A review of the major threats and challenges to global bat conservation

Article *in* Annals of the New York Academy of Sciences · April 2019

DOI: 10.1111/nyas.14045

3 authors:

Winifred Frick
Bat Conservation International
120 PUBLICATIONS 5,551 CITATIONS

Tigga Kingston
Texas Tech University
113 PUBLICATIONS 4,070 CITATIONS

Jon Flanders
Bat Conservation International
34 PUBLICATIONS 1,808 CITATIONS

Ann. N.Y. Acad. Sci. ISSN 0077-89

ANNALS OF THE NEW YORK ACADEMY OF SCIENCES
Special Issue: *The Year in Ecology and Conservation Biology*
REVIEW

A review of the major threats and challenges to global bat conservation

Winifred F. Frick,[1,2] Tigga Kingston,[3] and Jon Flanders[1,4]

[1]Bat Conservation International, Austin, Texas. [2]Department of Ecology and Evolutionary Biology, University of California Santa Cruz, Santa Cruz, California. [3]Department of Biological Science, Texas Tech University, Lubbock, Texas. [4]School of Biological Sciences, University of Bristol, Bristol, United Kingdom

Address for correspondence: Winifred F. Frick, Bat Conservation International, 500 North Capital of Texas Hwy Building 1, Austin, TX 78746. wfrick@batcon.org

Bats are an ecologically and taxonomically diverse group accounting for roughly a fifth of mammalian diversity worldwide. Many of the threats bats face (e.g., habitat loss, bushmeat hunting, and climate change) reflect the conservation challenges of our era. However, compared to other mammals and birds, we know significantly less about the population status of most bat species, which makes prioritizing and planning conservation actions challenging. Over a third of bat species assessed by the International Union for Conservation of Nature (IUCN) are considered threatened or data deficient, and well over half of the species have unknown or decreasing population trends. That equals 988 species, or 80% of bats assessed by IUCN, needing conservation or research attention. Delivering conservation to bat species will require sustained efforts to assess population status and trends and address data deficiencies. Successful bat conservation must integrate research and conservation to identify stressors and their solutions and to test the efficacy of actions to stabilize or increase populations. Global and regional networks that connect researchers, conservation practitioners, and local stakeholders to share knowledge, build capacity, and prioritize and coordinate research and conservation efforts, are vital to ensuring sustainable bat populations worldwide.

Keywords: bats; biodiversity; conservation; Chiroptera; threats; mammals

Introduction

Loss of biodiversity is a global crisis caused by pervasive threats from anthropogenic activities,[1] particularly land-use change,[2] overexploitation of species,[3] introduction of invasive species,[4] and climate change.[5] One fifth of vertebrate species around the world are considered by the International Union for Conservation of Nature (IUCN) to be threatened,[6] a patterned mirrored by the world's mammalian species.[7,8] Bats are the most widely distributed terrestrial mammals on Earth and constitute nearly a fifth of mammalian biodiversity, with almost 1400 species now recognized.[9,10] However, the nocturnal, elusive habits of bats, and a paucity of bat research in the regions of the world with the greatest bat diversity, challenge our ability to prioritize and effect conservation where it is most needed.[11]

Identifying the main anthropogenic stressors on natural populations is key to proposing actions that can decrease the risk of local or global extinctions and mitigate the drivers of species declines.[12] Examining threats within taxonomic groups sheds light on global patterns, identifies common conservation problems, and guides conservation action. When Mickleburgh *et al.*[13] reviewed the global conservation status of bats over 15 years ago, habitat loss or modification, roost site loss or disturbance, human health issues, persecution, lack of information, and overexploitation for food were identified as the major threats to bats globally. Many of these issues remain major threats, but in the intervening years, new threats have also emerged, including mass die-offs of pteropodid bats in Australia and South Asia from heat waves,[14] high rates of mortality at wind energy turbine installations,[15] and the emergence

doi: 10.1111/nyas.14045

of an infectious fungal disease of bats, white-nose syndrome (WNS), in North America.[16,17] The open-access book *Bats in the Anthropocene: Conservation of Bats in a Changing World* offers a recent and thorough review of the major conservation issues for bats, revealing the breadth and depth of anthropogenic stressors on bat populations globally.[11]

Here, we provide an overview of the global status of bat conservation by reviewing the major anthropogenic threats to bats and special challenges to bat conservation. Using data from the IUCN Red List, we visualize hotspots of threatened and data-deficient bat species around the globe and compare the proportions of threatened and data-deficient bats to other homeothermic vertebrates (i.e., other mammals and birds). We rank threats to bats using the IUCN threat classification schema and review the literature on the major threats identified by the IUCN Red List[18] to highlight what we currently know and still need to know. Although the IUCN Red List provides the most comprehensive global database on the status and conservation needs of species, the Red List is based on available information and expert opinion and as such is chronically incomplete and out of date. We discuss two habitats with particular significance for bat conservation, namely islands and subterranean features, and the value of bats to ecosystems. We conclude with some of the enduring challenges to global bat conservation and suggest next steps toward meeting those challenges.

Global status of bat populations

Global patterns of bat diversity are similar to biodiversity patterns for mammals, with diversity peaking in equatorial regions of the world (www.biodiversitymapping.org).[1,8] Using range maps from IUCN, we show areas with the highest density of species richness of known threatened and data-deficient bats and show that global patterns for threatened and data-deficient bats differ (Fig. 1). Range maps from IUCN are based on current taxonomy, available locality records, and expert opinion and should be viewed as hypotheses of the extent of occurrence of species. The density of listed threatened species peaks in Southeast Asia, whereas the density of data-deficient species is highest in the Amazon basin in South America. The difference in the distribution of data-deficient species may in part reflect a lag in species discovery in equatorial Africa and Southeast Asia compared to the neotropics, as newly described species are commonly data deficient. Island archipelagos across the globe, including the Caribbean, African islands, and islands throughout Asia and the south Pacific, are hotspots of threatened bats. To some extent, these patterns reflect the geographic biases in knowledge and inclusion of species on the IUCN Red List, but it is clear that islands and equatorial regions of Africa, Southeast Asia, and the neotropics are priority areas for research and conservation attention.

We investigated whether the global status of bats differed from similar taxa by comparing the proportion of bats considered threatened or data deficient by the IUCN Red List to other mammals and birds. Notably, while 15% of bats are considered to be threatened by the IUCN (assessed as Critically Endangered, Endangered, or Vulnerable on the Red List),[19] 18% of bat species are Data Deficient, a far greater proportion than reported for either other mammals (13%) or birds (1%) (Table 1; Fig. 2). Critically, over half of bat species assessed by IUCN (57%) have unknown population trends compared to 39% of other mammals and just 8% of all birds (Fig. 3A). The disparity in knowledge about population trends was also significant when just compared among species ranked as Least Concern or Near Threatened. Thirty-five percent of bat species classified as Least Concern have unknown population trends (Fig. 3B), showing a remarkable gap in knowing the status of many bat species not currently considered to be conservation priorities.

There has been rapid growth in the number of recognized bat species over recent decades[10,20] with over 270 new species described since 2005, when the last version of the Mammal Species of the World was published.[21] The increase in described bat species (>25%) over the past 15 years has outpaced that of other mammals.[10] Many of these species are not yet classified by IUCN, which currently has 1236 species compared to the 1395 species now recognized in the online global bat taxonomy database.[9] The pace of species discovery is consistently faster than that of species assessments by the IUCN. The Global Bat Taxonomy Database working group was recently created as part of the IUCN Bat Specialist Group to centralize and harmonize descriptions of new species and taxonomic revisions that can support more rapid assessments of new taxa. Despite these efforts, the number of data-deficient species

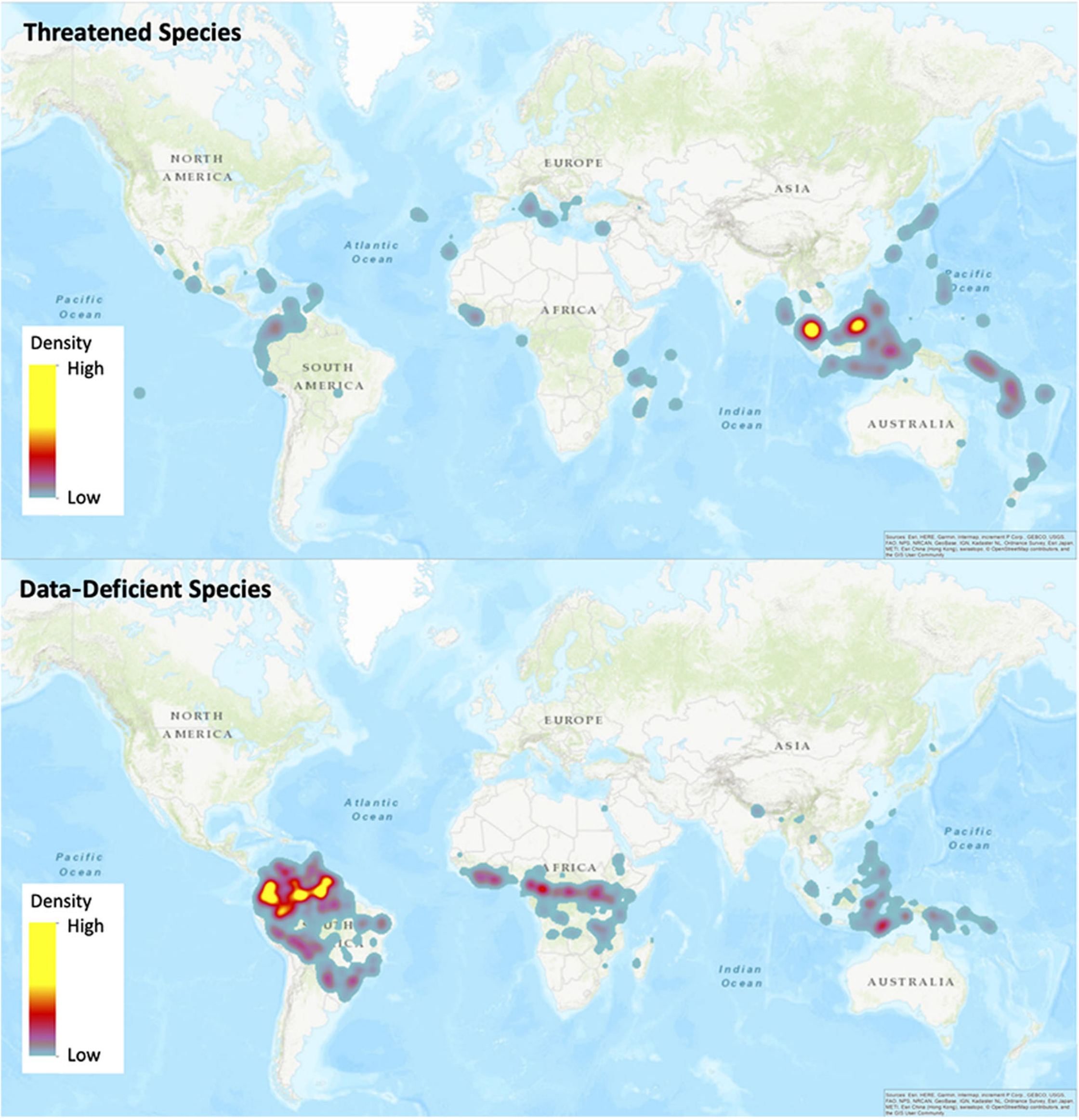

Figure 1. Heat maps showing areas of highest species density of threatened (top) and data-deficient (bottom) bat species. Data based on IUCN range maps and classifications.

on the IUCN Red List remains a minimum estimate. We recommend that descriptions of new species or taxonomic revisions suggest the appropriate IUCN status based on available data and Red List criteria to aid in rapid inclusion on the IUCN Red List.

