

Literature Review

North American Bat Ecology and Anthropogenic Disturbances

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ABSTRACT

As the only flying placental mammal today, the North American bat population faces certain extinction not just from climate change, but from a host of other issues that are anthropogenically induced. This review attempts to highlight important issues surrounding bat mortality that can provide a platform for conservation strategies. These include: climate-induced changes in range and dispersal, fatalities at wind turbines, the effects of resource partitioning and competition in spatial niches, and the devastating impacts of the rapidly spreading White-Nose Syndrome. I conclude with research strategies and solutions that are currently being investigated to conserve the biodiversity of several threatened bat species.

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1. Introduction

The fact that bats are nocturnal creatures may be a reason why society is overlooking the recent impacts on their population. Among other things, bats serve a vital ecological purpose as bioindicators for climate change (Jones et al. 2009). In this paper, I explore the current problems surrounding the lack of holistic research in this taxa--most notably as anthropogenic influences are contributing to increased range shifts and dispersal patterns of the bat community. For instance, I will provide evidence for major bat mortalities in relationship to the seemingly paradoxical rise of "green" energy in the form of wind turbines. I will also highlight the need for a major shift in how we think about bats and disease--in particular as it concerns the fungal infection, White Nose Syndrome (WNS), that is not only decimating populations of bats in North America, but may pose real-life concerns for human agriculture in the near future. In addition, I will emphasize the importance of appropriating novel modelling techniques that can help to minimize bias and provide more accurate empirical data to aid in conservation planning. For these reasons and more, I discuss growing concerns for why we, as a global community, should see bats as integral to our changing world.

2. Bat Communities

2.1 Migration

Bats are believed to have evolved from small, arboreal, nocturnal insectivores. Moreover, the act of aerial foraging could have co-evolved with increasing heterogeneity of slow-flying insects that can easily be captured (Black 1974). At present, the structure of the North American bat community is seasonal but poorly understood, due to variation in occurrence data that must be supplemented with inherently biased museum records (Cryan 2003). Cryan et al. (2003) report

that some tree bat species, in particular the hoary bat (*Lasiurus cinerius*), western red bat (*Lasiurus blossevillii*), eastern red bat (*Lasurius borealis*), and silver-haired bats (*Lasionycteris noctivagans*) are thought to be highly migratory (moving at distances greater than > 100km). As such, it is vital to consider the functional ecology of cave and foliage roosting bats not as a static event, but one that interacts with shifting ecological diversity, trophic structures and emerging viral infections (Kunz and Fenton 2005). Since bats spend over half of their lives subjected to conditions in their roost environment (Kunz and Fenton 2005), it would be useful to consider how anthropogenic disturbances and human-assisted climate change are affecting their migratory habits.

2.2 Changing landscapes and Distribution

There is increasing evidence that shifting vegetation in semi-arid landscapes has varied historically due to the encroachment of woody vegetation into grasslands and savannas (Archer et al. 1995). Landscape data over the past 26 years suggests that the mechanism of woody encroachment is not encroachment at all, but the result of a positive feedback loop of replicating clonal stems that has led to a 16-fold increase in shrub species (Ratajczak et al. 2011). Taken together, this indicates that future conservation work needs to identify how bat reproductive rates may potentially be influenced by shifting landscape mosaics, as most migratory tree bats rely on these shrubs for roosting. Although incomplete data on bat migration is nothing new (Vaughan and Krutzsch 1954), expanding edges in landscapes might provide important clues into how the genetic diversity of the local biota in these environments can sustain migratory bats (Hampe and Petit 2005). Therefore, a more complete process-based model is needed that can more accurately track changes in bat migration.

