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Bat Migration[☆]

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Abstract

This article summarizes current knowledge about the migratory behavior of temperate and tropical bats. A close association between migration and hibernation exists in temperate, but not in tropical, bats. Compared with birds, bats are relatively short-distance migrators, with maximum migration distances being <2000 km; intercontinental migration is likely to be uncommon in bats. Migratory bats have lower levels of population subdivision and larger genetically effective population sizes than nonmigratory bats. A variety of methods, including banding, genetic analyses, stable isotope analyses, and tracking with radio or satellite transmitters, are currently being used to study bat migration. The conservation of migratory bats poses special challenges that require national and international efforts. Migratory bats sometimes harbor pathogens that can be transmitted to humans. Overall, the beneficial aspects of migratory bats, including control of insect populations and dispersal of pollen and seeds over broad areas, far outweigh their negative aspects.

Keywords

Bats; Conservation; Fat deposition; Genetic structure; Hibernation; Metapopulations; Migration; Mitochondrial DNA; Reproduction; Stable isotopes; Transmitters; Viruses; White nose syndrome

Introduction

Migration is an essential feature of the life history of a substantial fraction of the world's animal fauna. Among vertebrates, migration, which can be defined as a seasonal, usually two-way, movement from one habitat to another to avoid unfavorable climatic conditions and/or to seek more favorable energetic conditions, is common in fish and birds. It is less common in amphibians, reptiles, and mammals. Among volant vertebrates, it is much more common in birds than in bats, and birds migrate much longer distances, on average, than bats. Nonetheless, a considerable number of bats, including both temperate and tropical species, undergo significant seasonal movements between habitats (Avgar *et al.*, 2014; Cryan and Diehl, 2009; Fleming and Eby, 2003). As I discuss in this article, these movements have important population and conservation consequences. In a world of global climate change and increased extinction risk for an estimated 25% of the world's mammals (Hoffmann *et al.*, 2010), migratory species are especially vulnerable to extinction risks and are of major conservation concern. These concerns include the effect of wind turbine farms on migratory bats and their roles as reservoirs for emerging diseases that can be fatal to humans.

An Overview of Bat Migration

Temperate Bats

Until recently, migration in bats had mostly been studied in temperate regions of North America and Europe where migratory behavior is closely associated with hibernation. Results of those studies indicate that temperate bats exhibit three broad patterns of spatial behavior: (i) sedentary (nonmigratory) behavior in which bats breed and hibernate within a 50-km radius or less; (ii) regional migration in which bats migrate 100–500 km between summer and winter roosts; and (iii) long-distance migrants in which bats migrate 1000 km or more between seasonal roosts (Fleming and Eby, 2003). Examples of European sedentary taxa include species of *Eptesicus*, *Plecotus*, and *Rhinolophus* and certain species of *Myotis*. Their North American counterparts include *Eptesicus fuscus*, *Corynorhinus rafinesquii*, and *Antrozous pallidus*. European regional migrants include several species of *Myotis*, and North American taxa include several species of *Myotis* and *Pipistrellus* (or *Perimyotis*) *subflavus*. European long-distance migrants include several species of *Nyctalus* as well as two species of *Pipistrellus* and *Vespertilio murinus*. Although they migrate relatively long distances between summer and winter roosts, they do so within, rather than between, continents, unlike many European migratory birds which are intercontinental migrants. In North America, long-distance migrants include species of *Lasiurus*, *Lasionycteris noctivagans*, and the subtropical/tropical seasonal migrants *Leptonycteris yerbabuena* (formerly *L. curasoae*), *L. nivalis*, *Choeronycteris mexicana*, and *Tadarida brasiliensis*. With the possible exception of *Lasiurus* species, these taxa are also intracontinental migrants. Unlike other temperate migrants, these species do not hibernate (but see Weller *et al.*, 2016 for hibernation in *Lasiurus cinereus*).

[☆]Change History: December 2017. T.H. Fleming updated the text and references based on articles written between 2010 and 2017 and added a discussion of white-nose syndrome, which is affecting North American migratory bats. This is an update of T.H. Fleming, Bat Migration, In Encyclopedia of Animal Behavior, edited by Michael D. Breed and Janice Moore, Academic Press, Oxford, 2010, Pages 145-149.