Major threats to bats

We review the major threats to bats, organized by the categories identified by the threat classification schema used by the IUCN[19] (Fig. 4). We used the first-level hierarchy of threat category, except for the category of "Biological resource use," which includes "Hunting and collecting animals" and "Logging and wood harvesting," two of the most widespread yet distinct threats to bats that we consider separately. We discuss threats in rank order based on the proportion of threatened bat species for which a threat was listed on the Red List.

Table 1. **Conservation status of bats compared to other mammals and birds**

Taxon	Species assessed	Threatened species (%)	Data-deficient species (%)
Bats	1236	180 (18%)[a]	227 (15%)[b]
Other mammals	4358	1030 (24%)	578 (13%)
Birds	10,961	1469 (13%)	58 (1%)

NOTE: Conservation status is summarized as species classified as threatened (Critically Endangered, Endangered, and Vulnerable) or Data Deficient by IUCN Red List (data accessed on July 26, 2018).
[a]Proportion of species in threatened categories was significantly lower ($P < 0.001$) for bats than other mammals, but not significantly different from birds ($P > 0.25$), based on a generalized linear model with binomial errors.
[b]Proportion of species classified as Data Deficient was significantly higher for bats ($P < 0.001$) than for other mammals and birds, based on a generalized linear model with binomial errors.

Logging and harvesting plants

Globally, the two most important habitats for bats are forests and subterranean features (i.e., caves and mines). Although caves capture our attention as uniquely important for bats, forests are the most critical habitats for supporting local abundance and species diversity for bats at a global scale.[22] Forests not only provide essential foraging habitats, but they also allow many bat species to roost in plant structures, such as hollows and cavities in standing and fallen trees, under bark, or in foliage.[23] Although subterranean habitats provide protected refuges for roosting for roughly 40% of the world's bat species, many of these species also depend on forest habitats for foraging.[24] The importance of forests is evidenced by global patterns of bat biodiversity that peak in tropical forest ecosystems.[25]

Continuing loss and degradation of tropical rainforests,[26] particularly in the neotropics[27] and Southeast Asia,[28] is a severe threat to global bat diversity.[22,29] The impacts of deforestation are obviously not unique to bats and conservation efforts focused on the protection of forests, both temperate and tropical, will benefit a large component of bat biodiversity.[22,30] Research on bat species responses and impacts of deforestation and land-use change on bats in Southeast Asia have historically trailed behind research effort in the neotropics but have gained more attention and funding in recent years in large part due to the efforts of the Southeast Asian Bat Conservation Research Unit (SEABCRU).[29,31] Unfortunately, studies on the impacts of deforestation on bats in Africa remain rare[32,33] and need more attention. In the managed timber-production forests of Europe, Australia, and North America,

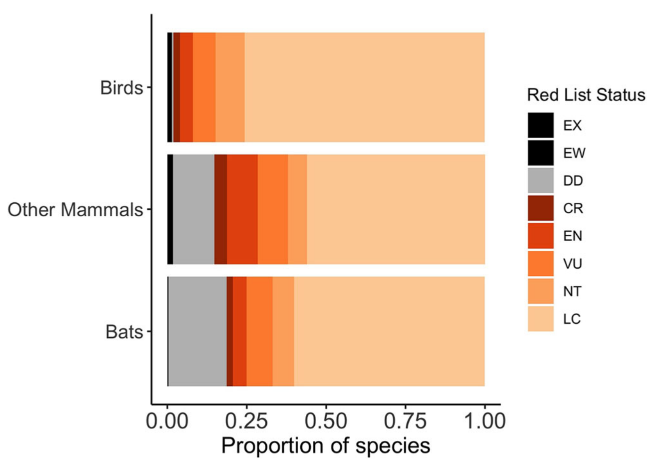

Figure 2. **The proportion of species in each category of the IUCN Red List is shown for bats, other mammals, and birds. The IUCN categories are EX (Extinct), EW (Extinct in the Wild), DD (Data Deficient), CR (Critically Endangered), EN (Endangered), VU (Vulnerable), NT (Near Threatened), and LC (Least Concern).**[19]

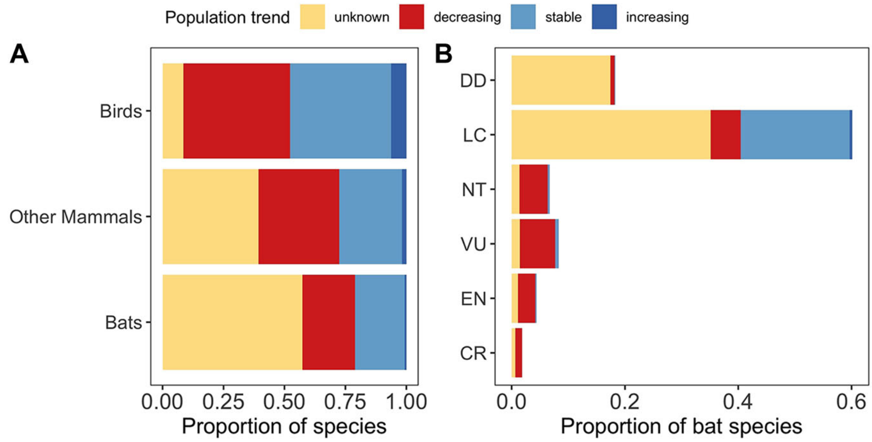

Figure 3. Population trend status from IUCN Red List assessments for (A) bats, other mammals, and birds and for (B) the Red List categories for bats. The proportion of species with unknown population trends was significantly higher for bats than other mammals ($P < 0.001$) or birds ($P < 0.001$).

historical silvicultural practices, such as removal of standing dead trees and even-aged management, have compromised forest value for bat diversity. Recent shifts to management practices that create spatial-temporal heterogeneity in forest age and structure at landscape scales and retain mature forest trees with cavities are likely to benefit bats, but need to be propagated across regions.[34,35]

Forest bats can be difficult to study, particularly in terms of quantifying population status and trends, given that they often roost in cryptic locations dispersed throughout forest habitats and recapture rates of individuals are usually too low to allow effective mark-recapture techniques for population or demographic studies.[23,36] Given that 80% of bats emit ultrasonic echolocation signals, acoustic

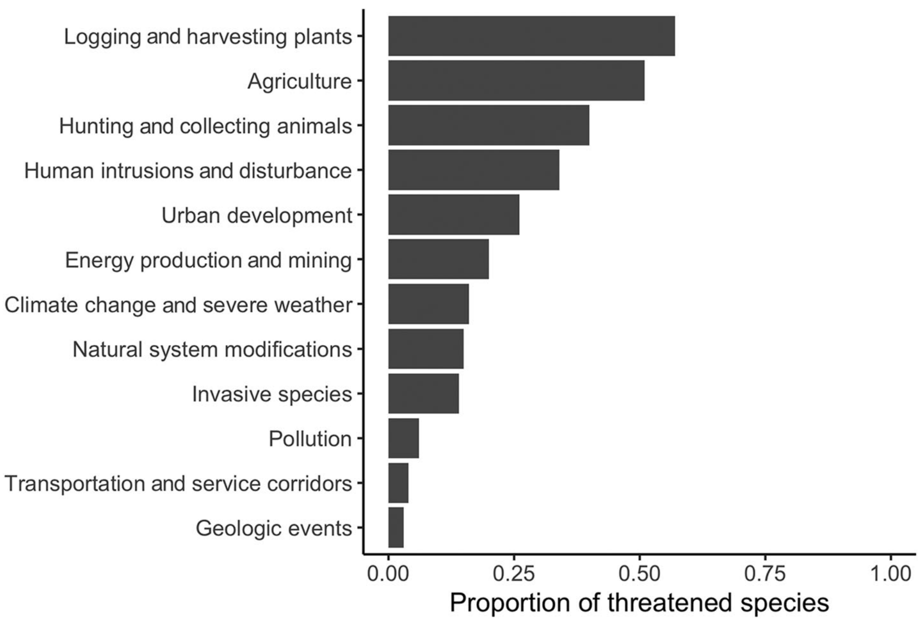

Figure 4. Ranking of major threat types for threatened bat species, based on IUCN Red List assessments. A total of 170 species (94% of assessed threatened species) had at least one threat type listed. For description of threat categories, see: www.iucnredlist.org.

monitoring can be used to conduct longitudinal studies to assess trends over time as well as compare across environmental gradients (e.g., land-use change) to provide a baseline understanding of bat habitat use and population trends.[37,38] However, while acoustic monitoring may be effective in temperate forests that are mostly populated with species that use high-intensity echolocation calls, assemblages of the interior of tropical rainforests are dominated by species that use low-intensity and/or high-frequency calls. These faint calls limit detection distances to a few meters. Consequently, acoustic approaches cannot characterize and monitor the diversity of the most vulnerable tropical ensembles. Rather, monitoring must rely upon standardized capture protocols that require substantial effort to detect population trends.[31,39,40]