2.3 Dispersal, Range Shifts and Climate change

Recent studies have shown a link between latitudinal and northward elevation shifts of terrestrial species (16.9km and 11.0 m per decade, respectively) due to an ever warming climate (Chen et al. 2011). However, dispersal patterns are still species-dependent. As such, a fuller account of species distribution relies on other trait proxies such as internal processes and external drivers at a local scale (Chen et al. 2011). While evolutionary theory predicts increases in dispersal at expanding range margins, it is important to consider the complex responses surrounding dispersal and changing climate (Travis et al. 2013). One case study of the Brazilian free-tailed bat (*Tadarida brasiliensis*) finds that the majority are now established in year-round colonies that were previously thought to be outside of their range limits--in other words, they are roosting in areas that have been historically cooler (McCracken et al. 2018). These geographic distributions are most certainly driven by global climate change. In addition, several "high confidence" studies predict that climate change is strongly impacting living systems (Parmesan and Yohe 2003; Loarie et al. 2008), and efforts to provide high-resolution measurements of range shifts is essential in lowering species extinction risk (Sekercioglu et al. 2008). However, it is equally important to consider scale when assessing not only range shifts, but local dispersal limitations and invasiveness of species. For instance, simulations of pine shrubs in Europe provide little evidence that the major effects of temperature have driven local-scale recruitment intensity over the past 50 years, suggesting that predictions are not yet truly "confident" unless they can incorporate a species-specific component (Dullinger et al. 2004). Therefore, future analyses must account equally for dispersal probability and persistence events in range shifts--both of which contribute to the future picture of what 'climate path' can be anticipated in the coming years (Early and Sax 2011).

3. Wind Turbines

A recent study estimated that nearly 500,000 migratory bats (hoary bats, being the most common) are killed annually by wind turbines across the United States and Canada (Frick et al. 2017). While this sharp rise in mortality is observable, bat migratory patterns continue to remain elusive due to climate change and other drivers causing range shifts, while wind energy continues to expand (Smallwood 2013). As such, improvements in acoustic monitoring and carcass search are vital in determining if bat fatalities are concentrated in certain areas, or more evenly distributed throughout the landscape (Baerwald and Barclay 2009). While the mortality rate of small passerines (songbirds) has also increased due to wind energy efforts (between 134,000 and 230,000 fatalities or 2.10 to 3.35 per megawatt (MW) of installed capacity), it is worth noting that billions more birds are killed due to anthropogenic disturbances, such as communication towers, buildings (windows) and domestic cats each year (Erickson et al. 2014). While the need to replace fossil fuels is ever-growing, alternative developments are urgently needed in order to reduce the number of fatalities at turbines (e.g. better quantification of why bats are attracted to turbines, more accurate predictive and risk assessment models) (Kunz et al. 2007). In actuality, little planning has been done to reduce the casualties according to recent Ecological Impact Assessments (Lintott et al. 2016).

4. Predator and prey

4.1 Moth specialist and Competition

A study of diet in 159 North American bats in 2003 found that migratory hoary bats are the least diverse in their eating habits (feeding on Lepidoptera--butterflies and moths--98% of the time),

while migratory silver-haired bats are moderately diverse (feeding on Lepidoptera (47.5%) and Diptera (two-winged true flies, 20%)). Interestingly, the diets of little brown bats (*Myotis Lucifugus*) and eastern pipistrelle bats (*Pipistrellus subflavus*) were the most diverse, consuming an even proportion of six orders of insect including: Coleoptera (beetles), Hemiptera/Homoptera (true bugs, cicadas and aphids), Lepidoptera, Diptera, Hymenoptera (sawflies, wasps, bees, ants) and Tricoptera (caddisflies) (Carter et al. 2003). Earlier studies have shown that in the absence of competition, the hoary bat in Hawaii had a much more generalized diet, which supports the idea that increased competition leads to specialization of resources (Whitaker and Tomich 1983). In light of this trend, orthological study of food habits as well as resource partitioning may help to elucidate a clearer boundary of spatial niches; however, presence data for bats remains limited, which seriously hinders landscape management plans. In addition, an increase in insect population (due to increasing edge habitat or human-related disturbances, such as introduction of street lamps that attract moths) can contribute to the rise and decline of one bat species over another (Arlettaz et al. 2000). Owing to this, it is reasonable to suspect that as ranges continue to shift, the competitive exclusion principle may become even more pronounced in the next coming years for bats.

4.2 Predators and Habitat Fragmentation

The owl is a common predator of avians, and to a lesser extent of bats--however, it is unclear how shifting roosts and foraging behavior may subsequently affect predatory behaviors of owl populations (Baxter et al. 2006). While evidence suggests that bats are able to detect predators and elicit an avoidance response (Baxter et al. 2006), the factors surrounding how their senses may be altered if climate and anthropogenic disturbances continue to change is yet unknown.

