that information from marked bats is not lost.

The techniques discussed in the previous paragraphs rely on marked individuals being found at sites remote from where they were originally tagged; however, most recaptures of banded bats occur at the original marking site (Griffin, 1970). Considering that bats often exhibit year-to-year fidelity to particular sites (Kunz, 1982; Willis et al., 2003), the future development of passive devices that record the geographic movements of bats while away from known roosts, but are then recovered and analyzed on their return, may be rewarding. For example, miniature

(5-g) daylight level recorders are currently being used to track the global movements of large pelagic birds and marine mammals (Delong et al., 1992; Croxall et al., 2005). These devices are relatively easy to build from components that cost approximately US$100 per unit; average location error on pelagic birds is approximately 180 ± 114 km (e.g., Afanasyev, 2004). Whereas the use of daylight loggers on bats will be limited because of direct-light requirements, development of other miniaturized passive location recording devices (e.g., GPS) will likely prove more practical than trying to relocate bats marked with passive tags at locations distant from the marking site. Currently use of such devices on bats is limited by their size and mass.

Active Tagging

As detailed by Amelon et al. (this volume), radio transmitters are a practical means of following the movements of bats. Unfortunately, the use of radio transmitters to track bats as they migrate has been limited, likely due to the perceived cost and logistical difficulty of such endeavors. To date, there is very little quantitative information on the flight behaviors or distances traveled on a daily basis by migratory bats and even minor attempts to study such aspects of bat ecology could be worthwhile. The most likely efforts to succeed are those that attempt to follow bats marked with radio transmitters using a combination of ground or water vehicles and aircraft, although it is likely that researchers will be able to pursue some species, in certain situations, using ground vehicles alone. Circumstantial evidence suggests that some migratory species forage as they migrate (Miller, 1897; Zinn and Baker, 1979; Valdez and Cryan, in press), a behavior that may slow their progress. Successful pursuit in ground vehicles will rely on the availability of roads, thus pilot efforts in geographically homogeneous, developed regions (e.g., American Midwest) would be advisable. It is likely that high-altitude flight behavior exhibited by some species of bats during migration (e.g., *Lasiurus cinereus* at an altitude of 2,438 m; Peurach, 2003) will make them easier to detect while migrating than is typical during foraging or roosting studies. Aircraft are an effective means of continuously following animals as they migrate but can be expensive and logistically difficult (e.g., flying at night without a predetermined flight plan). Most bat species have been observed flying at speeds less than 10 m/s, although slightly faster flight speeds (14 m/s) by migratory species have been recorded (Hayward and Davis, 1964; Ransome, 1990; Sahley et al., 1993). The minimum (stall) speed of a typical small aircraft such as a Cessna is approximately 30 m/s, or more than twice the flight speed of the fastest recorded bat. Thus, it is likely that the chase plane will far outpace any bat carrying a transmitter, necessitating frequent maneuvering. For detailed methods and considerations for tracking wildlife by aircraft, see Amelon et al., this volume, and Seddon and Maloney, 2004). A more cost-effective use of aircraft for tracking migratory movements is to use aircraft to find bats in their day roosts between nightly migration flights. Efforts to follow bats in ground vehicles during the night can inform such daytime searches with aircraft by providing the direction and approximate speed at which the marked bat was last detected. As it is probable that some species of bats migrate in groups, the deployment of numerous radio transmitters and use of radio receivers that rapidly scan multiple frequencies would increase the likelihood of successful pursuit by ground vehicles and aircraft. Any effort to follow migrating bats using radio transmitters must overcome the difficulty of determining the appropriate time to attach the transmitter. Most miniature (<1 g) radio transmitters have a limited life span (e.g., 10–15 days); therefore, it is crucial to attach them either at the commencement of migration or during migratory flight. Because prior knowledge of the period during which bats leave on migration may not exist, intercepting bats along their migration route may be the best starting point for new studies. Evidence of potential migration stopovers can be found throughout the literature (e.g., species of *Lasiurus* on the Farallon Islands; Tenaza, 1966; Cryan and Brown, 2007).