Agriculture

Conversion of land for agricultural production is one of the most significant land-use changes occurring across the planet, with an estimate of nearly 40% of terrestrial land cover now in agricultural production.[41,42] Agriculture is identified as a threat in IUCN Red List assessments for over 50% of threatened bat species (Fig. 4). Agriculture reduces bat populations through direct habitat loss and modification, as agricultural habitats present reduced foraging and roosting resources for most species. For insectivorous species, widespread use of insecticides and insect-resistant varieties of crops reduces foraging resources by reducing insect prey abundance, and can directly poison bats, particularly in countries lacking regulation of organochlorines. In regions where bats feed on fruit crops, direct conflict between bats and farmers has led to lethal persecution by both individuals and government programs.[43,44] A geographical bias toward North America and Europe exists for studies estimating the consequences for bats of agricultural conversion and intensification, although some studies in tropical regions have focused on agroforestry, particularly in the neotropics.[41] The current evidence from these regions is that lower intensity agriculture, such as organic farming and shaded agroforestry, supports higher activity and species richness compared to more intensive methods, indicating management interventions that focus on lower intensity agriculture may benefit bats.[41,42]

Hunting and collecting animals (including persecution/control)

One hundred and sixty-seven bat species (roughly 13% of species) are hunted for food or medicine, and bushmeat hunting is increasingly recognized as a major conservation threat for bats, primarily in Southeast Asia and West and Central Africa.[3,45,46] Hunting disproportionately affects Old World fruit bats (Pteropodidae), with roughly half of pteropodid bat species (92/183) hunted, primarily for food but in some cases for traditional medicine and sport. The most intensely hunted species are typically large (>100 g body mass) and roost in large accessible aggregations in trees or caves where they can be predictably encountered.[46] Despite increased awareness and concern about bushmeat hunting of bats, even at noncommercial scales (e.g., subsistence or local-scale markets), there are few empirical estimates of population impacts from hunting.[45] The few available studies indicate that harvest rates are alarmingly high and appear unsustainable based on what is known of local population sizes and bat population dynamics.[47–51] Harvesting bats for tourist souvenirs, curios, and decoration is also a growing concern[52] particularly as the online market is global in extent. Only species of *Pteropus* (65 spp.), *Acerodon* (5 spp.), and *Platyrrhinus* (1 sp.) are listed on the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) appendices that prohibit or control trade.[53]

In addition to overexploitation of bats hunted for food, bats are intentionally killed for a variety of reasons,[54,55] including fear of bats as a source of zoonotic disease transmission,[56,57] cultural beliefs that bats are evil or "creepy,"[55] eradication of bats living in human structures,[58] and illegal and legal culling intended to reduce damage to fruit crops.[43] The threat of intentional killing of bats varies geographically,[54] depending on cultural context, existence (or lack thereof) of wildlife protection laws and their enforcement, and the type of bat fauna present in a region.[55] As loss of natural habitat accelerates, bat–human conflicts become more common as bats increasingly depend on human-dominated habitats.

A recent example of human–wildlife conflict threatening bats is the culling of an endemic flying fox, *Pteropus niger*, on the island of Mauritius in 2015 and 2016.[59–61] The conflict derives from consumption of fruit crops, primarily lychee, by bats, but has been exacerbated by misinformation and misperception about the extent of damage caused by bats compared to other sources of fruit damage (e.g., non-native birds, fungal infection, rats, and wind). Political, economic, and capacity barriers currently prevent extensive use of crop netting, a technique that has successfully mitigated bat predation of fruit crops in Australia and Thailand. Local political motivations to cull bats have overridden scientific evidence that shows culls fail to improve crop yield.[61] In two mass culling events ordered by the government, over 38,000 individuals were reported killed, a loss of more than a third of the population in just 2 years.[59,62] The rapid and severe population loss from the government cull, and associated increases in hunting and persecution by the public, resulted in a change in status on the IUCN Red List from vulnerable to endangered.[44] In November 2018, a third cull with a target of 20% of the remaining 65,000 bats began. Continued population declines are projected for *P. niger* from the 2018 and future culls, illegal killing by farmers, hunting, reductions in natural forest habitat, and risk of mortality from cyclone events, highlighting how island bat species face multiple threats that are interrelated.[44,59] For island flying foxes, including *P. niger* in Mauritius, loss of natural habitat from deforestation increases conflicts with local farmers as bats become dependent on domesticated fruit trees for food in the absence of adequate forest habitat.[59,62]

In Central and South America, vampire bats are a vector of rabies transmission to livestock and are culled in an attempt to control rabies transmission.[54,57,63] Methods of killing have been largely indiscriminate, with whole caves being destroyed or gassed, resulting in mortality and loss of roosts for species that share roosts with vampire bats.[63,64] Research on transmission dynamics has shown that culling does not reduce transmission and in some cases has the opposite effect.[57] Improving methods and reducing illegal and legally sanctioned culls of vampire bats is an area of active conservation. Culling animals for attempted control of other zoonotic diseases, such as Marburg virus, has also proven ineffective and leads to unnecessary extermination of local populations without human health benefit or, worse, can even increase disease prevalence.[65]

Resolving bat–human conflicts requires understanding of human behaviors and rigorous approaches to developing effective interventions to promote behavioral change.[55,66] Biologists often lack the training to address questions related to human behavior. Collaborations with social scientists are needed to extend research beyond the boundaries of the natural sciences.[55,67] As Kingston[55] points out, many bat biologists believe promoting positive messages about bats and emphasizing their ecosystem services will *de facto* lead to cultural shifts toward positive views of bats, which will then translate into protection or conservation measures. Yet, there is little empirical evidence to support this belief and we need to test the efficacy of educational campaigns and ways to resolve bat–human conflicts.[55,64,68]

Human intrusions and disturbance

Bats that roost in caves are particularly vulnerable to disturbance because they form large, concentrated aggregations.[24] Large colonies of cave-roosting bats are relatively easy to locate—by local communities and researchers alike—resulting in documented cases of intentional disturbance (e.g., persecution, hunting, vandalism, etc.) or roost destruction (e.g., mineral extraction and mining).[24] The effects of unintentional disturbance are more difficult to measure due to the variety and nature of recreational activities in caves. Cave tourism, which was estimated to attract 20 million people worldwide by the mid-1990s, continues to increase in popularity, adding stress to species dependent on subterranean habitats.[24] Disturbance affects over a third of threatened bat species (Fig. 4). Installing bat-friendly gates that permit bats to continue to use caves or mines while limiting human access can reduce disturbance to bats and increase use and colony size of bats for some species and regions.[69,70] Some species may be intolerant of gating structures and installation should be tested and bat use monitored prior to wide-scale implementation to ensure that gating leads to roost protection rather than abandonment.[71,72] Gating may also require education and communication efforts to target audiences, such as recreational users, or the gates may be destroyed.

The IUCN threat category of "Human intrusions and disturbance" includes threats posed by war, civil unrest, and military exercises. Although political unrest is only listed as a direct threat for six bat species, political instability and conflict often intensify other threats, such as exploitation of bats for bushmeat when human food resources are scarce, or encroachment into protected areas. More generally, war and political instability frequently restrict or prohibit access to research areas, and greatly constrain or preclude research and conservation activities. At worst, academic institutions, collections, and researchers may be directly at risk.

Urban development

Urbanization drastically alters habitats and is predicted to increase in land cover by 1.2 million km^2 by 2030, tripling in extent over 30 years, with disproportionate expansion in biodiverse areas such as tropical Africa and Asia.[73] The impact of urbanization on bats is generally negative, although the response can be species specific.[74,75] Some bat species are synanthropic and have adapted to roosting in human-made structures such as buildings and bridges for either all or some of their annual life cycle (e.g., maternity or hibernation roost sites).[58,75] Although populations of some species may increase in some urban settings, the effect of urban living on the fitness and population dynamics of synanthropic species is still not well understood, and urban environments could serve as ecological traps.[75] As urbanization increases in the biodiverse tropics, especially in regions such as Africa where there is less regulatory protection of wildlife and greater concerns regarding the potential for bats to transmit disease, it also increases bat–human conflicts. Bat colonies that depend on human structures after loss of natural roost sites become vulnerable to persecution and extirpation.[58,75]

Energy production and mining (including renewable energy)

Mining and quarrying activities threaten bats by destroying subterranean habitats used for roosting as well as degrading or destroying surface habitats. Of particular concern is the global demand for limestone extraction, which typically occurs in karst regions with a high density of natural cave roosts.[24] Bat roosts in natural caves are associated with high species richness of other cave organisms and can indicate high priority sites for biodiversity conservation in areas threatened by resource extraction.[76] In addition to roost destruction, some mining operations produce tailing impoundments and toxic surface water that may poison or harm bats that depend on surface water for drinking.[54] Inactive mines often provide suitable roosting habitats for bats and may provide critical roosts for populations.[77,78] Some countries, such as the United States and Australia, have government-sponsored programs to close abandoned mines due to human health and safety concerns and have developed best management practices, such as installing bat-friendly gates and requiring preclosure bat surveys, prior to mine closures. Destruction of inactive mines, either from intentional closure or renewed mining activities, is a major concern for habitat loss for bats globally.

Only two species are currently listed as threatened by “renewable energy” in IUCN assessments. However, fatalities from collisions with wind energy turbines are now one of the leading causes of observed mortality of bats globally.[54] Over 500,000 bats are estimated to be killed annually across Canada and the United States[79–81] and over 300,000 killed annually at wind energy facilities in Germany alone.[82,83] Current fatality rates from wind turbines are high enough to cause rapid declines in populations and increase the risk of extinction for some migratory species.[15] Much of the research attention has occurred in North America and Europe, but there is growing awareness and efforts to understand the impact of wind energy facilities on bats in other regions, especially as the number of wind energy facilities increases globally.[84–86]

In North America and Europe, the majority of bats killed by turbines are migratory species[83,87,88] that generally lack regulatory protection.[89] Research showing effective mitigation solutions to reduce mortalities has been known for nearly a decade.[90,91] Limiting wind turbine operation during the high-risk periods of nights with low wind speeds during autumn migration can reduce bat fatalities by as much as 44–93%, with minimal impact on power generation.[90,91] Other solutions, such as acoustic deterrents installed on turbines, may also reduce fatalities, although further research is needed on efficacy in different settings before broad-scale implementation.[92]

Although scientific research has shown how to reduce fatalities and demonstrated the need to reduce fatalities to prevent rapid population declines,[15] implementing regulatory management solutions has proven challenging.[93] Furthermore, strategies to reduce fatalities of bat species in tropical habitats, on islands, and in other regions experiencing rapid growth in turbine installment are necessary. In 2017, four North American migratory bat species (*Lasiurus* spp.) were added to the Convention on Migratory Species, but since Canada, Mexico, and the United States are not parties to the treaty, the listing does not impose transnational regulatory protection.