Furthermore, studies indicate that increasing habitat fragmentation gives rise to more inhospitable matrices which tend to result in lower rates of migration (Collingham and Huntley 2000). How this will affect the already tenuous predator-prey dynamics of both species is still unclear.

5. White Nose Syndrome (WNS)

5.1 Origin and Europe

The North American uptick in *Pseudogymnoascus destructans* (Pd) (Pd, formerly *Geomyces destructans*, Gd) or more commonly, White-Nose Syndrome (WNS), has resulted in the swift and devastating decline of cave-dwelling bats since its discovery in the caves of Albany, New York in 2006 (Warnecke et al. 2012). Pd is a cold-adapted fungus that causes epidermal wing damage by altering torpor (cold)-arousal cycles in bat hibernation that leads to dehydration of the epidermal layer. Studies by Warnecke and al. (2012) support the 'novel pathogen hypothesis' (i.e. that the disease has recently spread into new geographic areas) which neatly explains why North American bats are more susceptible to the disease than European bats, as opposed to there being a more endemic pathogenicity of Pd itself. Furthermore, molecular comparison of DNA in North American and European bats reveal a high degree of genetic similarity, indicating that the source population for Pd most likely originated in Europe (Leopardi et al. 2015). As bats do not engage in trans-oceanic migratory patterns, this suggests that humans may have been a causal vector for the spread of the disease. The death toll so far has reached between 5-6 million bats since 2006 (the most affected of which is the little brown bat, *M. lucifugus*), and is rising rapidly (Leopardi et al. 2015). This 'pathological pollution' not only poses significant threats to global biodiversity, but can also be very expensive: the present cost of an introduced disease to human, livestock and

crop plant health alone is \$41 billion annually in the United States (Daszak et al. 2000, see figure 1). Therefore, it is imperative to understand the mechanism by which Pd spreads in order to prevent both ecological and financial collapse.

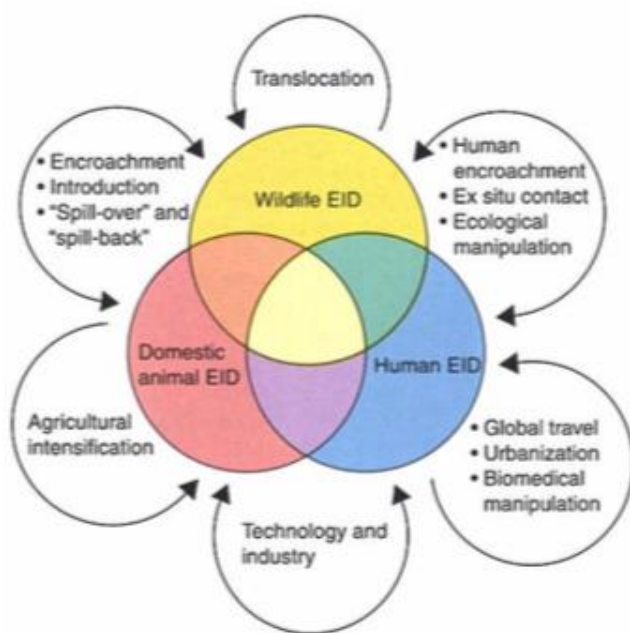


Fig. 1. The host-parasite ecological continuum (here parasites include viruses and parasitic prokaryotes). Most emerging diseases exist within a host and parasite continuum between wildlife, domestic animal, and human populations. Few diseases affect exclusively any one group, and the complex relations between host populations set the scene for disease emergence. Examples of EIDs that overlap these categories are canine distemper (domestic animals to wildlife), Lyme disease (wildlife to humans), cat scratch fever (domestic animals to humans) and rabies (all three categories). Arrows denote some of the key factors driving disease emergence.

Fig.1. The ecological connectivity between species of Emerging Infectious Diseases (Daszak et al. 2000).