Problems of detecting active tags over long distances are generally overcome with the use of satellite transmitters. Platform transmitter terminals (PTTs) emit UHF (ultra high frequency) signals (401.650 MHz) to polar-orbiting satellites and their locations are subsequently calculated from Doppler shift information as the satellites pass overhead (ARGOS, 2005). After processing, locality coordinates are emailed to the researcher on a daily, weekly, or monthly basis. PTTs are an expensive yet effective means of tracking large bats over long distances and periods; transmitters cost US$1,000–3,000 and location acquisition and processing by ARGOS is approximately US$35 per day of tracking. The smallest PTT devices currently available weigh about 12 g (not including the mass of an attachment collar), and thus their use is limited to bats weighing at least 240 g (largest members of the family Pteropodidae, such as species of *Eidolon*, *Pteropus*, *Acerodon*, *Dobsonia*, and *Hypsignathus*). Tidemann and Nelson (2004) successfully used PTTs to track the long-distance movements of two gray-headed flying foxes (*Pteropus poliocephalus*) in Australia. Both animals moved approximately 2000 km and across more than 4 degrees of latitude during the course of their annual migrations. Location errors of PTTs range from several meters to tens of kilometers and are dependent on the position of satellites as they pass overhead and obstruction of the transmitted signal. Error estimates are provided with the PTT location coordinates sent by ARGOS. As with other tracking devices, lighter

PTTs may be developed during the coming years, but limitations of contemporary batteries to current power requirements, as well as the problem of increased location error with decreased size (Britten et al., 1999), are impeding such miniaturization (F. Riskey, pers. comm.).

An effort is currently underway to establish a system for tracking the signals of conventional, miniature radio transmitters (<1 g) using earth-orbiting satellites (Wikelski et al., 2007). If implemented, such a system would be ideally suited for following the long-distance movements of small, insectivorous migratory bats.

INFERRING BAT MOVEMENTS

Although it is preferable to follow the migratory movements of known individuals, the difficulty of doing so makes researchers often settle for inferential techniques. By monitoring bat movements at the population level, certain demographic data are sacrificed, but potentially important information on the timing and direction of migratory movements can be gained.

Observational Techniques

Observing migrants from a fixed point as they pass is a simple and effective way of collecting information on the migratory movements of animals (Dingle, 1996). Geographical features where birds are often observed in high numbers during migration include ridges, peninsulas, isthmuses, rivers, coastlines, and offshore islands. Circumstantial evidence indicates that concentrations of migrating bats may occur at similar features (Miller, 1897; Tenaza, 1966; Strelkov, 1969; Timm, 1989; Cryan, 2003; Cryan and Brown, 2007), although visual observations of groups of migrating bats are rare (Mearns, 1898; Howell, 1908; Hall, 1946; Heppenstall, 1960). Whereas monitoring the night sky for bats during migration periods has proven impractical in the past, new methods of "watching" bats in the dark might increase the utility of fixed-point observations. Infrared thermal imaging techniques, as described by Kunz, Betke, Hristov, and Vonhof (this volume), offer promise toward monitoring the movements of migratory bats, particularly at sites with wind turbines, where their movements through an area may be of conservation concern, and radar techniques, described below, may offer additional methods for monitoring migrating bats.

The use of radar for biological purposes began shortly after World War II (Lack and Varley, 1945). Since that time, biologists studying aerial animal movements have benefited from continuing advances in radar technology. Today's radars are sophisticated, digital instruments capable of yielding enormous quantities of data on biological processes such as migration. For a review of the efficacy of different types of radars used in biological research, see Larkin (2005). Herein we will consider basic operational differences in two general classes of radar commonly used by biologists and consider their value as tools in the study of bat migration.

The most common types of pulsed radars used for biological purposes fall roughly into two categories, based on the scale of information they provide. The first category is comprised of large and stationary surveillance radars (hereafter, *surveillance radar*), which emit longer wavelength signals to capture patterns in the broad distributions of hundreds to millions of aerial targets across large spatial scales. In particular, weather surveillance radars such as those within the United States NEXRAD (NEXt generation RADar) system have seen considerable use in biological studies during recent years. The second category of pulsed radars include small portable radar units (hereafter, *portable radar*), which emit shorter wavelength signals to capture the specific movements of individual targets across relatively small spatial scales; these include commercial marine radars and military tracking radars. Unfortunately, given the difficulties of acquiring and maintaining tracking radars, we are aware of only one currently in use in North America for biological work, although several are in use across Europe. All of the systems described above differ considerably in design constraints, operation, and portability; therefore, they complement rather than overlap in their usefulness for biological research and monitoring.