Climate change

There is mounting evidence that changing climatic conditions, including extreme events such as drought and flooding, are causing shifts in species richness and distribution patterns of biodiversity at an unprecedented rate.[94] Climate change is now recognized as a significant threat to global biodiversity and its effects could surpass those of land use change by 2070.[95] Developing frameworks to identify species at greatest risk from climate change by predicting species response[96–100] is an urgent need. The high mobility of bats may enable some species to respond to changing climates with rapid range shifts,[101,102] and the ability to use diverse habitats or alter behavior may buffer some species from extinction risk.[103] Climate shifts may disrupt or change migratory behavior,[104,105] survival and reproduction,[106,107] foraging behavior,[108] and disrupt food availability for pollinating species through alterations in flowering phenology.[109]

The negative forces of climate change are most likely to impact species that are already vulnerable. An increase in extreme weather events, such as unusually hot or dry conditions, or an increase in the frequency of natural disasters caused by typhoons and hurricanes, can cause rapid population declines that further decrease the resiliency of populations already threatened by small population sizes due to anthropogenic degradation or loss of natural habitats.[110,111] Bats on tropical islands are particularly vulnerable to cyclones, and drastic declines (80–90% of some *Pteropus* populations) arising from direct mortality and loss of forest resources have been observed throughout the Pacific Islands.[112] Extreme heat events on continents are increasing in intensity and frequency. Sustained high temperatures (>42 °C) lead to physiological stress, resulting in the mortality of flying foxes in South Asia and Australia.[14,113] Die-offs from heat stress of flying foxes that roost colonially in trees are readily observable, but the impact of extreme weather events on other bat species may be harder to observe and quantify.

While climate change is a global problem necessitating a global solution, local interventions can play a critical role in protecting species from its adverse effects. Protecting and restoring wetlands and forests can reduce the levels of carbon released into the atmosphere and make habitats more resilient to extreme weather events and provide bat foraging habitats.[114] In semiarid areas, where the combined effects of drought and increases in human demand for water are predicted to be a primary driver of biodiversity loss,[115] strategies that focus on restoration of water courses and provisioning water to wildlife may be successful.[116,117]

Invasive species

Although invasive species are one of the major threats to biodiversity globally,[118,119] there has been relatively little attention on estimating the effects of invasive species on bats.[120] An exception is the invasive fungal pathogen that causes WNS in North America, a disease that has caused severe mortality among hibernating bats.[17] Welch and Leppanen[120] provide a review of the threat of invasive species on bats and identified 37 invasive species as threats to 40 bat species based on searching the IUCN Red List and the literature. Although 40 bat species represent less than 5% of the fauna, over 60% of bat species threatened by invasives occur on islands, where impacts from invasives are generally compounded by other stressors and the risk of extinction is generally greater.[121] Welch and Leppanen note that over half of the cases they identified were speculative or circumstantial, indicating that better documentation and empirical research are needed to determine the impact of invasive species on bat populations. Online databases, such as the Threatened Island Biodiversity database (http://tib.islandconservation.org/) maintained by Island Conservation, a conservation organization focused on eradicating invasive species, provides a starting point to identify where island bats are most vulnerable to invasive species.

WNS is an infectious disease of hibernating bats caused by the fungal pathogen *Pseudogymnoascus destructans* that has spread widely across North America in the past decade.[122–124] The disease emerged in New York State in 2006 and quickly drew attention as a major conservation crisis in North America when mass die-offs that led to rapid and dramatic population declines were observed for hibernating bats, raising alarms about regional or global extinction of species previously considered stable or increasing.[125–127] The fungus infects hibernating bats and in some species causes a lethal cutaneous skin infection by disrupting physiology.[124,128–130] Although WNS currently impacts a small percentage of the global bat fauna, the dramatic nature of the die-offs elevated public and scientific interest in bat conservation beyond the species under immediate threat from the disease.

Pollution

Studies on chemical pollutants and bats have declined over the past few decades despite general increases in chemical products and growing interest in bats and their conservation.[89] Most of what we know about the impacts of pesticides on bats comes from North America and the impact of organochlorine pesticides,[41] and a few specific studies on direct mortality[131] or demographic impacts.[132] In temperate areas, concentrations of organic contaminants found in bat tissues have declined since the 1970s and 1980s, when use of the persistent organochlorine pesticide dichlorodiphenyltrichloroethane (DDT) was banned in the United States and Canada, Australia, and most European countries.[133] However, DDT, as well as pyrethroids, is still widely used in Africa and parts of Asia, including India, for the control of malaria and other vector-borne diseases, although mostly applied indoors.[134] We need more research on ecotoxicology and quantification of acute and chronic (sublethal) effects of exposure to pesticides on bats.[133,135] Persistent organic compounds concentrate in tissues with higher fat content and could impact physiological processes for bats that depend on seasonal fat deposition.[133] Recent reviews on bats and pollutants raise the need for standardized monitoring protocols and online data repositories for better information sharing on ecotoxicology.[133,135] Other types of pollution, such as light pollution[136] and noise pollution,[137] have received recent attention given their propensity to disrupt the foraging of bats, but these threats have yet to be explicitly listed in IUCN assessments for threatened bat species.

Transportation and service corridors

Transportation and service corridors threaten biodiversity by serving as mortality sinks and by causing habitat loss and fragmentation. The scale and severity of the threat of roads to bats remains poorly investigated and only within the last decade has research attention focused on the effect of roads on bat populations.[138–140] Current evidence suggests that roads serve as a substantial source of mortality for many bat species and create barrier effects and fragmented habitats.[138,139] For example, a recent study from Brazil showed that 44 species (25% of the local fauna) were observed as roadkill, with frugivorous species identified as most vulnerable.[141] Road corridors degrade and fragment habitats, thus creating barriers to movement, and they increase levels of noise, light, and chemical pollution.[138,139] These effects can lead to reduced foraging efficiency, lower reproductive success, and ultimately lower species diversity near roads.[142,143] In addition, the expansion of road corridors facilitates land conversion in areas that were previously inaccessible and intact. Most of the research on bats and roads has occurred in temperate regions (mostly in Europe) and more research attention is needed on mortality rates and barrier effects of roads in tropical areas.[139,141]

Geologic events

Geologic events, such as volcano eruptions, earthquakes, and landslides, are included in the IUCN threat classification scheme and were mentioned in Red List assessments for five bat species. These threats are not addressable by direct conservation action but demonstrate the vulnerability of small populations, particularly on islands, to natural disasters.

Two special habitats for bats as conservation targets

Islands

Islands are key areas for conservation, with a disproportionate number of rare and endemic taxa compared to mainland habitats.[144] Island ecosystems tend to be small, isolated, and vulnerable to a variety of threats.[144] An estimated 75% of recorded terrestrial vertebrate extinctions occur on islands and 40% of species threatened with extinction live only on islands.[145] Because bats can disperse across wide expanses of water, they are often the only native mammals on islands and are particularly important to island ecosystems.[146] Bats help maintain island ecosystems, particularly in forests, by dispersing seeds over wide distances.[147] Roughly, a quarter of all bat species are island endemics and 50% of these species are threatened.[113,148] Notably, the five species of bats that have gone extinct were all island endemics.[149]

Although bats on islands face many of the same threats as mainland species, the small size and isolation of habitats magnify these threats, resulting in a higher background rate of extinction.[113,148] Naturally occurring threats, such as extreme weather events (e.g., typhoons, hurricanes, or extended drought), put island species at higher risk of episodic catastrophic losses of population. However, anthropogenic pressures, such as habitat loss and intentional killing, that reduce population sizes decrease resiliency, making insular bat species more vulnerable to extinction. Furthermore, the frequency and intensity of catastrophic weather events is increasing with climate change.[150] The combined effect of habitat change, hunting, disturbance, and invasive species[4] has intensified the risk of extinction. Indeed, these threats contributed to the decline and global extinction of the Christmas Island pipistrelle (*Pipistrellus murrayi*), which was formally declared extinct in 2017, and six extinct species of island flying fox (*Pteropus* spp.).[59,151]

Conservation efforts for island bats are hampered by a lack of information about species' habitat needs, drivers of population declines, and effective ways to implement conservation measures that improve resilience to stressors.[152] Research on threatened bat species endemic to islands currently lags that on continental faunas,[148] which is likely driven by challenges of capacity and access on islands. Despite the challenges facing island bats, there is also opportunity to make meaningful conservation gains. Efforts to protect species on islands are likely to focus over smaller geographic areas and involve fewer government agencies, facilitating a quicker, more nimble approach to implementing conservation strategies. Research findings can be quickly disseminated to a small group of stakeholders, enabling practical and achievable conservation action.

Subterranean refuges

Subterranean habitats are a different type of "island" but share many similarities to islands with supporting fragile faunas. Although caves account for a relatively small proportion of the landscape compared to other habitats, they support a disproportionate number of endemic species.[153,154] Subterranean habitats support some of the largest and most diverse aggregations of bat species in the world.[149] In turn, bats play a key role in cave ecosystems and surrounding habitats, especially when they form aggregations in the thousands to millions. Bats depositing guano in caves provide some of the only allochthonous nutrient inputs into cave environments, thus contributing substantially to cave ecosystem food webs and supporting cave-specialist organisms.[155] In addition, bats commuting and foraging to and from a centralized cave roost provide ecosystem services as consumers of nocturnal insects, pollinators of tropical plants, and dispersers of tropical seeds.[156]

With an estimated 40% of all threatened bat species[149] known to use subterranean habitats, researchers and conservation practitioners need to place a greater emphasis on implementing effective measures in these high-risk habitats. While some caves and cave-dwelling bats receive some legal protection, the extent and impact of these protections vary considerably across the world.[157] Legal protection relies on available and accurate information and may not always be enforceable without local support. For example, although caves are protected by law in the Philippines (Republic Act No. 9072) and there has been significant progress in protecting karst habitats, challenges arise if local communities and interest groups are not aware of the value of habitat restoration and protection, demonstrating the importance of incorporating education and awareness campaigns as part of strategies to designate protected areas.[158] Increasingly, conservation practitioners recognize that direct actions to protect caves (e.g., land purchase and management) must include efforts to protect and restore the surrounding landscape where cave-roosting bats commute and forage. Additionally, environmental education programs with local communities are necessary to ensure local support and enforcement of conservation measures.