5.2 Clonal reproduction

While early studies in New York have mostly been pseudoreplications of isolates in neighboring geographic areas (Pd can spread through air, soil and water) the one surprising piece of evidence is that while Pd reproduces asexually, some populations in North America have undergone recombination events (Rajkumar et al. 2011). However, since WNS in bats is confirmed by morphological appearance and histopathology, there exists a reasonable sampling bias in confirming the existence of the disease (Ren et al. 2012). Therefore, more recent studies have

supported the asexual clonal expansion theory, which explains why substantial phenotypic variation is present with increased distance from the original epicenter (Forsythe et al. 2018).

5.3 Temperature and microclimates

However, there are some recent insights which may shed light on the mechanistic process. For instance, optimal temperatures for its growth are between 12.5 and 15.8° C, and research indicates that there is reduced Pd proliferation and dispersal at higher temperatures (Verant et al. 2012). However, timing of mortality is largely dependent on colony size (larger extinctions experience greater declines), and species (those that seek a more humid microclimate (caves), such as *M. lucifugus*) tend to experience early mortality (Wilder et al. 2011). This may be due to their decreased ability to cope with evaporative water loss from wing damage. However, while this highlights the link between Pd transmission, density-dependence of bat colonies, and microclimate (that is so far geographically independent), newer and more accurate simulation models are desperately needed to assess future impacts of Pd (Langwig et al. 2012).

5.4 Impacts on biodiversity

While increasing efforts are underway to control the spread of this disease, the potential quantitative effects on biodiversity are not yet known. Evidence suggests that increases of torpor-arousal correlate positively with increased mortality (Reeder et al. 2012), but the lack of a mechanistic model severely limits intervention strategies. It is estimated that mortality rates in WNS-affected colonies frequently exceed 90 percent (Wilder et al. 2011) and they cannot be explained by antibody-mediated immune responses in the species with the highest mortality

(Johnson et al. 2015). Therefore, the future of infected bats would rely on the rate at which cellular-adaptation can confer immunity. What's more is that echolocation calls (an indicator of bat activity) within approximately 100 km of the WNS epicenter has reduced by 78 percent in the summer months since 2006, indicating that winter die-offs have the potential to alter species' home ranges in other seasons (Dzal et al. 2011). So how do these severe shifts in bat ecology relate to human ecosystems? One study predicts that the progression of the disease may, in turn, cause the collapse of food security for much of North America (Fisher et al. 2012). As such, a targeted and more comprehensive analysis of year-round data for bats is needed in order to prevent potential agricultural catastrophe.

6. Potential Solutions

6.1 Wind Turbines and Echolocation

At this time, wind energy developments depend on a complex interaction among economic, technological, political and other unknown factors that cannot be easily predicted (Kunz et al. 2007, see Table 1). Better probability models that specifically match the functional processes to the appropriate scale (by way of clustering data or other methods to minimize biases) are sorely needed to represent survival estimation (O'Shea et al. 2004). Environmental impact assessments should also gather data more efficiently in order to reduce aggregation of turbines at specific locations (Schaub 2012). Two studies suggest that introducing broadband acoustic deterrents as well as altering turbine speed may be effective at reducing bat fatalities, but future efforts must evaluate the cost-effectiveness of these approaches (Arnett et al. 2011; Arnett et al. 2013).

<p>Panel 1. Hypotheses for bat fatalities at wind energy facilities</p> <p>We propose 11 hypotheses to explain where, when, how, and why insectivorous bats are killed at wind energy facilities. These hypotheses are not mutually exclusive, given that several causes may act synergistically to cause fatalities. Nevertheless, testing these and other hypotheses promises to provide science-based answers to inform researchers, developers, decision makers, and other stakeholders of the observed and projected impacts of wind energy development on bat populations.</p> <p>Linear corridor hypothesis. Wind energy facilities constructed along forested ridgetops create clearings with linear landscapes that are attractive to bats.</p> <p>Roost attraction hypothesis. Wind turbines attract bats because they are perceived as potential roosts.</p> <p>Landscape attraction hypothesis. Bats feed on insects that are attracted to the altered landscapes that commonly surround wind turbines.</p> <p>Low wind velocity hypothesis. Fatalities of feeding and migrating bats are highest during periods of low wind velocity.</p> <p>Heat attraction hypothesis. Flying insects upon which bats feed are attracted to the heat produced by nacelles of wind turbines.</p> <p>Acoustic attraction hypothesis. Bats are attracted to audible and/or ultrasonic sound produced by wind turbines.</p> <p>Visual attraction hypothesis. Nocturnal insects are visually attracted to wind turbines.</p> <p>Echolocation failure hypothesis. Bats cannot acoustically detect moving turbine blades or miscalculate rotor velocity.</p> <p>Electromagnetic field disorientation hypothesis. Wind turbines produce complex electromagnetic fields, causing bats to become disoriented.</p> <p>Decompression hypothesis. Rapid pressure changes cause internal injuries and/or disorient bats while foraging or migrating in proximity to wind turbines.</p> <p>Thermal inversion hypothesis. Thermal inversions create dense fog in cool valleys, concentrating both bats and insects on ridgetops.</p>