The usefulness of radar as a tool for studying bat migration is currently uncertain, although that uncertainty is more a consequence of problems with target identification (see below) than an inadequacy of any particular radar system. Because the design and use of surveillance radars often centers on monitoring air traffic or severe weather, physical constraints and policy usually predetermine scan strategies, radar siting, and other aspects of operation that may not be optimal for studying biological processes. Despite these constraints, mobility is less important when surveillance radars are numerous and comprehensive in their coverage, as is usually the case in the U.S. (e.g., NEXRAD; see Crum and Alberty, 1993), and the biological phenomenon of interest occurs over large spatial scales, as migration often does (Baker, 1978).

Reliable identification of radar targets is a prerequisite for using radar as a research instrument. The greatest challenge in applying radar to studies of bat migration lies in target identification; in particular, whether bats can be distinguished from other biological targets. Separating biological from nonbiological targets such as precipitation is more straightforward and beyond the scope of this discussion. Because surveillance and portable radars differ considerably in spatial and temporal resolution, the kinds of data used in target discrimination differ as well. Spatial resolution is determined by the size of the radar's "pulse volume," the smallest volume of airspace within which

echoes are quantified. Portable radars typically quantify, at high sampling rates, the echo in volumes of airspace small enough to contain single biological targets. Consequently, these radars gather highly detailed data on the behaviors of individuals (e.g., wing beat rate, climb rate, and changes in track). Surveillance radars quantify, at comparatively low sampling rates, the amount of echo from pulse volumes large enough to contain tens to thousands of individuals (depending on the target type and the manner of their distribution in the airspace). Because many individuals contribute to a single measure of radar echo, the details of individual behavior are traded in favor of providing less specific information on larger numbers of individuals over larger spatial scales. Surveillance radars quantify such large amounts of airspace that single pulse volumes frequently contain multiple taxa. Accordingly, target discrimination on surveillance radars is not absolute, but focuses instead on determining what kinds of animals dominate the airspace. Portable radars benefit by generally not being subject to these ambiguities.

Ornithologists have long been challenged by the need to separate bird from nonbird targets (Emlen, 1974; Flock, 1974; Larkin, 1991; Gauthreaux and Belser, 1998), and their experiences offer insight into the challenges facing the use of radars to study bat migration. Biologists typically make discriminations between target types based on differences in behavior and, to a lesser degree, size as apparent to radar (Diehl and Larkin, 2005). Organisms that differ in body size and shape can be distinguished by some specially equipped radars that are not yet widely available (Zrnic and Ryzhkov, 1998, 1999). However, when body size (e.g., body height or length) is similar to the wavelength of the radar—as is often the case—the amount of radio energy reflected by a target is not easily predicted from the target's size. As a result, in many circumstances a target's size on radar is typically not a useful factor for distinguishing taxa (Vaughn, 1985; Larkin, 2005).

Differences in natural history and behavior have proven useful in general target discrimination. Behaviors used in discriminating among target types include habitat preference, range of a species, response to weather, timing in the onset of flight, height and speed of flight, variability in flight behavior among individuals, and dates of migration. Numerous taxa have been associated with distinctive spatiotemporal patterns of radar echo using this approach, thereby permitting productive use of radar in biological research; however, migratory animals often show considerable overlap in such behaviors. Because behavior and natural history during migration are often poorly understood, especially among bats, only coarse taxonomic resolution is currently possible through radar. Biologists are challenged to develop means of identifying biological radar targets below the taxonomic levels of Class and even Order (e.g., foraging bats, foraging waterfowl, migrating raptors, migrating songbirds, migrating insects, aerial plankton). Nonetheless, as research has progressed in the area of target identification, the number of taxa discernable from idiosyncratic signal patterns has increased.