Accordingly, some of the most effective conservation initiatives for cave-roosting bats have come from multipartner projects that include groups with the skills and expertise to address multiple threats. As one example, a bi-national consortium of researchers, NGOs, landowners, and government agencies worked on local and range-wide conservation programs to protect and recover populations of the lesser long-nosed bat (*Leptonycteris yerbabuenae*), a migratory species that depends on caves and forms large aggregations (>10,000 bats) across its migratory range from Mexico into the southwestern United States.[159] Conservation measures in both Mexico and the United States, including roost protection measures and research efforts to obtain better estimates of population size and trends, resulted in removal of the species from the Mexican endangered species list in 2013 followed by removal from the Endangered Species Act in the United States in 2018.[160–162]

In the immediate term, conservation of cave-dwelling bats requires identifying and protecting key roost sites of vulnerable populations before local, regional, or global populations spiral toward extinction (e.g., UNEP/EUROBATS Conservation of Key Underground Sites Database).[163] At local to regional scales, correlates of bat diversity, such as land-use change and cave complexity, can be used to help identify priority caves.[164] Criteria, such as those developed as part of the IUCN Key Biodiversity Area initiative,[165] could be used to identify target areas for conservation action. The IUCN's Key Biodiversity Area criterion D focuses on large demographic aggregations in a local habitat, which applies readily to bat species that form mass colonies in caves.[165] Sustainable conservation will also require investing in research to determine the relative impacts of different stressors that contribute to population declines of cave-dwelling bats[166] and monitoring the effectiveness of conservation actions to protect populations. Direct conservation actions, such as gating sites to control human access, purchasing caves to establish reserves, or mitigating roost loss by adapting underground sites or creating artificial roosts, should be conducted as adaptive management so that populations are monitored to determine whether protective measures result in desired outcomes of stabilizing or increasing populations. Guidelines that minimize the impact of some cave activities have been developed (e.g., guano harvesting),[167] but greater efforts to reach relevant communities are needed. Finally, efforts to protect cave-dwelling bats will only succeed if cultural traditions, sensitivities, and cave use are considered.[164]

Value of bats to ecosystems

Bats provide ecosystem services of both economic and ecological value in addition to their intrinsic value to global biodiversity.[156,168] As the primary consumer of nocturnal insects, bats consume agricultural insect pests, and their annual services to the agricultural industry in the United States alone have been estimated in the billions.[169,170] Experimental studies have documented that bats reduce crop damage in a number of agricultural settings in both temperate and tropical regions,[171,172] showing that bats provide quantifiable value to agricultural economies by consuming crop pests.[168] Nectar-feeding and fruit-eating bats perform ecosystem services by pollinating plants and dispersing seeds.[156,168] Diet specialization for nectar-feeding and fruit-eating occurs primarily in just two families of bats, the old-world Pteropodidae and new-world Phyllostomidae, but these diverse phytophagous bats pollinate or disperse seeds for well over 1000 different plants worldwide.[173–175]

Bats are important contributors to forest ecosystem health and provide both ecological and economic value to neotropical and paleotropical forest ecosystems.[176] Frugivorous bats have been studied as potential agents to facilitate forest restoration and regeneration efforts in degraded landscapes due to their potential to naturally disperse seeds,[177,178] but approaches require refinement to demonstrate success at facilitating seedling recruitment in highly degraded areas.[179] Flying foxes are often the only effective seed dispersers on paleotropical islands[180] and therefore are critical for maintaining forest structure and health on oceanic islands in the Pacific and Indian Oceans.[62]

Some plants that rely heavily on bats for pollination or seed dispersal have significant commercial or ecological value,[156,168] including baobabs in Africa (*Adansonia digitata*),[181] durian (*Durio zibethinus*) and petai (*Parkia speciosa*) in southeast Asia,[182–184] and pitaya cactus (*Stenocereus* spp.) and agave (*Agave* spp.) in Mexico.[185,186] A recent meta-analysis showed that bat-pollinated plants are more dependent on their bat pollinators than plants primarily pollinated by other vertebrate pollinators such as birds or rodents, suggesting that loss of bat pollinators could have strong impacts on plant reproductive success, particularly in tropical habitats.[187]

The ecosystem consequences of declining bat abundances, local extirpations, and global extinctions need greater research attention, as our current understanding is based primarily on inferences from what we know of the primary ecological roles of bats (e.g., insect predators, plant pollinators, and seed dispersers). General theory about ecological integrity and the impacts to ecological communities from loss of biodiversity components should apply to bats.[113] In some cases, we may expect ecological resilience to reductions in population sizes or loss of species, but in other cases we may expect cascading and negative impacts resulting from removal or reduced numbers of key ecological actors.

Challenges and next steps for global bat conservation

While many of the threats that bats face (e.g., habitat loss, bushmeat hunting, and climate change) reflect the broader conservation challenges of our era, there are aspects of bat ecology that present specific challenges and opportunities for conservation action. For example, bat species that aggregate in large numbers in concentrated habitats, such as caves or mines, are particularly vulnerable to direct mortality threats; loss of large colonies can have a disproportionate impact on populations. But conversely, focal habitats, such as caves, can be tractable targets for conservation that can have a significant impact through protecting and safeguarding species from extinction, if executed effectively.[157] Identifying the stressors and solutions that overlap among taxa or require taxon-specific efforts improves the efficiency of deploying limited conservation resources.

A particular challenge for bat conservation is the pervasive lack of data on population status and trends (Fig. 3). Data deficiency hinders accurate assessment of conservation status, which impedes efforts to prioritize conservation attention when resources are limited. Data-deficient species can be under immediate threat and require urgent conservation action, as a recent paper highlights for the gray flying fox (*Pteropus griseus*), a species classified as data deficient but rapidly disappearing because of hunting pressures in Indonesia.[188] Lack of data on populations also inhibits scientific inquiry to identify stressors or determine whether conservation actions result in desired outcomes. Unsurprisingly, the problem of data deficiency is not evenly distributed across the planet and vexingly peaks in tropical regions, such as Amazonia and equatorial Africa, where bat species richness is highest but resources for research and management are more limited (Fig. 1).

The rapid pace of species discovery of bats (>25% increase in described species over the past 15 years)[10] highlights the importance of systematics for conservation. Voucher specimens from biodiversity surveys in remote or undersampled areas provide critical documentation of bat diversity in a changing world, can confirm species identification of poorly known taxa or those in need of resolution, and are essential for the description of new species.[40] However, lethal sampling for routine collecting or as part of studies searching for zoonotic viruses can be excessive or unnecessary, especially as nonlethal alternatives are available.[189,190] Training, guidance, and protocols for researchers on safe handling and nonlethal sampling techniques could reduce lethal sampling practices and minimize collateral damage from injury and disturbance to sensitive colonies.[189]

Successfully conserving bats globally will require creative and collaborative efforts to tackle the urgent needs of already imperiled species while simultaneously working to improve understanding of the status and needs of a diverse fauna. Monitoring schemes capable of quantifying whether bat populations are decreasing, stable, or increasing are still needed. Yet, we must design programs that are effective and sustainable. Some species or faunas may be intractable to effective monitoring with current technologies or capacities. For example, bat species that roost inconspicuously in trees and do not have echolocation signals that are reliably detectable with ultrasonic microphones present especially formidable challenges for estimating population changes with reasonable effort and accuracy. In tropical areas, commitments to long-term monitoring (e.g., 20 years) are recommended to provide sufficient power for estimating population change.[39]

Passive acoustic monitoring has been used for bat research for several decades, but recent improvements in sensor technologies,[191,192] progress on data science toolkits to process and interpret large audio data streams and classify bat sounds,[193] as well as advances in statistical modeling[194] now enable broad-scale monitoring schemes to determine the status and trends of bat populations.[195] With appropriate study design and implementation, such monitoring programs could also help identify potential drivers of population declines and feed directly into conservation decision making.[37,74] National-scale programs, such as the British Bat Monitoring Program[37] and the North American Bat Monitoring Program,[196] are currently operating and continue to refine ways to use acoustic data to monitor and inform decision makers about the status and trends of bat species. These programs depend on sustained governmental investment, dedicated coordination and management, as well as citizen science participation, which may limit their scalability in developing countries. Implementation of acoustic monitoring programs in areas where we know the least about bat populations, including tropical ecosystems, will require investments in monitoring infrastructures, including further development of echolocation call libraries,[197] and commitments to long-term systematic data collection.

Species that are observable while roosting can be monitored by directly counting roosting bats. Annual or biennial counts of hibernating bats are used throughout temperate regions to monitor populations of hibernating species and were responsible for the detection of mass mortality events during the emergence of WNS in the northeastern United States.[125,126] Counts of hibernating bats provide some of the most reliable data on population trends, but researchers should coordinate and plan efforts to minimize disturbance to sensitive colonies[198] and practice field hygiene to reduce spread of pathogens.[199] Internal roost surveys during maternity season should generally be avoided to reduce disturbance; instead, maternity colonies can be monitored during exit flights.[200] Monitoring efforts at roosts should be designed with consistency to account for inter- and intraseasonal variation in colony size and roost use.[196,200]

Online databases and sharing portals (e.g., AfriBats on iNaturalist.org) offer new opportunities for recording species observations, coordinating datasharing, and potentially facilitating monitoring of species that are readily observable. For example, the Eidolon Monitoring Network was piloted using trained citizen science volunteers across sub-Saharan Africa to monitor the migratory African straw-colored fruit bat (*Eidolon helvum*) across its range, given concerns about declining colony sizes at major roosts.[201] However, sustained funding to train and incentivize data collection by citizen groups are needed for these efforts to provide consistent collection of data usable for monitoring population trends and informing conservation planning.

