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STUDYING THE MIGRATORY BEHAVIOR OF INDIVIDUAL BATS: CURRENT TECHNIQUES AND FUTURE DIRECTIONS

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Migrating bats are among the most poorly understood of migratory taxa, with relatively little information available on their behavior and ecology during migration compared to other taxa. This arises because of the ''small animal problem,'' namely the limitations of current technology to track individual animals that weigh <190 g. In this paper (which is not a comprehensive review of bat migration) we assess the limits of current techniques available to study the migratory behavior of individual bats and what is needed to take the study of the behavior and ecology of migrating bats forward.

Key words: bat, behavior, ecology, global positioning system, migration, radiotracking, satellite telemetry

Every year billions of birds, bats, and insects make migratory movements of thousands of kilometers around the globe. The impact that these animals have on humanity is difficult to quantify but must surely be vast, both positive and negative (Wikelski et al. 2007). The reason their impact on us is so difficult to quantify is that although we are able to study the broadscale patterns of their movements, we know relatively little about their individual behavior during the journey. This lack of information about behavior during migration applies to migratory bats more than any other species. There have been some excellent reviews on the overall pattern of bat migration (Fenton and Thomas 1985; Fleming and Eby 2003; Griffin 1970), all of which suggest that bat migration is a relatively rare phenomenon, and demonstrate that much less is known about migration in bats than in migratory birds (Fleming and Eby 2003). However, the rarity of the phenomenon of bat migration may in part be an artifact of the lack of knowledge about tropical species, for which relatively little is known with regard to migratory behavior (Popa-Lisseanu and Voigt 2009).

Why is it so difficult to study the behavior of migrating animals such as small insectivorous bats over the course of their journey? This is because of what we define here as the ''small animal problem.'' The general rule for transmitter weight is that it should not exceed 5% of the animal's body mass (Aldridge and Brigham 1988; Caccamise and Hedin 1985). Although there are satellite transmitters that allow the tracking of animals over large distances and even a number of years (Jouventin and Weimerskirch 1990), these devices weigh a minimum of 9.5 g and so are currently limited to animals that weigh >190 g. This precludes the tracking of 60% of mammals (Wikelski et al. 2007). Although some fruit bats can be tracked using satellite transmitters (Richter and Cumming 2008; Tideman and Nelson 2004), the insectivorous migratory bats of Europe and North America are certainly all below this 190-g size threshold: an examination of the weights of bats indicates that for known migratory bat species, 90% cannot be tracked with currently existing technology (Fig. 1). Five-gram satellite tags have successfully been tested and may soon become available from Microwave Telemetry, Inc. (Columbia, Maryland), but even using these tags would only increase the percentage of migratory bat species that can be tracked globally to 15%.

The importance of tracking small animals in a natural setting to solve a number of pure and applied scientific questions has been discussed recently (Altmann and Altmann 2003; Holland et al. 2007; Wikelski et al. 2007). Many bat species are endangered, and because they have a high mortality at wind turbines there is an urgent need to discover more about their behavior at these facilities (Baerwald et al. 2008; Kunz et al. 2007). Furthermore, the recently discovered white nose syndrome, a fungal agent that may cause very high mortality in temperate zone bats (Blehert et al. 2009), causes further concerns about the movement of these animals. The impact of this disease on the migratory bats of North America is currently unknown. Additionally, along with birds, bats represent 1 of only 2 vertebrate taxa that fly and make rapid, wide-ranging movements. This makes bats highly interesting in comparison with migratory birds in understanding how

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evolution has shaped the migratory mechanism in these 2 taxa (Bingman and Cheng 2006). Bats are thus a flagship taxon for the small animal problem.

When compared with birds, for which there are 50 years of research on individual mechanisms during migration, it is amazing that so little is known about the migratory mechanisms of bats (Holland 2007). It is vital to study migratory phenology, stopover ecology, migratory flyways, and behavioral decisions so that this knowledge can be applied to the conservation of these mammals. Given that there is currently no method to track most bats globally with high spatial definition, how can we study their behavior, and what needs to be done to achieve the final goal of tracking bats individually on a global scale? In this paper, which is not a comprehensive review of bat migration, we will discuss current techniques for tracking the behavior of individual bats and the technological advances required to provide the ultimate goal of solving the small animal problem.