The primary challenge in using radar to study bat migration lies in discriminating bats from migrating songbirds, which also move in large numbers during the night. Because migratory bats and songbirds overlap considerably in body size and shape, morphological differences are of little use in target identification. Furthermore, similarities in body size between bats and birds result in many overlapping flight characteristics. Similarities in airspeed, altitude, wingbeat rate, and other attributes of flight (Hayward and Davis, 1964; Williams et al., 1973; Sahley et al., 1993; Larkin, 1991; Rayner, 1995) limit the range of behaviors available for distinguishing taxa using portable radars, which examine the finer details of individual flight. Unfortunately, because migration in bats is so poorly understood, little knowledge of behavior or natural history can be brought to bear on the problem of discriminating migratory bats from songbirds. For example, both bats and birds migrate in spring and autumn over much of North America (Griffin, 1970; Baker, 1978; Fleming and Eby, 2003), but are there regions of the continent where bat migration dominates? How large are migratory populations? Do migrating bats and birds exhibit similar flight speeds and heights during migration? How long do migrating bats remain aloft and do their flights occupy specific times of the nocturnal period? Foraging bats frequently exhibit erratic flight unlike that of songbirds, but is migratory flight similarly erratic (Gauthreaux and Livingston, 2006)? More research into the behavior of bats during migration, together with the wider application of more sophisticated radar technology (specifically tracking radar), may allow biologists to identify differences in radar echoes that distinguish bats from birds.

Conversely, differences between the behavior of bats and birds may be too subtle to be captured by radar, leaving biologists to make broad generalizations about the likelihood that monitored targets are one taxa or another based on their supposed relative abundances in the airspace. In North America, hundreds of bird species thought to number in the billions (Gaston and Blackburn, 1997) migrate long distances each spring and fall. On the whole, migrating birds likely outnumber migrating bats by a considerable amount and therefore explain the bulk of biological radar echoes during this time; however, the relative proportions of migrating bats and birds in the airspace are not well known and certainly vary locally. In certain locations and at certain times of year, migrating bats may dominate the airspace. If patterns in the relative abundance of migrating bats and birds in the airspace are discernable, then application of large surveillance radars

to studies of migrating bats may be relegated to relatively small scales where bats and birds exhibit little spatiotemporal overlap. Future studies that use radio transmitters, PTTs, or other devices to track bats as they move through an airspace while simultaneously monitoring the airspace by radar may shed light on the question of how we discern bats from other taxa.

Analysis of Occurrence Records

A wealth of information on the seasonal distribution patterns and potential migration routes of bats lies untapped in the form of disparate occurrence records. Mapping the monthly or seasonal distribution of occurrence records is an effective yet underutilized technique. For examples of studies that mapped the seasonal distribution of occurrence records see Dalquest (1943), Findley and Jones (1964), Hoffmeister (1970), and Cryan (2003). The difficulty of accessing, consolidating, and mapping occurrence records has historically limited the use of such techniques, but recent advances in information management and analysis make them ever more practical. Geographic information systems (GIS) provide an effective means of storing, displaying, and analyzing occurrence data. At the forefront of accessibility and verifiability are data associated with museum specimens. Scientific museum collections are the best source of information on historical bat occurrences because, unlike other types of records, museum data are well archived and are associated with verifiable specimens. Furthermore, several large museum collections are computerizing specimen data, adding geographic coordinates to specimen localities, and then making them available on the internet. For data not available on the Internet, museums can be queried for occurrence records, and geographic coordinates can be assigned based on place names of the collection locality using internet resources such as the U.S. Geological Survey's Geographic Names Information Server (http://geonames.usgs.gov/redirect.html), Environment Canada's Canadian Geographic Names Server (http://geonames.nrcan.gc.ca/index_e.php), and the Geographic Names Server of the U.S. National Geospatial-Intelligence Agency (http://earth-info.nga.mil/gns/html). A list of active mammal collections and their associated contact information can be found in Hafner et al. (1997). Researchers should be cautioned that even the most reputable museum collections sometimes misidentify bats. Therefore, when possible, museum collections should be visited so that specimens can be examined and verified. Although museum records offer a convenient means of mapping the seasonal distributions of bats, interpretation of these occurrence data should be treated cautiously. Museum records indicate presence only and absence of records from an area does not necessarily mean that bats do not occur there. Biases associated with variable collection techniques (e.g., shooting or hand-capture versus netting) and variation in seasonal activity levels must be considered. For example, many species of bats use torpor or hibernation, and the northward progression of occurrence records during spring, indicative of population movement, may be also be indicative of previously dormant individuals becoming active with the northward progression of warm temperatures (Baker, 1978). Other potential biases to occurrence data include underrepresentation of records from seasons during which biologists are not conducting fieldwork, or lack of records from areas where specimen collection is not commonly practiced. Additionally, the age and reproductive condition of bats may also affect likelihood of encounter (e.g., pregnant females and juveniles may be more likely to be captured). Despite these inherent biases of museum records, trends in the data such as the summer disappearance of records from wintering areas or disappearance of only one sex from an area probably indicate true movement patterns. Currently underutilized, yet more biased, sources of occurrence data include bats submitted to state health departments for rabies testing, capture data submitted through permitting compliance with state wildlife agencies, and information from acoustic detectors.