As is the case in birds, temperate zone long-distance migrant bats tend to differ morphologically from more sedentary species and are adapted for rapid, energetically efficient flight (Norberg and Rayner, 1987). They have wings with high aspect ratios (i.e., they are long and narrow), pointed wing tips, and high wing loading. As a result, most insectivorous long-distance migrants forage in uncluttered air space away from vegetation where slow, highly maneuverable flight is not needed. In addition, many long-distance migrants (e.g., the European species plus *Lasiurus* and *Lasionycteris* in North America) roost in small colonies (or are solitary) in trees and buildings rather than in large numbers in caves, as is often the case in regional migrants and sedentary species. Exceptions to this include North American *T. brasiliensis* and *L. yerbabuena* which are highly gregarious cave dwellers year round (Fleming and Nassar, 2002; McCracken and Gassel, 1997).

Not all individuals of species of temperate migratory bats undergo seasonal migrations. Partial migration (in which some populations are sedentary whereas others are migratory) occurs in a number of species, including long-distance migrants. In Europe, partial migrants include species of *Nyctalus* and *Pipistrellus* and *V. murinus* (e.g., O'Mara et al., 2016; Rydell et al., 2014). In North America, partial migrants include *Lasiurus cinereus*, *L. noctivagans*, *L. curasoae*, and *T. brasiliensis*. In Europe, sedentary populations of *P. nathusii* share hibernation caves with migratory populations, whereas sedentary and migratory populations of *V. murinus* have geographically separate ranges year round (Roer, 1995). A situation similar to that of *V. murinus* is seen in North American *T. brasiliensis* in which western and southeastern populations in the United States are sedentary and seasonal populations in the south-central United States overwinter in Mexico (McCracken and Gassel, 1997).

Regardless of the distances involved, most temperate zone migratory bats undergo a characteristic annual physiological and reproductive cycle that is closely tied to hibernation. This cycle includes hyperphagia and fat deposition in the fall and mating in the fall or winter. Unlike birds, which sometimes increase their body mass by 50% by fat deposition prior to migration, bats increase their mass by only 12%–26% by fat deposition (e.g., Krulin and Sealander, 1972). Also, unlike birds, bats must use most of the fat they deposit prior to or during migration as a fuel source during hibernation (Herlekar, 2015). Conservation of stored fat for use during hibernation is an important reason why many temperate bats migrate relatively short distances. Finally, the annual reproductive cycle of temperate bats usually involves mating in the fall prior to hibernation. In some species (e.g., *N. noctula*, *P. nathusii*), mating occurs along female migratory pathways with males defending roost sites which are visited by females for mating (McCracken and Wilkinson, 2000). In other species (e.g., *Myotis* species in North America), individuals of both sexes form 'swarms' at the entrances of hibernation or other caves, probably for mating. After mating, females of hibernating species store viable sperm in their oviducts during the winter and ovulate and undergo fertilization in the spring prior to migrating to their summer maternity roosts. In nonhibernating long-distance migrants such as *Lasiurus borealis*, *L. yerbabuena* and *T. brasiliensis*, mating and fertilization occur simultaneously prior to or during spring migration.

Tropical Bats

Migratory behavior is much less common in tropical bats than in temperate bats and is never associated with hibernation (Fleming and Eby, 2003). Whereas temperate bats migrate and hibernate to avoid habitats that are energetically and physiologically unfavorable during winter, tropical, and subtropical bats usually migrate along food resource gradients or among seasonally ephemeral resource patches. A clear example of this is the nectar-feeding, long-distance migrant *L. yerbabuena* in Mexico and the southwestern United States (Fleming and Nassar, 2002). During the fall and winter, populations in western Mexico live in tropical dry forest and visit flowers produced by trees and shrubs during an annual flowering peak. After mating, many pregnant females (but few males) migrate 1000 km or more to the Sonoran Desert of northwestern Mexico and Arizona along a 'nectar corridor' of blooming columnar cacti (Fleming et al., 1993). Once in the Sonoran Desert, they form maternity colonies and feed at a super-rich source of nectar and pollen produced by several species of spring-blooming columnar cacti. Populations of this species living in central or southern Mexico are more sedentary because their floral resources are available year round. In Africa, several species of fruit-eating pteropodid bats, including *Eidolon helvum*, *Myonycteris torquata*, and *Nanonycteris veldkampii*, migrate up to 1500 km away from equatorial forests to savanna woodlands to feed on seasonal bursts of fruit (Thomas, 1983). In eastern Australia, the pteropodid bat *Pteropus poliocephalus* contains sedentary coastal populations that feed on fig fruits year round and inland populations that migrate hundreds of kilometers between ephemeral but rich patches of flowering eucalypt trees (Eby, 1991). Finally, several species of insectivorous rhinolophid and vespertilionid bats undergo short-distance migrations between coastal and inland habitats in East Africa in response to seasonal changes in food availability (O'Shea and Vaughan, 1980).