Traditional Techniques for Monitoring Movement

The most widespread method of tracking the movement of animals involves mark by banding (called ringing in Europe) and recapture. This has been used with great success to categorize breeding and wintering areas and occasionally stopover sites in a vast number of bird species (Bairlein 2001). Banding studies in bats have been fewer, in comparison, but nevertheless a coordinated European effort has revealed a highly useful data set on the movement of bats within this area (Hutterer et al. 2005). A concerted banding effort also has revealed which populations of *Tadarida brasiliensis* are migratory and which are sedentary in the southern United States and Mexico (Cockrum 1969), and some African fruit bats are known to be migratory on this basis (Thomas 1983). In the United States, it is much rarer to recover temperate zone migratory bats that have been banded, and they are usually found near where they were initially captured (Cryan and Diehl, in press; Griffin 1970). Coordinated efforts across national borders are lacking. As a result little is known about even the maximum scale of movement of the migratory tree bats of North America based on banding recoveries (Cryan 2003; Cryan et al. 2004). This may be a problem caused by the roosting habits of the tree-roosting bats, which generally make capture and recovery of banded bats more difficult than for cave-roosting species. In fact, anecdotal observations have been more informative than banding studies about the behavior of tree bats during migration (Cryan and Diehl, in press) and at least 2 more species of the genus *Lasiurus* may be migratory, but hard data are lacking (P. M. Cryan, United States Geological Survey, Ft. Collins, Colorado, pers. comm.). Population genetic studies also have been used to infer a migratory lifestyle, because migratory bat species are expected to have far less genetic differentiation between populations than sedentary bats (Burland et al. 1999; Petit and Mayer 2000; Russell et al. 2005). Although population genetics can be used to imply migratory behavior, and even indicate distance of movement (Ceballos et al. 1997), it cannot be used to study the behavior of individual bats. In some cases population genetic methods are unable to distinguish between migratory and nonmigratory populations within the same species (Russell et al. 2005). Other techniques such as the implanting of passive integrated transponder tags may improve recoveries in bats. Similarly, stable isotope studies (Cryan et al. 2004) and records for museum specimens (Cryan 2003) have been used to answer questions about range of movement and seasonal distribution of migrating bats at a population or species level. Nevertheless, these techniques are insufficient to investigate individual behavioral decisions, which may be crucial in categorizing migratory movements of bats. Radar also has been used to monitor migratory animals including bats (Horn and Kunz 2008), and some radar can resolve individuals (Bruderer and Popa-Lisseanu 2005). However, it is difficult to identify species using radar, and the range of radar is limited, making it less useful for tracking an entire migratory journey (Cryan and Diehl, in press). To study the behavior of individual bats it is necessary to track their movement actively. In the remainder of this paper we discuss the techniques that can be used to track small insectivorous bats. We also highlight the limits of such methods and what is necessary to investigate migratory behavior of bats over the whole range of their migration.

Tracking Individual Small Animals

As noted previously the ''small animal problem'' arises because 90% of migrating bat species cannot be tracked by global satellite telemetry (Fig. 1). Furthermore, the smallest satellite tags require solar power, and it is uncertain whether they would be effective for bats, which are mostly nocturnal or crepuscular; it will be necessary to test these tags in low-light conditions. Indeed, in the study of Richter and Cumming (2008) in which the straw-colored fruit bat (*Eidolon helvum*; mean mass 290 g) was tracked using a 12-g solar-powered Argos tag (Microwave Telemetry, Inc.), problems were encountered with recharging and thus fewer data than expected were obtained. Other options for tracking the path of migrating bats are geolocation (Croxall et al. 2005) and radiotelemetry (Lord et al. 1962).

Geolocation. This technique relies on calculating latitude and longitude from the changing times of sunset and sunrise and is currently being used successfully in tracking songbirds (Stutchbury et al. 2009). Current devices (about 1 g) are small enough to be used for the heavier migratory insectivorous bats that weigh more than 20 g such as *Nyctalus noctula* and *Lasiurus cinereus*, but as data-logging devices, they require the animals to be recaptured for data recovery. Geolocation loggers have not yet been tested on bats but, given that many species are faithful to the same roosts year after year (Lewis 1995), the possibility of recapture is high, particularly for cave-roosting species such as *N. noctula*. Geolocation techniques are less likely to be as effective in tree-roosting

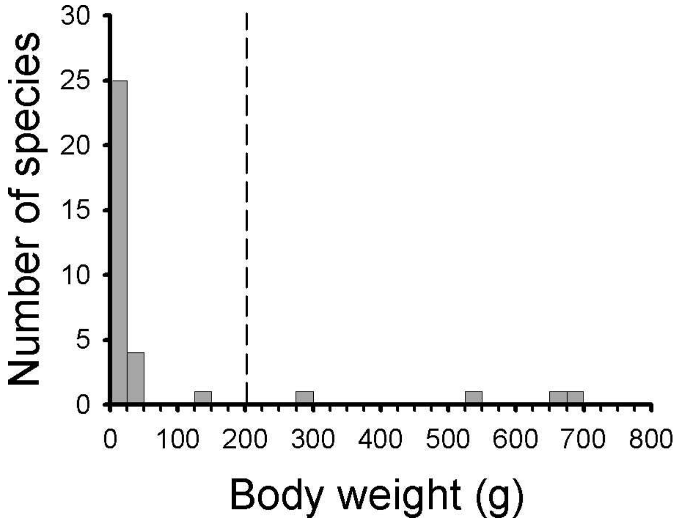

Fig. 1. Frequency histogram of the weight classes of all 34 known migratory bat species as defined by Fleming and Eby (2003). The dashed line at 190 g indicates the lower size limit of animals that can be tracked by global satellite systems using a platform transmitter terminal, according to the 5% weight rule (Aldridge and Brigham 1988). The upper limit of each class is a 25 g interval. Classes to the left of the line are those that cannot be tracked by a 9.5 g satellite transmitter, which is currently the lightest available platform transmitter terminal.