Monitoring alone is insufficient for conservation success. Mitigating threats and protecting populations from stressors requires direct action and strategic planning to identify how actions will protect conservation targets. The open standards of the practice of conservation offer guidance and tools developed from the tenets of the theory of change and adaptive management to aid conservation practitioners in planning and executing conservation delivery.[202] The open standards can also be instructive to scientists and academic researchers interested in how hypothesis-driven research can be used to directly inform conservation decisions. Better collaboration and integration between academic researchers, conservation NGOs, and local stakeholders is needed to support building a body of evidence to inform conservation decisions and conducting conservation in ways that improve scientific knowledge and ecological integrity.[203]

The Conservation Evidence initiative compiles existing evidence for conservation interventions through an interactive online database and an open-access journal (www.conservationevidence.com). In the first edition of the synopsis of evidence for bat conservation published in 2014,[70] there were 78 interventions for bat species identified. In the soon-to-be-released edition, 188 interventions have been identified, representing a 141% increase. However, the majority of interventions are listed with "no evidence" and the increase in interventions may simply reflect efforts to petition a broader set of practitioners. The effort to collate and synthesize available knowledge relevant to direct conservation actions is a useful and promising tool. Researchers are encouraged to submit findings to the Conservation Evidence online journal or other journals that provide ready access to information so that evidence is available to the global conservation community. Similarly, the North American Bat Conservation Alliance launched a wiki site in 2017 to collate, share, and discuss findings and practices to address threats facing bats in North America (http://batconservationalliance.wikidot.com/). These efforts to share knowledge openly can hopefully advance efforts and propel us toward adopting evidence-based solutions for bat conservation globally.

Bats are taxonomically and ecologically diverse and face complex, pressing threats. A wide range of expertise and rapid responses are thus needed for effective mitigation. Addressing these needs requires effective collaborative networks of diverse individuals and groups (e.g., researchers, NGOs, and conservation practitioners) and a rapid increase of in-country research capacity in hotspots of bat diversity. Countries and regions supporting some of the highest diversity of bats in the world lack expertise entirely or are reliant on one or two dedicated researchers to garner knowledge on dozens of bat species. Training people and building more academic capacity is fundamental to accelerating research that identifies targets for conservation. To meet these needs, at least 10 regional bat conservation networks have arisen in recent years, allowing rapid knowledge development and sharing, research capacity building, consensus approaches to priority setting, and coordination of conservation effort and advocacy.[204] We endorse Kingston *et al.*[204] and advocate for a global network for bat conservation that unifies and connects existing regional networks to share knowledge, build capacity, prioritize and coordinate research effort, and provide a voice for advocacy that can ensure sustainable bat populations worldwide.

With over a third of bats considered either threatened or data deficient and well over half of species ranked with either unknown or decreasing population trends, a total of 988 known species (80% of bats classified by IUCN) require conservation or research attention. When so many species need attention, researchers and conservation practitioners may feel overwhelmed or even paralyzed when choosing or prioritizing where to target efforts. Prioritization of efforts is obviously necessary since resources are chronically insufficient to match global needs. However, criteria for prioritization will depend on the capacity, objectives, and desired outcomes and may differ even among groups who share similar values and goals. Ultimately, we must heed Voltaire's warning that "The best is the enemy of the good," roll up our proverbial sleeves, and get to work.

Acknowledgments

We thank Douglas Braaten, editor-in-chief of *Annals of the New York Academy of Sciences*, for his patience, support, and sustained interest in this review. We thank Bruce Patterson and one anonymous reviewer for constructive reviews.

Competing interests

The authors declare no competing interests.

References

1. Pimm, S.L., C.N. Jenkins, R. Abell, *et al.* 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344:** 1246752.
2. Foley, J.A., R. Defries, G.P. Asner, *et al.* 2005. Global consequences of land use. *Science* **309:** 570–574.
3. Ripple, W.J., K. Abernethy, M.G. Betts, *et al.* 2016. Bushmeat hunting and extinction risk to the world's mammals. *R. Soc. Open Sci.* **3:** 160498.
4. McCreless, E.E., D.D. Huff, D.A. Croll, *et al.* 2016. Past and estimated future impact of invasive alien mammals on insular threatened vertebrate populations. *Nat. Commun.* **7:** 12488.
5. Maclean, I.M.D. & R.J. Wilson. 2011. Recent ecological responses to climate change support predictions of high extinction risk. *Proc. Natl. Acad. Sci. USA* **108:** 12337–12342.
6. Hoffmann, M., C. Hilton-Taylor, A. Angulo, *et al.* 2010. The impact of conservation on the status of the world's vertebrates. *Science* **330:** 1503–1509.
7. Hoffmann, M., J.L. Belant, J.S. Chanson, *et al.* 2011. The changing fates of the world's mammals. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **366:** 2598–2610.
8. Ceballos, G. & P.R. Ehrlich. 2006. Global mammal distributions, biodiversity hotspots, and conservation. *Proc. Natl. Acad. Sci. USA* **103:** 19374–19379.
9. Simmons, N.B. & A.L. Cirranello. Accessed November 19, 2018. www.batnames.org.
10. Burgin, C.J., J.P. Colella, P.L. Kahn, *et al.* 2018. How many species of mammals are there? *J. Mammal.* **99:** 1–14.
11. Voigt, C.C. & T. Kingston. 2016. *Bats in the Anthropocene: Conservation of Bats in a Changing World*. Springer International Publishing.
12. Dirzo, R., H.S. Young, M. Galetti, *et al.* 2014. Defaunation in the Anthropocene. *Science* **345:** 401–406.
13. Mickleburgh, S.P., A.M. Hutson & P.A. Racey. 2002. A review of the global conservation status of bats. *Oryx* **36:** 18–34.
14. Welbergen, J.A., S.M. Klose, N. Markus, *et al.* 2008. Climate change and the effects of temperature extremes on Australian flying-foxes. *Proc. Biol. Sci.* **275:** 419–425.
15. Frick, W.F., E.F. Baerwald, J.F. Pollock, *et al.* 2017. Fatalities at wind turbines may threaten population viability of a migratory bat. *Biol. Conserv.* **209:** 172–177.
16. O'Shea, T.J., P.M. Cryan, D.T.S. Hayman, *et al.* 2016. Multiple mortality events in bats: a global review. *Mamm. Rev.* **46:** 175–190.
17. Frick, W.F., S.J. Puechmaille & C.K.R. Willis. 2016. White-nose syndrome in bats. In *Bats in the Anthropocene: Conservation of Bats in a Changing World*. C.C. Voigt & T. Kingston, Eds.: 245–262. Springer International Publishing.

18. IUCN Red List of Threatened Species. The IUCN Red List of Threatened Species. Accessed November 19, 2018. https://www.iucnredlist.org/en.
19. International Union for Conservation of Nature and Natural Resources & IUCN Species Survival Commission. 2001. IUCN Red List categories and criteria. IUCN.
20. Tsang, S.M., A.L. Cirranello, P.J.J. Bates, *et al.* 2016. The roles of taxonomy and systematics in bat conservation. In *Bats in the Anthropocene: Conservation of Bats in a Changing World.* C.C. Voigt & T. Kingston, Eds.: 503–538. Springer.
21. Wilson, D.E. & D.M. Reeder. 2005. *Mammal Species of the World: A Taxonomic and Geographic Reference.* D.E. Wilson & D.M. Reeder, Eds. Johns Hopkins University Press.
22. Meyer, C.F.J., M.J. Struebig & M.R. Willig. 2016. Responses of tropical bats to habitat fragmentation, logging, and deforestation. In *Bats in the Anthropocene: Conservation of Bats in a Changing World.* C. Voigt & T. Kingston, Eds.: 63–103. Springer International Publishing.
23. Kunz, T.H. & L.F. Lumsden. 2003. Ecology of cavity and foliage roosting bats. In *Bat Ecology*. T.H. Kunz & M.B. Fenton, Eds.: 3–89. Chicago, IL: University of Chicago Press.
24. Furey, N.M. & P.A. Racey. 2016. Conservation ecology of cave bats. In *Bats in the Anthropocene: Conservation of Bats in a Changing World.* C. Voigt & T. Kingston, Eds.: 463–500. Springer International Publishing.
25. Willig, M.R., B.D. Patterson & R.D. Stevenson. 2003. Patterns of range size, richness, and body size in the Chiroptera. In *Bat Ecology*. T.H. Kunz & F.M. Brock, Eds.: 580–621. Chicago, IL: University of Chicago Press.
26. Hansen, M.C., P.V. Potapov, R. Moore, *et al.* 2013. High-resolution global maps of 21st-century forest cover change. *Science* **342:** 850–853.
27. Hansen, M.C., S.V. Stehman, P.V. Potapov, *et al.* 2008. Humid tropical forest clearing from 2000 to 2005 quantified by using multitemporal and multiresolution remotely sensed data. *Proc. Natl. Acad. Sci. USA* **105:** 9439–9444.
28. Brook, B.W., N.S. Sodhi & P.K.L. Ng. 2003. Catastrophic extinctions follow deforestation in Singapore. *Nature* **424:** 420–426.
29. Kingston, T. 2010. Research priorities for bat conservation in Southeast Asia: a consensus approach. *Biodivers. Conserv.* **19:** 471–484.
30. Lacki, M.J., J.P. Hayes & A. Kurta. 2007. *Bats in Forests: Conservation and Management.* JHU Press.
31. Kingston, T. 2013. Response of bat diversity to forest disturbance in Southeast Asia: insights from long-term research in Malaysia. In *Bat Evolution, Ecology, and Conservation.* R. Adams & S.C. Pedersen, Eds.: 169–185. Springer.
32. Meyer, C.F.J., M.J. Struebig & M.R. Willig. 2016. Responses of tropical bats to habitat fragmentation, logging, and deforestation. In *Bats in the Anthropocene: Conservation of Bats in a Changing World.* C. Voigt & T. Kingston, Eds.: 63–103. Springer International Publishing.
33. Webala, P.W., J. Mwaura, J.M. Mware, *et al.* 2019. The effect of habitat fragmentation on the bats of Kakamega Forest, western Kenya. *J. Trop. Ecol.* **35:** 260–269.
34. Russo, D., G. Billington, F. Bontadina, *et al.* 2016. Identifying key research objectives to make European forests greener for bats. *Front. Ecol. Evol.* **4:** 87.
35. Law, B., K.J. Park & M.J. Lacki. 2016. Insectivorous bats and silviculture: balancing timber production and bat conservation. In *Bats in the Anthropocene: Conservation of Bats in a Changing World.* C.C. Voigt & T. Kingston, Eds.: 105–150. Springer.
36. O'Shea, T.J., L.E. Ellison & T.R. Stanley. 2004. Survival estimation in bats: historical overview, critical appraisal, and suggestions for new approaches. In *Sampling Rare and Elusive Species.* W.L. Thompson, Ed.: 297–336. Washington, DC: Island Press.
37. Barlow, K.E., P.A. Briggs, K.A. Haysom, *et al.* 2015. Citizen science reveals trends in bat populations: the National Bat Monitoring Programme in Great Britain. *Biol. Conserv.* **182:** 14–26.
38. Gibb, R., E. Browning, P. Glover-Kapfer, *et al.* 2018. Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. *Methods Ecol. Evol.* https://doi.org/10.1111/2041-210X.13101.
39. Meyer, C.F.J., L.M.S. Aguiar, L.F. Aguirre, *et al.* 2010. Long-term monitoring of tropical bats for anthropogenic impact assessment: gauging the statistical power to detect population change. *Biol. Conserv.* **143:** 2797–2807.
40. Kingston, T. 2016. Bats. In *Core Standardized Methods for Rapid Biological Field Assessment.* T.H. Larsen, Ed.: 59–82. Conservation International.
41. Williams-Guillén, K., E. Olimpi, B. Maas, *et al.* 2016. Bats in the anthropogenic matrix: challenges and opportunities for the conservation of Chiroptera and their ecosystem services in agricultural landscapes. In *Bats in the Anthropocene: Conservation of Bats in a Changing World.* C.C. Voigt & T. Kingston, Eds.: 151–186. Springer.
42. Park, K.J. 2015. Mitigating the impacts of agriculture on biodiversity: bats and their potential role as bioindicators. *Mamm. Biol.* **80:** 191–204.
43. Aziz, S.A., K.J. Olival, S. Bumrungsri, *et al.* 2016. The conflict between pteropodid bats and fruit growers: species, legislation and mitigation. In *Bats in the Anthropocene: Conservation of Bats in a Changing World.* C.C. Voight & T. Kingston, Eds.: 377–426. Springer.
44. Kingston, T., V. Florens, R. Olesky, *et al.* 2018. *Pteropus niger*. IUCN Red List of Threatened Species.
45. Mildenstein, T., I. Tanshi & P.A. Racey. 2016. Exploitation of bats for bushmeat and medicine. In *Bats in the Anthropocene: Conservation of Bats in a Changing World.* C.C. Voigt & T. Kingston, Eds.: 325–375. Springer.
46. Mickleburgh, S., K. Waylen & P. Racey. 2009. Bats as bushmeat: a global review. *Oryx* **43:** 217.
47. Epstein, J.H., K.J. Olival, J.R.C. Pulliam, *et al.* 2009. *Pteropus vampyrus*, a hunted migratory species with a multinational home-range and a need for regional management. *J. Appl. Ecol.* **46:** 991–1002.
48. Brooke, A.P. & M. Tschapka. 2002. Threats from overhunting to the flying fox, *Pteropus tonganus*, (Chiroptera: Pteropodidae) on Niue Island, South Pacific Ocean. *Biol. Conserv.* **103:** 343–348.
49. Harrison, M.E., S.M. Cheyne, F. Darma, *et al.* 2011. Hunting of flying foxes and perception of disease risk in Indonesian Borneo. *Biol. Conserv.* **144:** 2441–2449.
50. Kamins, A.O., O. Restif, Y. Ntiamoa-Baidu, *et al.* 2011. Uncovering the fruit bat bushmeat commodity chain and