Table 1. Potential hypotheses to reduce mortality of bats at wind turbines (Kunz et al. 2007)

6.2 Predator and Prey

Novel geometrical models of bat-moth interactions are continuously being developed at higher resolutions in order to analyze flight trajectories, and this can significantly alter the risk of starvation for bats (Corcoran and Conner 2016). Of course, as ranges continue to shift northwards, these process-based models will be extremely vital in providing accurate occurrence data for migratory bats.

6.3 WNS

The negative effects of WNS on future crops is a looming possibility, however, there may still be some hope--when given time to heal away from the wild, little brown bats showed a full recovery rate within a year (Dobony et al. 2011). This suggests that banding and netting practices of bats should be improved as a means to preserve future bat colonies (O'Shea et al. 2004). Additional measures seek to quantify WNS-related wing damage in terms of an index and give further credence to the observable healing capacity of free-ranging little brown bats (Fuller et al. 2011), however not all responses are conclusive due to fluctuating neutrophil response as well as inflammatory pathology on an individual basis (Meteyer et al. 2011). Equally important is working to limit the human-vectored transport of Pd by both cave visitors and researchers by devising effective decontamination techniques (Reynolds et al. 2015). To achieve this, a greater respect and understanding for bat ecology is needed (Maher et al. 2012) as well as a more thorough investigation of the environmental conditions that can facilitate the spread of the disease (Flory et al. 2012).

6.4 ENM and SDM

Lastly, useful modelling methods such as Ecological Niche Modelling (ENM) and Species' Distribution Modelling (SDM) stand at the forefront of research to deliver improved predictive models of species' occurrences and potential distribution. The theory of the ecological niche has long been discussed in biology (Grinnell 1917), and pioneering studies at the end of the 20th century served to provide more reliable evidence of species' occurrences as climate change continues to impact range shifts (Parmesan 1996). Predictive habitat modeling for spatial and temporal niches has already been indispensable to conservation planning (Guisan and

Zimmermann 2000) and specific habitat demography must be quantified in order to accurately depict variation (Pulliam 2000). The usefulness of these models will of course be contingent upon the questions asked by the scientific community, with an inherent understanding that perfect validation is unrealistic (Araujo and Rahbek 2006; Araujo and New 2007).

7. Conclusions

The future of bat ecology looks hopeful, in that technology is improving at a rate that might outstep the rate of extinction. However, the measure of uncertainty that comes from novel climate change impacts cannot be underestimated. Therefore, there must be a concerted effort among scientists, conservationists, resource managers and educators to enforce strategies, even in the face of this uncertainty (Wiens et al. 2009). However, it still remains a race against the clock to limit the many threats contributing to the decline of several bat species in North America. As the magnitude of global emissions and climate change continue to make seasons more extreme, in addition to severely melting snowpacks and affecting the water resources in the United States (Hayhoe et al. 2004), shifting attitudes in politics and intergovernmental panels must also occur in order to provide wildlife safeguarding strategies. As our global ecology continues to change, the need to provide resource managers with a "rule of thumb" measurement (McPherson and Jetz 2007) for the likely behavior and presence of bats will be paramount, not just for the livelihood of bats, but for human ecosystems as well.

Conflict of Interests

The author declares that there are no conflicts of interest regarding the submission of this paper

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