Methods for Studying Bat Migration

Obtaining precise quantitative data on the distances that bats migrate and their migratory pathways have been technologically challenging (reviewed in O'Mara et al., 2014). From the 1930s until recently, placing numbered aluminum bands on bats was the predominant method used to study bat (and bird) migration. This method involves banding bats at one roost (either a summer or winter roost), and then attempting to recapture banded bats (or recover their bands) somewhere else. This method is very labor intensive and inefficient because only a tiny fraction (=1%) of banded bats are usually ever recovered away from their original banding sites. For example, over 400,000 *T. brasiliensis* were banded in winter roosts in Mexico and summer roosts in the southern United States in the 1950s and 1960s, and only a handful were ever recovered away from their banding sites (Cockrum, 1969).

In addition to banding, methods that are currently being used to study bat migration include analyses involving DNA and stable isotopes and tracking studies using radio or satellite transmitters, GPS devices, and data loggers. Control region mitochondrial DNA is potentially very informative about genetic connections among distant roosts from which migratory connections can be inferred. A

study of *L. yerbabuena* using this technique, for example, was able to identify two pathways along which females moved from south-central Mexico into the Sonoran Desert and southeastern Arizona, respectively, using data from only 49 individuals captured at a total of 13 roosts (Wilkinson and Fleming, 1996). Since this species is federally endangered in the United States and Mexico, large-scale banding operations were not feasible and other methods were needed to determine the scale of its migratory movements. Genetic analysis proved to be a very efficient method to obtain this information and to identify roosts in Mexico of special conservation concern (e.g., mating roosts). Other species whose migratory behavior has been studied using genetic techniques include *Miniopterus schreibersii*, *N. noctula*, and *T. brasiliensis* (reviewed in Moussy et al., 2013).

Another analytical technique that has provided important new insights into the migratory behavior of hard-to-study bats is stable isotope analysis. Stable isotopes of carbon and hydrogen are especially useful for this. The ^{13}C stable isotope of carbon allows one to determine whether herbivorous animals are feeding on plants that use the CAM, C4, or C3 photosynthetic pathway. The first two pathways are used by succulent plants (e.g., cacti and agaves) or tropical grasses (e.g., corn), respectively, and are enriched in ^{13}C compared with the more common C3 plants. By analyzing carbon stable isotopes in muscle tissue taken from museum specimens collected throughout its geographic range in Mexico and the southwestern United States, Fleming et al. (1993) found that individuals of *L. curasoae* use CAM plants (primarily columnar cacti in the spring and agaves in the fall) as food sources during migration and C3 plants during the winter. Knowing that columnar cacti occur in the Pacific coastal lowlands of Mexico and that agaves occur in upland portions of the Sierra Madre, they were able to identify the likely 'nectar corridors' along which these bats fly during migration.

Deuterium (D), the stable isotope of hydrogen, is useful for determining the migration distances of solitary roosting insectivores such as *L. cinereus* and *L. noctivagans* (Sullivan et al., 2012). Values of D vary inversely with latitude, elevation, and distance from coasts and can indicate approximately where bats were living when new tissue such as hair was produced. Since the aforementioned bats tend to molt before migrating in the fall, an analysis of hair samples from bats caught during migration or in their winter locations can be used to determine how far they migrated after molting. This technique has been used to determine migration distances of 1800–2600 km for both males and females of *L. cinereus* in North America (Cryan et al., 2014a). Some bats molting during the summer in Canada were captured in Mexico in the winter. The researchers concluded that this technique holds considerable promise for studying long-distance migration in bats.