Population Genetics

The growing field of population genetics offers much promise in the study of bat migration. Details on the background and methods of population genetics as they apply to bat migration studies can be found in Ruedi and McCracken (this volume).

Stable Hydrogen Isotope Analysis

Analyzing the stable isotope ratios of biogenic materials (e.g., hair, feathers, whale baleen, butterfly wings) is a useful way to infer the long-distance movements by migratory animals (Hobson, 1999). The basic procedure of such methods is to measure the isotopic ratio of a given element in an animal's tissues and then relate that isotopic "signature" back to the most likely geographic region where the tissue was grown.

The analysis of hydrogen isotopes (deuterium [D]: hydrogen [H]) is particularly useful for animal migration studies, because no other element (except oxygen, which is highly correlated with hydrogen) exhibits such consistent patterns of distribution across the globe. The stable hydrogen isotope ratio (δD) of precipitation is inversely related to latitude, elevation, and distance from the coast across all continents (Rozanski et al., 1993):

$$\delta D = \left[\frac{(D/H)sample}{(D/H)reference} \right] \times 10^3$$

After initial shifts in δD between precipitation and primary producers (Ziegler, 1988), isotopic signatures tend to

change systematically across trophic levels (Birchall et al., 2005). Thus, in most cases, δD values of the tissues that an animal grows correlate in a systematic way with the hydrogen isotope ratios of local precipitation (δD_p; Hobson and Wassenaar, 1997). This relationship between δD_p and the δD values of animal tissues has enabled researchers to infer the geographic origins of migratory animals by analyzing tissues collected at different seasons and in different parts of their range (Chamberlain et al., 1997; Hobson and Wassenaar, 1997, 2001; Meehan et al., 2001). Cryan et al. (2004) used stable hydrogen isotopes to infer migratory movements of up to 2,000 km by hoary bats in North America.

There are two major criteria that must be satisfied in order to use stable isotopes. The first criterion is that the animal tissue being analyzed was grown before migration took place and that there has been little change in its isotopic composition after growth. Bat hair seems ideally suited for use in migration studies as it is biochemically inert and not subject to subsequent isotopic turnover once it is formed. Therefore, bats carry the hydrogen isotope signatures of the places where they grew their fur. Bat species in temperate latitudes typically molt into new pelage just once per year (Quay, 1970) and pelage replacement at such latitudes tends to occur from mid to late summer (Constantine 1957, 1958; Jones and Genoways, 1967). Evidence suggests that some variation in the timing of molt between age and sex groups may occur, with reproductive females molting later than males and juveniles (Jones and Genoways, 1967; Quay, 1970; Cryan et al., 2004). Despite such variation, it is likely that the majority of new hair growth occurs before migration takes place. Body tissues other than hair may not be well suited for migration studies because their different isotope turnover rates likely reflect pooled dietary inputs over recent weeks (e.g., blood, heart, liver) or years (e.g., bone), rather than a discrete time period before migration.

The second criterion required to apply stable isotopes is that δD of the animal tissue in question reflects δD_p of the geographic location where the tissue was grown. Excellent correlation between δD of fixed tissues and precipitation at the location of tissue formation has been shown for several species (e.g., Wassenaar and Hobson, 1998; Hobson et al., 1999b). For bats, Cryan et al. (2004) showed that the stable hydrogen isotope ratio of hair (δD_h) collected from hoary bats during summer in North America was correlated with δD_p of the collection site and the relationship was similar to that observed among birds. Although mammal hair is composed of α-keratin and bird feathers are made of β-keratin, processes of hydrogen uptake from food and water into these tissues are apparently similar. However, given the nature of the way that the data were collected by Cryan et al. (2004) it is unknown how well the relationship observed between δD_h and δD_p in hoary bats describes that of bats in general. Controlled laboratory experiments, in which several species of captive bats are fed a diet of known isotopic composition, would help refine our understanding of the relationship between δD_h and δD_p in bats.