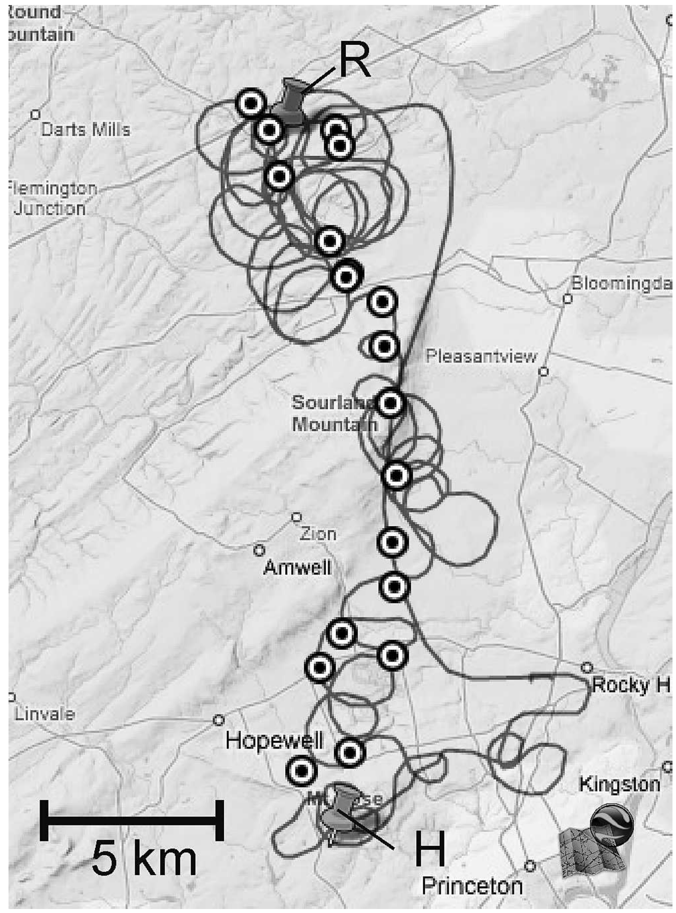

Fig. 2. The track of a male big brown bat (*Eptesicus fuscus*) released 20 km from the home roost (control bat from Holland et al. [2006]). R indicates the release site and H indicates the home roost. Tracks were obtained by an aircraft circling the transmitter signal emitted and taking a global positioning system reading at the point of strongest signal. The line indicates path of the plane and circles indicate global positioning system points taken on the route. The total time taken for the bat to return was 1 h 15 min. The data are plotted in Google Maps (www.maps.google.com).

species, where lower densities and unknown roost fidelity makes recapture less likely. One main problem with geolocation technology is location error, which can be in the region of 180 km (A. Fudikar, pers. comm.). Such a large location error makes identification of stopover roosts or flyways difficult using this technique. Additionally, it is unknown to what extent the general nocturnal habit and roosting ecology would affect the accuracy of the device at this stage. Nevertheless, geolocation remains a promising but challenging technology for studying bat migration.

Radiotracking. Radiotracking has been used to track birds since the early 1960s (Lord et al. 1962), and shortly thereafter was used to track bats (Williams and Williams 1967, 1970). Radiotracking uses a transmitter that emits a signal in the megahertz range, which can be detected by a radioreceiver tuned to the appropriate frequency. This is known as active tracking. Unlike satellite transmitters, which transmit locations via a satellite so that the tag or the animal need never be recovered, with radiotracking the researcher must maintain contact with or periodically relocate the transmitter signal to locate the animal. This receiver may be fixed to a tower, held in the hand and used on foot, or mounted in a vehicle; it can be used on land, sea, or air. Much radiotracking is done on foot for many animal species. Operators use handheld receivers to locate the position within a habitat by triangulation, and radiotracking can be used to determine home range, habitat use, or daily movements (Kenward 2000). It is relatively easy to track on foot animals such as mammalian carnivores or ungulates, but it is more challenging to track a flying animal, and radiotracking has been used much less often to track migration of flying vertebrates. Nevertheless, much insight has been gained using radiotracking on mostly nonmigratory bats (Fenton et al. 1998; Kalko et al. 1999). A reduction in weight of radiotransmitters in the last 10 years means that, with a tag size of as little as 0.2 g, animals as small as 4 g can be tracked. Radiotracking studies have now successfully revealed aspects of behavior in migrating songbirds (Cochran and Kjos 1985; Cochran et al. 2004; Thorup et al. 2007), homing bats (Holland et al. 2006, 2008), and even migrating insects (Sword et al. 2005; Wikelski et al. 2006).