Radio-tagging and satellite tracking are two methods for directly studying the migratory behavior of bats. Radio transmitters weighing <1 g are readily available and have been used to study the foraging and roosting behavior of many species of bats, including species weighing <10 g. Except for the Australian *Pteropus poliocephalus*, which can carry transmitters with large batteries because of their large size, they have not yet been used to study bat migration for at least two reasons: (i) the battery life of these transmitters is short (about 2 weeks) and limits the amount of data that can be gathered from individual bats; (ii) since they migrate at night and sometimes at substantial altitudes (up to 2400 m), following radiotagged bats during migration involves potentially dangerous night time airplane flights over unknown terrain. Less dangerous but more costly in terms of transmitters (which cost US\$1–3K) and daily or weekly downloads, satellite transmitters offer great potential for studying migration in bats, as it does for birds. Solar-powered satellite transmitters now weigh 12 g and have been used to study foraging and migration movements of one species of pteropodid bat that roosts in tree canopies (rather than in caves) during the day. Richter and Cumming (2008) studied the movements of four individuals of the 300 g frugivore *Eidolon helvum* that they tagged in central Zambia, Africa. These bats foraged up to 59 km from their day roost and traveled 878–1975 km over a period of two or more weeks when flying north to the Democratic Republic of Congo. During the return trips, these bats averaged 90 km per night. Satellite transmitters equipped with conventional batteries (total package weight=33–40 g) have been placed on two young males of *Pteropus poliocephalus* weighing 790 and 857 g in south-eastern Australia. Over the course of about a year, these bats made round trips of >2000 km spanning over 4° latitude as they moved up to 400 km among roosts in response to changes in the local availability of eucalypt blossoms (Eby, 1991). Satellite tracking of *Pteropus vampyrus* in Malaysia has revealed that individuals are highly mobile and often move hundreds of kilometers to Indonesia and Thailand (Epstein et al., 2009). Similar long-distance cross-border movements have also been reported in two other satellite transmitter-tagged Australasian species of *Pteropus* (Breed et al., 2010). As discussed below, these movements in migratory bats have important implications concerning the spread of infectious viruses as well as conservation.

Population and Genetic Consequences of Migration

Migration can have strong effects on the population and genetic structure of bats (Burns and Broders, 2014; Moussy et al., 2013). In temperate bats, males and females typically hibernate in the same caves and are largely trophically inactive during winter. During the trophically active season, the behavior of males and females of migratory species often differs with respect to distances they migrate and locations where they spend the summer. In many species, females migrate longer distances and form larger summer (maternity) colonies than males (Fleming and Eby, 2003). As a result, the sexes are often geographically separated at a variety of spatial scales during the summer. An extreme example of this is *Lasius cinereus* in which males spend the summer in the mountains of western North America and females roost in north-central and northeastern United States and Canada. Sex-biased migration and seasonal spatial segregation of males and females also occur in *L. yerbabuena* and *T. brasiliensis* in North America. In both species, females migrate north from south-central Mexico to form large maternity colonies in the Sonoran Desert and south-central United States, respectively.

Seasonal movements can also have community consequences whenever regional and long-distance migrants move into and out of habitats containing resident species. In West Africa, for example, three species of frugivorous pteropodid bats migrate from

equatorial forests to more northern savanna woodlands where they join a resident community of several species of frugivorous bats and birds (Thomas, 1983). Differences in habitat and fruit preferences reduce potential competition among these species. A similar situation is seen in East Africa where several species of migrant insectivorous bats join a community of resident insectivores during periods of increased insect availability. Differences in morphology and foraging behavior again allow these species to coexist. Finally, seasonal influxes of migrant nectarivores and insectivores increase the species richness of bats in Sonoran Desert communities during the summer. As in the other two examples, differences in diets and foraging behavior minimize competition between residents and migrants.

As might be expected given their high mobility, the genetic structure of migrant species also differs from that of nonmigrants in a predictable way: a lower degree of genetic subdivision and larger effective population sizes in migratory species (Olival, 2012). An extreme example of a sedentary species is the Australian megadermatid *Macroderma gigas* in which widely separated colonies seldom exchange genes. As a result, Wright's index of subdivision F_{st} for this species is about 0.87 (out of 1.0 for complete subdivision; a value of 0.0 represents complete panmixia). At the other extreme is the long-distance migrant *N. noctula* whose F_{st} is 0.006 and whose region of panmixia in central Europe has a diameter of about 3000 km. Other species in both mobility classes have less extreme levels of F_{st} , but values for nonmigratory species are generally >0.10 whereas those of migrant species are <0.10 (Moussy *et al.*, 2013).