Sample Collection and Preparation

Hair is a well-suited tissue for stable hydrogen isotope analysis because it is easy to collect, it stores well, and only miniscule amounts (less than 0.5 mg) are needed for analysis. At present, very little is known about variability in δD_h across the pelage of an individual bat. Because considerable intra-individual variation has been observed among the flight feathers of birds (Kelly et al., 2001; Meehan et al., 2003; Smith and Dufty, 2005), it is prudent to assume that such variation occurs in bats as well, until proven otherwise. Hair samples should always be cut from the same area of the bat's pelage and as close to the base of the hair shaft as possible. Samples can be stored in any type of clean and dry container for indefinite periods. Prior to analysis, hair should be cleaned of surface oils using a 2:1 chloroform:methanol solution. An effective technique for cleaning samples is to (1) place them in small glass vials; (2) pipette the cleaning solution directly into the sample vial; (3) slowly turn the vial so that most of the hair adheres to the sides; (4) pour off the solution through a clean screen; and (5) allow the samples to air-dry for 48 hours under a fume hood. After the samples are cleaned, it is important that they not be handled with anything but clean instruments, as contamination by surface oils can influence analysis results. Clean samples should be weighed into small increments on a microbalance (typically 0.25–0.35 mg); sample weights usually specified by the analysis laboratory. The weighed sample is then placed into a silver foil capsule and rolled or crushed using forceps to secure the hair within. Foil-wrapped samples can then be loaded into a sample tray for transport to the analysis lab.

Sample Analysis and Laboratory Standards

Several commercial and academic laboratories now provide stable isotope services. Cost of analysis of biogenic organic materials for δD currently ranges between approximately US$10–30 per sample. At the laboratory, hair samples and their silver foil capsules are typically pyrolyzed in a thermal combustion elemental analyzer and the resultant gas is analyzed using continuous-flow isotope ratio mass spectrometry. Values derived from mass spectrometers are reported in δ-notation as parts per million (‰) relative to Vienna Standard Mean Ocean Water (VSMOW). For detailed information on stable isotopes and their use in ecological studies, see Lajtha and Michener (1994).

There are several important considerations to make before commencing a study using stable hydrogen isotopes and bat hair. About 20% of the hydrogen in keratinous tissue (i.e., hair, feathers) exchanges freely with hydrogen in ambient water vapor (Wassenaar and Hobson,

2000a). Cryan et al. (2004) determined that 17% of the hydrogen in the hair of hoary bats could exchange with the environment; this value is similar to proportions of exchangeable hydrogen reported for other vertebrate tissues (about 16–22%; Wassenaar and Hobson, 2000a). Because the proportion of freely exchangeable hydrogen may vary among different types of mammal hair, preliminary experiments should be carried out to quantify such amounts for the species of interest using the steam-equilibration method described by Wassenaar and Hobson (2000a).

The free-exchangeable hydrogen in organic samples presents a problem for stable isotope analyses because temporal or geographical differences in the isotopic composition of ambient moisture can affect analytical results (Wassenaar and Hobson, 2003). Thus, the total hydrogen isotope ratio (δD_t) of a sample derived from mass spectrometry must be corrected for exchangeable proportions of hydrogen if results are to be comparable among analysis runs, studies, and laboratories. This requires a calibrated laboratory standard to correct for variation in the isotopic composition of ambient moisture over time and space. Unfortunately, widely available laboratory standards for hydrogen isotope analysis of organic samples having exchangeable hydrogen (i.e., keratin standards) are not yet widely available, thus researchers or analysis laboratories must develop their own. At least two keratin standards are needed with δD_h values that span the entire range of the samples being analyzed. Sufficient quantities of keratinous tissue, preferably mammal hair, should be acquired so that 0.25–0.35 mg increments of each standard can be included during all sample analysis runs. Large quantities of hair can be cleaned (as described above) and homogenized into a fine powder (< 200 micron sieved particle size) using a cryogenic grinder. Once appropriate keratin standards are obtained, comparative equilibration methods (Wassenaar and Hobson, 2000a) must be used to determine the nonexchangeable hydrogen isotope ratio (δD_n) of each standard. Standards should be included and reported for each batch of samples to be analyzed. If standards are used, analysis results from the laboratory will include measures of δD_t from the keratin standards, which can then be plotted against their known δD_n values to develop a regression equation for calculating δD_n of all other samples in the batch (Wassenaar and Hobson, 2003).