A common theme in most experiments that tracked migration over long distances has been the combination of vehicle-based and aircraft-based tracking of the animal in order to fix its location in time and space. There are 2 options for collecting such locations. The 1st is to maintain active contact with the animal while it is moving to create a relatively high-resolution track of the animal's movement (Fig. 2). This is possible by using a ground vehicle in areas with uniform flat terrain, such as the American Midwest, and it was used successfully to track a Swainson's thrush

(*Catharus ustulatus*) over a total distance of 1,512 km (Cochran and Kjos 1985). In more built-up areas it is difficult to maintain contact with a flying animal from the ground, and if the animal is highly mobile, terrain and road directions can make tracking frustrating. In these cases an aircraft has been used to track the animal. It may be possible to track the animal actively as it moves, by circling the aircraft to find the point of strongest signal (as shown in Fig. 2). One of us (MW) has confirmed, with transmitters hidden on the ground, that this can give an accuracy of ±100 m. If many animals are being released simultaneously or contact is lost, another option is to survey aerially by flying back and forth over the region. For migrating bats and night-migrating birds, most movement is at night, so daytime surveys can often locate the stopover position where the animal is resting. Daily surveys provide less resolution than actively following a moving animal, but they allow for a larger number of individuals to be tagged at a time when only 1 aircraft is available, or if animals fly during bad weather when it would be dangerous for small aircraft to fly. Such daily survey techniques have been used successfully to study navigation of migratory songbirds (Thorup et al. 2007) and migration in dragonflies (Wikelski et al. 2006).

An aircraft has not yet been used successfully to track an animal over its entire migratory journey, however. Although this may theoretically be possible, in practice manpower and resources have not been sufficient to accomplish it. Currently, therefore, although radiotracking is the best way to study the movement behavior of individual migratory bats, with our current detection methods it is unlikely to solve the problem of tracking them globally.

Future Directions—How Do We Solve the Small Animal Problem?

Clearly, what is needed to globally track small animals such as most bats is an active radiotag weighing <1 g that can be detected by a satellite system that relays the location of the animal to the researcher without the need for active tracking or recapture. The Argos system uses platform transmitter terminals, which are attached to the animal and calculate its position using Doppler shift of the radiosignal emitted. This system meets many of these criteria but is still too heavy to track an insectivorous migratory bat. The recent development of solar-powered receivers has started to address the main cause of the weight limit: battery size. With a new generation of platform transmitter terminals weighing 5 g now in the prototype stage (Microwave Telemetry, Inc.) it may not be too long before a lighter tag is available. Accuracy is a problem with such tags, however, because the error of fixes can range from a few hundred meters to a few kilometers. Accuracy can be increased by adding global positioning system receivers, which allow data to be downloaded remotely through the Argos system. However, these devices now weigh ≥22 g and it is not likely they will become significantly smaller with current limitations on technology (F. Kümmeth, E-obs GmbH, pers. comm.). The limiting factors for the global positioning system are not only battery size (required for processing power) but also size of the antenna or ground plane, because the global positioning system satellite constellation orbits at a high altitude.

An alternative to waiting for current satellite-based systems to become smaller would be to install a highly sensitive radioreceiver in low-earth orbit that could detect radiotransmitters (Cochran and Wikelski 2005; Wikelski et al. 2007). Theoretically, currently available radiotransmitters can be detected from a satellite in a low earth orbit (400 500 km). There are 2 large issues with such a system, though: the effects of signal-to-noise ratios between small transmitters on animals and a receiver in orbit are currently unknown and expensive to test, and cost of launching such a system is substantial. Although it may seem redundant to recommend building a new satellite system when the Argos system already exists, the urgent need for the information that would be available from such a small-animal tracking system should not be underestimated. There are billions of small animals in addition to bats migrating around the globe every year, and we are still quite ignorant about their impact on ourselves and the environment. We have some knowledge of the extent to which they provide services to the ecosystem (Cleveland et al. 2006), but the role they play in emerging infectious diseases is still debated (Dobson 2006; Fenton et al. 2006). We believe that the importance of information about these movements for both pure and applied science has been ignored for far too long. We conclude by arguing that there has been a trend for scientists to bring research into the laboratory to study the details of behavior and ecology. In practice, biology does not exist in such environments, and techniques that allow us to comprehensively study migratory behavior in a natural setting are not out of reach, but urgently need to be developed to advance ecological research in the 21st century.

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