Conservation Consequences of Migration

Because their annual ranges often encompass substantial geographic areas that usually cross different federal or international boundaries, the conservation of migratory bats, like that of migratory birds, can be challenging (Racey and Entwistle, 2003; Rodhouse *et al.*, 2015). Consequently, conservation efforts need to be geographically and politically broad in scope. This conservation must involve protecting a variety of different roost sites, including those used for mating, migration, and maternity, as well as the foraging habitats around critical roost sites. In addition, habitats used en route during migration, including stopover habitats where bats can refuel, need protection. Plant-visiting bats such as the nectarivore *L. yerbabuena* and the frugivore *E. helvum* likely migrate along specific food corridors that also need protection. Based on their satellite-tracking results, for example, Richter and Cumming (2008) noted that only a fraction of the migratory pathway along which *E. helvum* flies between the Democratic Republic of the Congo and Zambia is currently protected. Loss of forest habitat containing fruiting trees along this pathway could seriously disrupt its annual migration. Similarly, destruction of parts of the columnar cactus 'nectar corridor' along the Pacific coast of Mexico would have a strong negative effect on migrating pregnant females of *L. yerbabuena*. Based on levels of fat that these bats deposit prior to and during migration, Fleming has estimated that the maximum flight range of these bats is about 550 km (Fleming, 2004). If the average distance between rich patches of cacti exceeds this value, then the migration of thousands of bats could be disrupted. And because intact populations of fall-blooming agaves are also needed by this species to complete the return leg of its migration, habitat protection over a large portion of western Mexico is needed. Migration of insectivorous bats is usually much more diffuse geographically than that of plant visitors, but they also need intact foraging habitat, as well as protected stopover roost sites (Racey and Entwistle, 2003; Wiederholt *et al.*, 2013). A landscape that is devoid of safe caves, intact forests, and unpolluted lakes and streams is just as threatening to the existence of migrating insect bats as a landscape devoid of flowering and fruiting plants is to plant visitors.

In addition to the usual litany of threats to bats and other wildlife (e.g., habitat destruction, pollution, and specifically for bats, malicious destruction of their colonies in caves and other roosts), a new threat to their conservation has emerged recently – wind turbine farms. In an effort to tap alternate sources of energy, wind farms have increased markedly in number and size in Europe, Australia, and North America in recent years (Arnett *et al.*, 2008; Baerwald and Barclay, 2011; Thaxter *et al.*, 2017; Zimmerling and Francis, 2016). While these establishments clearly have positive value for energy production, they can have negative value for wildlife because they kill migratory birds and bats. In North America and Europe, for example, peak bat fatalities occur in late summer and fall and are heavily concentrated in long-distance migrants such as species of *Nyctalus* and *P. nathusii* in Europe and species of *Lasiurus* in North America. In the United States, wind farms located in forested parts of the east coast experience higher kill rates than those located in the Rocky Mountains and Pacific Northwest. Why lasiurine bats, which migrate in flocks despite being solitary roosters during the summer, are more vulnerable to fatal interactions with wind turbines is not yet known (but see Cryan *et al.*, 2014b). Fatalities are most common on nights with low wind speed ($<6 \text{ m s}^{-1}$) and before and after the passage of storm fronts when large numbers of bats (and birds) are likely to be migrating. Bat fatalities occur only when turbines are spinning, not when they are stationary. After reviewing available data, Arnett *et al.* (2008) concluded that the number of bat fatalities at wind farms could be reduced substantially by temporarily stopping turbines at night at certain times of the year and under certain climatic conditions.

Migratory Bats as Disease Reservoirs

My final topic – one that also has important conservation implications, especially for migratory bats, as well as health implications for humans – is bats as reservoir hosts for emerging viruses and other pathogens (Brierley *et al.*, 2016; Han *et al.*, 2016; Messenger *et al.*, 2003). It has long been known that bats are important reservoirs for rabies virus and that they sometimes (but rarely) transmit