the true extent of fruit bat hunting in Ghana, West Africa. *Biol. Conserv.* **144:** 3000–3008.

51. Sheherazade, & S.M. Tsang. 2015. Quantifying the bat bushmeat trade in North Sulawesi, Indonesia, with suggestions for conservation action. *Glob. Ecol. Conserv.* **3:** 324–330.
52. Lee, B.P.Y.-H., M.J. Struebig, S.J. Rossiter & T. Kingston. 2015. Increasing concern over trade in bat souvenirs from South-east Asia. *Oryx* **49:** 204.
53. Checklist of CITES species. Accessed November 19, 2018. http://checklist.cites.org.
54. O'Shea, T.J., P.M. Cryan, D.T.S. Hayman, *et al.* 2016. Multiple mortality events in bats: a global review. *Mamm. Rev.* **46:** 175–190.
55. Kingston, T. 2016. Cute, creepy, or crispy—how values, attitudes, and norms shape human behavior toward bats. In *Bats in the Anthropocene: Conservation of Bats in a Changing World.* C.C. Voigt & T. Kingston, Eds.: 571–595. Springer.
56. Schneeberger, K. & C.C. Voigt. 2016. Zoonotic viruses and conservation of bats. In *Bats in the Anthropocene: Conservation of Bats in a Changing World.* C.C. Voigt & T. Kingston, Eds.: 263–292. Springer.
57. Streicker, D.G., S. Recuenco, W. Valderrama, *et al.* 2012. Ecological and anthropogenic drivers of rabies exposure in vampire bats: implications for transmission and control. *Proc. Biol. Sci.* **279:** 3384–3392.
58. Voigt, C.C., K.L. Phelps, L.F. Aguirre, *et al.* 2016. Bats and buildings: the conservation of synanthropic bats. In *Bats in the Anthropocene: Conservation of Bats in a Changing World.* C.C. Voigt & T. Kingston, Eds.: 427–462. Springer.
59. Vincenot, C.E., F.B.V. Florens & T. Kingston. 2017. Can we protect island flying foxes? *Science* **355:** 1368–1370.
60. Florens, F.B.V. 2016. Biodiversity law: Mauritius culls threatened fruit bats. *Nature* **530:** 33.
61. Florens, F.B.V. & C. Baider. 2019. Mass-culling of a threatened island flying fox species failed to increase fruit growers' profits and revealed gaps to be addressed for effective conservation. *J. Nat. Conserv.* **47:** 58–64.
62. Florens, F.B.V., C. Baider, V. Marday, *et al.* 2017. Disproportionately large ecological role of a recently mass-culled flying fox in native forests of an oceanic island. *J. Nat. Conserv.* **40:** 85–93.
63. Johnson, N., N. Aréchiga-Ceballos & A. Aguilar-Setien. 2014. Vampire bat rabies: ecology, epidemiology and control. *Viruses* **6:** 1911–1928.
64. Reid, J.L. 2016. Knowledge and experience predict indiscriminate bat-killing intentions among Costa Rican men. *Biotropica* **48:** 394–404.
65. Amman, B.R., L. Nyakarahuka, A.K. McElroy, *et al.* 2014. Marburgvirus resurgence in Kitaka Mine bat population after extermination attempts, Uganda. *Emerg. Infect. Dis.* **20:** 1761–1764.
66. Madden, F. & B. McQuinn. 2014. Conservation's blind spot: the case for conflict transformation in wildlife conservation. *Biol. Conserv.* **178:** 97–106.
67. St John, F.A.V., G. Edwards-Jones & J.P.G. Jones. 2010. Conservation and human behaviour: lessons from social psychology. *Wildl. Res.* **37:** 658.
68. Madden, F. 2004. Creating coexistence between humans and wildlife: global perspectives on local efforts to address human–wildlife conflict. *Hum. Dimens. Wildl.* **9:** 247–257.
69. Martin, K.W., D.M. Leslie, M.E. Payton, *et al.* 2003. Internal cave gating for protection of colonies of the endangered Gray Bat (*Myotis grisescens*). *Acta Chiropt.* **5:** 143–150.
70. Berthinussen, A., O.C. Richardson & J.D. Altringham. 2014. *Bat Conservation: Global Evidence for the Effects of Interventions.* Pelagic Publishing Ltd.
71. Tobin, A., R.J.M. Corbett, F.M. Walker, *et al.* 2018. Acceptance of bats to gates at abandoned mines. *J. Wildl. Manage.* **82:** 1345–1358.
72. Spanjer, G.R. & M. Brock Fenton. 2005. Behavioral responses of bats to gates at caves and mines. *Wildl. Soc. Bull.* **33:** 1101–1112.
73. Seto, K.C., B. Guneralp & L.R. Hutyra. 2012. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc. Natl. Acad. Sci. USA* **109:** 16083–16088.
74. Border, J.A., S.E. Newson, D.C.J. White, *et al.* 2017. Predicting the likely impact of urbanisation on bat populations using citizen science data, a case study for Norfolk, UK. *Landsc. Urban Plan.* **162:** 44–55.
75. Russo, D. & L. Ancillotto. 2015. Sensitivity of bats to urbanization: a review. *Mamm. Biol.* **80:** 205–212.
76. Jaffé, R., X. Prous, R. Zampaulo, *et al.* 2016. Reconciling mining with the conservation of cave biodiversity: a quantitative baseline to help establish conservation priorities. *PLoS One* **11:** e0168348.
77. Monadjem, A., L. Richards & C. Denys. 2016. An African bat hotspot: the exceptional importance of Mount Nimba for bat diversity. *Acta Chiropt.* **18:** 359–375.
78. Kurta, A. & S.M. Smith. 2014. Hibernating bats and abandoned mines in the Upper Peninsula of Michigan. *Northeast. Nat.* **21:** 587–605.
79. Arnett, E.B. & E.F. Baerwald. 2013. Impacts of wind energy development on bats: implications for conservation. In *Bat Evolution, Ecology, and Conservation.* R. Adams & S.C. Pedersen, Eds.: 435–456. Springer.
80. Hayes, M.A. 2013. Bats killed in large numbers at United States wind energy facilities. *Bioscience* **63:** 975–979.
81. Smallwood, K.S. 2013. Comparing bird and bat fatality-rate estimates among North American wind-energy projects. *Wildl. Soc. Bull.* **37:** 19–33.
82. Lehnert, L.S., S. Kramer-Schadt, S. Schönborn, *et al.* 2014. Wind farm facilities in Germany kill noctule bats from near and far. *PLoS One* **9:** e103106.
83. Voigt, C.C., A.G. Popa-Lisseanu, I. Niermann, *et al.* 2012. The catchment area of wind farms for European bats: a plea for international regulations. *Biol. Conserv.* **153:** 80–86.
84. Millon, L., C. Colin, F. Brescia, *et al.* 2018. Wind turbines impact bat activity, leading to high losses of habitat use in a biodiversity hotspot. *Ecol. Eng.* **112:** 51–54.
85. Arnett, E.B., E.F. Baerwald, F. Mathews, *et al.* 2016. Impacts of wind energy development on bats: a global perspective. In *Bats in the Anthropocene: Conservation of Bats in a*

Changing World. C.C. Voigt & T. Kingston, Eds.: 295–323. Springer.