Interpreting Hydrogen Isotope Data

The greatest difficulty associated with the application of stable hydrogen isotope methods to studies of continental migration lies in the interpretation of laboratory results. Currently, the relationship between δD_h and δD_p in bats is not well defined. For example, Cryan et al. (2004) were unable to account for 40% of the variation observed between δD_h and δD_p in hoary bats. Potential sources of variation in δD_h include differences in temperature (McKechnie et al., 2004) or relative humidity (Cormie et al., 1994) across sites or years, input of water from sources other than precipitation (Wassenaar and Hobson, 2000a), drinking water effects (Hobson et al., 1999a), potential differences between adults and juveniles (Meehan et al., 2003; Smith and Dufty, 2005), or movement by bats over large areas as they molt into new pelage. Furthermore, values of δD_p on which relationships are investigated are usually taken from maps of weighted growing season δD_p (Bowen and Wilkinson, 2002; Meehan et al., 2004; Bowen et al., 2005; Dutton et al., 2005). Such maps are derived by interpolating climate data from relatively few sampling sites, and these data have been averaged over months and years, thus obscuring the potential seasonal, annual, and geographic variation in δD_p. Thus, a better approach may be the construction of species-specific isotopic base maps (cf. Wassenaar and Hobson, 1998). Until variation in δD_h and δD_p is better understood, it is unlikely that stable hydrogen isotope techniques will provide accurate (i.e., potential error less than hundreds of kilometers) quantitative measures of distances traveled by migratory bats. Regardless, the technique is very promising for relative measures of migration movement. For example, there is a current need to determine whether bats killed at wind power facilities are local residents or migrants from other areas. Stable hydrogen isotope analysis is well suited to answering such questions.

Use of Other Stable Isotopes

Several studies with migratory birds have shown that the incorporation of other stable isotopes (carbon, nitrogen, and sulfur) into analyses of movement can increase the probability of inferring the source areas of migrants (Caccamise et al., 2000; Wassenaar and Hobson 2000b; Hebert and Wassenaar, 2001; Hobson and Wassenaar, 2001; Rubenstein et al., 2002; Lott et al., 2003; Pain et al., 2004; Hebert and Wassenaar, 2005a, 2005b; Wunder et al., 2005). For a discussion of problems associated with the interpretation of data derived from multi-isotope migration studies see Wunder et al. (2005). Although the stable isotopes of carbon, nitrogen, and sulfur are not known to vary in a systematic way across continents, known distribution patterns of these isotopes in the environment can sometimes be used to study migratory movements at smaller scales. For an example and discussion of how stable carbon isotopes can be incorporated into studies of bat migration see Fleming et al. (1993), and Fleming (1995). These authors observed monthly changes in the stable carbon isotope ratios of tissues from nectarivorous bats (*Leptonycteris curasoae*), indicating seasonal shifts from a diet comprised of mostly cactus and species of *Agave* (CAM photosynthetic pathway) during spring and summer to a diet of mostly other types of flowering plants (C3 photosynthetic pathway) during winter (Fleming et al., 1993). This information supported hypotheses of migration movement by the species as well as identified a region where migration may not occur.

HOMING AND ORIENTATION

It is well established that bats are capable of returning to specific sites after making long migrations. The details of how bats consistently find their way across such distances, however, remain unknown. Most experimental studies into the navigational abilities of bats are those that examined homing ability. The majority of homing experiments on bats involved simply releasing marked individuals at various distances from their known roosts and waiting for them to return (see Griffin, 1970, for an in-depth review). The major assumptions of such homing experiments are that (1) the relocated animal actually wants or needs to return to the original roost, and (2) the point at which the bat is released is outside of its familiar area. Given our limited understanding of site fidelity and distance traveled in the course of a lifetime by individuals of most bat species, such assumptions are hard to assess. To further eliminate biases, homing experiments must be designed to address hypotheses of random scattering and systematic searching for familiar territory (Griffin, 1970; Wilson and Findley, 1972), as well as to account for the possibility that bats often return to different day roosts near the home roost after marking (Griffin, 1970) or frequently switch between several alternate day roosts (Lewis, 1995).