it to humans. According to a review by Calisher *et al.* (2006), bats are known to harbor a substantial number of viruses only a few of which are known to be pathogenic when transmitted to mammals, including humans. In addition to rabies, these include other lyssaviruses (Family Rhabdoviridae) as well as Hendra and Nipah viruses (Family Paramyxoviridae) and possibly SARS-Coronavirus-like viruses (Family Coronaviridae). Hendra virus has been found in species of *Pteropus* in Australia; Nipah virus has been found in species of *Pteropus* in South and Southeast Asia, and SARS coronavirus occurs in species of *Rhinolophus* in Eurasia. Both Hendra and Nipah viruses have been found in humans via transmission from intermediate host mammals (e.g., pigs). Ebola virus RNA (Filoviridae) has been found in three species of African pteropodids, including *E. helvum*. Marburg virus, another Filoviridae, has also been isolated from several species of African bats (Buceta and Johnson, 2017).

Because they are geographically wide ranging, migrant bats have the potential to spread pathogenic viruses over wide areas. Outbreaks of rabies virus in Europe, for example, have occurred along the migration routes of *P. nathusii*, and different geographic variants of this virus have been found in two North American migrants, *P. subflavus* and *T. brasiliensis*. Migrant bats in general have a classic metapopulation structure featuring discrete populations (roosts) interconnected by dispersal or migration; between-colony movements can expose resident as well as migrant populations to new variants of rabies or exchange virus variants among colonies. Calisher *et al.* (2006) suggested that this kind of population structure has the potential for seasonal virus transmission, annual outbreaks of viral diseases, and periodic outbreaks among spatially separate populations. Geographically discrete outbreaks of rabies in the (nonmigratory) vampire bat *Desmodus rotundus* or outbreaks of Hendra virus in migratory Australian *Pteropus* bats may reflect this. Finally, the long-distance migrant *E. helvum* has the potential for spreading infectious diseases over large areas of sub-Saharan Africa (Buceta and Johnson, 2017).

My final example deals with a pathogen that affects migratory (and sedentary) bats but not humans. Beginning in 2006, several species of migrant hibernating bats in eastern North America have become infected with a cold-tolerant fungus (*Pseudogymnoascus destructans*, Pd) resulting in the white-nose syndrome (WNS, Escobar *et al.*, 2014; Miller-Butterworth *et al.*, 2014). Nine species, all members of the Vespertilionidae, have been confirmed to suffer from this disease, and another six species have been diagnosed as Pd positive. First described in upstate New York, WNS now occurs in 30 U.S. states and five Canadian provinces. Some species, such as the very common little brown bat (*Myotis lucifugus*), have suffered massive population losses to the point that Frick *et al.* (2010) predicted that *M. lucifugus* would be regionally extinct in New England in less than 20 years. While mechanisms allowing this pathogen, which is native to much of Eurasia, to spread so rapidly are not yet known, its occurrence in very mobile bats many of which migrate hundreds of kilometers between winter and summer roosts and which often switch roosts, even during the winter, suggests that bat mobility must play an important role in its spread.

The conservation implications of the fact that bats harbor pathogenic organisms are enormous. A major reason why bats in general are persecuted throughout Latin America is the fear of ‘vampiros y la rabia.’ The association between rabies and bats, in vampires or otherwise, is well known throughout the world, and bats tend to be maligned worldwide as a result. Because of this association, the ecologically beneficial ‘services’ provided by bats such as control of injurious insect populations (e.g., *T. brasiliensis* and cotton-boll worms), and the broad dispersal of pollen and seeds (e.g., by *L. yerbabuena* and *E. helvum*) tend to be overlooked. In truth, the positive benefits of migratory (and nonmigratory) bats far outweigh their negative aspects. Migratory bats play an important role in many ecosystems around the world, and their conservation is essential (Kunz *et al.*, 2011).

Conclusions

Many species of bats are migratory and serve as ‘mobile links’ between geographically separate habitats and ecosystems. They move energy and nutrients among ecosystems, help to control insects on a broad scale, and serve as wide disseminators of pollen, seeds, and pathogens. Like their avian counterparts, migratory bats have many morphological, physiological, and behavioral adaptations for ‘life on the move.’ Because of their mobile lifestyles, these bats have special conservation needs that must be addressed politically at the national or international level. Although they sometimes harbor pathogenic organisms, their positive attributes far outweigh their negative attributes. Increased public awareness of the lives of these fascinating bats worldwide is the key to their conservation.

See also: Migration and Orientation: Bird Migration; Migratory Connectivity; Orientation, Navigation and Homing in Bats.

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