Several studies investigated the role of vision in long-distance orientation by either permanently or temporarily blinding bats during homing trials (Griffin, 1970). Techniques for temporarily obstructing the vision of bats include blindfolds (Mueller and Emlen, 1957) and miniature goggles (Williams and Williams, 1967). Williams and Williams (1967) radio-tracked bats with both impeded (treatment) and unimpeded (control) vision during homing flights of 10 km. Surprisingly, there has been only one subsequent attempt to follow homing bats using radio transmitters (Holland et al., 2006).

Although relatively biased, homing experiments on blinded animals conducted during the latter part of the 20th century offered important insight into the long-distance navigation of bats. Through these experiments, the general conclusion was reached that vision plays a key role in the ability of bats to orient during long-distance flights (Williams and Williams, 1967; Mueller, 1968; Griffin, 1970). Furthermore, because high frequency sound attenuates quickly in air, it is unlikely that echolocation plays a major role in long-distance orientation (Griffin, 1971). In the words of Donald Griffin (Griffin, 1970, p. 257), the discoverer of bat echolocation and pioneer of bat migration studies, "If we accept these indications that migrating and homing bats navigate by vision, we must then face the question of what they are looking at." To this day, the details of how bats use vision and other cues to navigate over long distances remain relatively unexplored.

At present, the possibility that bats navigate using celestial, solar, or magnetic cues cannot be discounted. Laboratory experiments on trained big brown bats, *Eptesicus fuscus*, demonstrated that they were capable of detecting light levels similar to those produced by bright stars (Childs and Buchler, 1981). Additionally, field and laboratory experiments indicated that *E. fuscus* orients using the postsunset glow as a reference point, apparently compensating for seasonal changes in solar azimuth at twilight (Buchler and Childs, 1982). Bats may also orient using certain acoustic cues from the environment (Griffin, 1970; Buchler and Childs, 1981). Magnetic materials have been detected in the carcasses of bats, suggesting the possibility of their perception of the earth's magnetic field, but early laboratory and field experiments to test for magnetic perception in bats were unsuccessful (August, 1984; Buchler and Wasilewski, 1985). However, Holland et al. (2006) recently exposed *E. fuscus* displaced from a summer roost to magnetic fields at sunset and observed experimental effects in the flight paths of bats as they returned home. These results suggested the bats were using a sunset-calibrated magnetic compass. As has been experimentally demonstrated with migratory birds (Berthold et al., 2003), it is likely that migrating bats navigate using a combination of sensory inputs that are informative at different spatial scales (Holland et al., 2006; Holland, 2007). Radio tracking of experimentally manipulated bats over various distances during migration may be a useful means of determining the relative importance of different sensory systems. Such techniques have been useful for studying orientation behavior of resident bats and migratory birds and, in combination with laboratory experiments, may work for bats as well. For example, Cochran et al. (2004) exposed migrating thrushes to artificial east-west magnetic fields at sunset and then radio-tracked them after release; the results indicated that migrating thrushes orient with a magnetic compass calibrated daily from twilight cues. Anyone interested in studying the navigation and orientation behavior of bats would benefit by familiarizing themselves with the considerable headway made in these areas by avian biologists (e.g., Alerstam, 1990; Berthold, 2001; Berthold et al., 2003), yet not let such information limit their thinking about potential migration behaviors that are unique to bats. Holland (2007) recently provided a thorough review of information on homing and orientation in bats, and identified several directions for future research.

SUMMARY

Tracking bats over long distances has proven extremely difficult, but recent advances in technology offer much promise toward our future understanding of this important phenomenon. Active efforts to follow bats as they migrate, as well as the application of techniques used to study bird migration, will likely reward those with the patience and energy to undertake such endeavors.

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THOMAS H. KUNZ

and

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