86. Chou, C.-H., T.-Y. Hsieh, W.-T. Liu, *et al.* 2017. Bat fatalities at wind farms in Taiwan. *Mamm. Study* **42:** 121–124.
87. Kunz, T.H., E.B. Arnett, W.P. Erickson, *et al.* 2007. Ecological impacts of wind energy development on bats: questions, research needs, and hypotheses. *Front. Ecol. Environ.* **5:** 315–324.
88. Cryan, P.M., P.M. Gorresen, C.D. Hein, *et al.* 2014. Behavior of bats at wind turbines. *Proc. Natl. Acad. Sci. USA* **111:** 15126–15131.
89. Weller, T.J., P.M. Cryan & T.J. O'Shea. 2009. Broadening the focus of bat conservation and research in the USA for the 21st century. *Endanger. Species Res.* **8:** 129–145.
90. Arnett, E.B., M.M.P. Huso, M.R. Schirmacher, *et al.* 2011. Altering turbine speed reduces bat mortality at wind-energy facilities. *Front. Ecol. Environ.* **9:** 209–214.
91. Baerwald, E.F., J. Edworthy, M. Holder, *et al.* 2009. A large-scale mitigation experiment to reduce bat fatalities at wind energy facilities. *J. Wildl. Manage.* **73:** 1077–1081.
92. Arnett, E.B., C.D. Hein, M.R. Schirmacher, *et al.* 2013. Evaluating the effectiveness of an ultrasonic acoustic deterrent for reducing bat fatalities at wind turbines. *PLoS One* **8:** e65794.
93. Arnett, E.B., R.M.R. Barclay & C.D. Hein. 2013. Thresholds for bats killed by wind turbines. *Front. Ecol. Environ.* **11:** 171–171.
94. Pecl, G.T., M.B. Araújo, J.D. Bell, *et al.* 2017. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* **355**. https://doi.org/10.1126/science.aai9214.
95. Newbold, T. 2018. Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios. *Proc. Biol. Sci.* **285**. https://doi.org/10.1098/rspb.2018.0792.
96. Rebelo, H., P. Tarroso & G. Jones. 2010. Predicted impact of climate change on European bats in relation to their biogeographic patterns. *Glob. Change Biol.* **16:** 561–576.
97. Hughes, A.C., C. Satasook, P.J.J. Bates, *et al.* 2012. The projected effects of climatic and vegetation changes on the distribution and diversity of Southeast Asian bats. *Glob. Change Biol.* **18:** 1854–1865.
98. Aguiar, L.M.S., E. Bernard, V. Ribeiro, *et al.* 2016. Should I stay or should I go? Climate change effects on the future of Neotropical savannah bats. *Glob. Ecol. Conserv.* **5:** 22–33.
99. Zamora-Gutierrez, V., R.G. Pearson, R.E. Green, *et al.* 2017. Forecasting the combined effects of climate and land use change on Mexican bats. *Divers. Distrib.* **24:** 363–374.
100. Razgour, O., J.B. Taggart, S. Manel, *et al.* 2018. An integrated framework to identify wildlife populations under threat from climate change. *Mol. Ecol. Resour.* **18:** 18–31.
101. Sherwin, H.A., W. Ian Montgomery & M.G. Lundy. 2012. The impact and implications of climate change for bats. *Mamm. Rev.* **43:** 171–182.
102. McCracken, G.F., R.F. Bernard, M. Gamba-Rios, *et al.* 2018. Rapid range expansion of the Brazilian free-tailed bat in the southeastern United States, 2008–2016. *J. Mammal.* **99:** 312–320.
103. Solari, K.A., H.K. Frank, L.O. Frishkoff, *et al.* 2016. Opportunity for some, extinction for others: the fate of tetrapods in the Anthropocene. *Evol. Ecol. Res.* **17:** 787–813.
104. Adams, R.A. 2017. Dark side of climate change: species-specific responses and first indications of disruption in spring altitudinal migration in myotis bats. *J. Zool.* **304:** 268–275.
105. Stepanian, P.M. & C.E. Wainwright. 2018. Ongoing changes in migration phenology and winter residency at Bracken Bat Cave. *Glob. Change Biol.* **24:** 3266–3275.
106. Frick, W.F., D.S. Reynolds & T.H. Kunz. 2010. Influence of climate and reproductive timing on demography of little brown myotis *Myotis lucifugus*. *J. Anim. Ecol.* **79:** 128–136.
107. Nurul-Ain, E., H. Rosli & T. Kingston. 2017. Resource availability and roosting ecology shape reproductive phenology of rain forest insectivorous bats. *Biotropica* **49:** 382–394.
108. Frick, W.F., P.M. Stepanian, J.F. Kelly, *et al.* 2012. Climate and weather impact timing of emergence of bats. *PLoS One* **7:** e42737.
109. Gómez-Ruiz, E.P. & T.E. Lacher. 2016. Modelling the potential geographic distribution of an endangered pollination corridor in Mexico and the United States. *Divers. Distrib.* **23:** 67–78.
110. Bennett, J.M., D.G. Nimmo, R.H. Clarke, *et al.* 2014. Resistance and resilience: can the abrupt end of extreme drought reverse avifaunal collapse? *Divers. Distrib.* **20:** 1321–1332.
111. Mac Nally, R., R.M. Nally, S. Nerenberg, *et al.* 2013. Do frogs bounce, and if so, by how much? Responses to the "Big Wet" following the "Big Dry" in south-eastern Australia. *Glob. Ecol. Biogeogr.* **23:** 223–234.
112. Scanlon, A.T., S. Petit, M. Tuiwawa, *et al.* 2018. Response of primary and secondary rainforest flowers and fruits to a cyclone, and implications for plant-servicing bats. *Glob. Change Biol.* **24:** 3820–3836.
113. Jones, G., D.S. Jacobs, T.H. Kunz, *et al.* 2009. Carpe noctem: the importance of bats as bioindicators. *Endanger. Species Res.* **8:** 93–115.
114. Parker, K.A., B.T. Springall, R.A. Garshong, *et al.* 2018. Rapid increases in bat activity and diversity after wetland construction in an urban ecosystem. *Wetlands* https://doi.org/10.1007/s13157-018-1115-5.
115. Kingsford, R.T. 2011. Conservation management of rivers and wetlands under climate change—a synthesis. *Mar. Freshwater Res.* **62:** 217.
116. Lisón, F. & J.F. Calvo. 2011. The significance of water infrastructures for the conservation of bats in a semiarid Mediterranean landscape. *Anim. Conserv.* **14:** 533–541.
117. Adams, R.A. & M.A. Hayes. 2008. Water availability and successful lactation by bats as related to climate change in arid regions of western North America. *J. Anim. Ecol.* **77:** 1115–1121.
118. Bellard, C., P. Cassey & T.M. Blackburn. 2016. Alien species as a driver of recent extinctions. *Biol. Lett.* **12:** 20150623.
119. Doherty, T.S., A.S. Glen, D.G. Nimmo, *et al.* 2016. Invasive predators and global biodiversity loss. *Proc. Natl. Acad. Sci. USA* **113:** 11261–11265.

120. Welch, J.N. & C. Leppanen. 2017. The threat of invasive species to bats: a review. *Mamm. Rev.* **47:** 277–290.
121. Spatz, D.R., K.M. Zilliacus, N.D. Holmes, *et al.* 2017. Globally threatened vertebrates on islands with invasive species. *Sci. Adv.* **3:** e1603080.
122. Blehert, D.S., A.C. Hicks, M. Behr, *et al.* 2009. Bat white-nose syndrome: an emerging fungal pathogen? *Science* **323:** 227–227.
123. Lorch, J.M., C.U. Meteyer, M.J. Behr, *et al.* 2011. Experimental infection of bats with *Geomyces destructans* causes white-nose syndrome. *Nature* **480:** 376–378.
124. Warnecke, L., J.M. Turner, T.K. Bollinger, *et al.* 2012. Inoculation of bats with European *Geomyces destructans* supports the novel pathogen hypothesis for the origin of white-nose syndrome. *Proc. Natl. Acad. Sci. USA* **109:** 6999–7003.
125. Frick, W.F., J.F. Pollock, A.C. Hicks, *et al.* 2010. An emerging disease causes regional population collapse of a common North American bat species. *Science* **329:** 679–682.
126. Frick, W.F., S.J. Puechmaille, J.R. Hoyt, *et al.* 2015. Disease alters macroecological patterns of North American bats. *Glob. Ecol. Biogeogr.* **24:** 741–749.
127. Langwig, K.E., W.F. Frick, J.T. Bried, *et al.* 2012. Sociality, density-dependence and microclimates determine the persistence of populations suffering from a novel fungal disease, white-nose syndrome. *Ecol. Lett.* **15:** 1050–1057.
128. Meteyer, C.U., E.L. Buckles, D.S. Blehert, *et al.* 2009. Histopathologic criteria to confirm white-nose syndrome in bats. *J. Vet. Diagn. Invest.* **21:** 411–414.
129. Langwig, K.E., W.F. Frick, R. Reynolds, *et al.* 2015. Host and pathogen ecology drive the seasonal dynamics of a fungal disease, white-nose syndrome. *Proc. Biol. Sci.* **282:** 20142335.
130. Reeder, D.M., C.L. Frank, G.G. Turner, *et al.* 2012. Frequent arousal from hibernation linked to severity of infection and mortality in bats with white-nose syndrome. *PLoS One* **7:** e38920.
131. Kunz, T.H., E.L.P. Anthony & W. Timothy Rumage III. 1977. Mortality of little brown bats following multiple pesticide applications. *J. Wildl. Manage.* **41:** 476.
132. Frick, W.F., W.E. Rainey & E.D. Pierson. 2007. Potential effects of environmental contamination on *Yuma myotis* demography and population growth. *Ecol. Appl.* **17:** 1213–1222.
133. Bayat, S., F. Geiser, P. Kristiansen, *et al.* 2014. Organic contaminants in bats: trends and new issues. *Environ. Int.* **63:** 40–52.
134. van den Berg, H., M. Zaim, R.S. Yadav, *et al.* 2012. Global trends in the use of insecticides to control vector-borne diseases. *Environ. Health Perspect.* **120:** 577–582.
135. Zukal, J., J. Pikula & H. Bandouchova. 2015. Bats as bioindicators of heavy metal pollution: history and prospect. *Mamm. Biol.* **80:** 220–227.
136. Stone, E.L., S. Harris & G. Jones. 2015. Impacts of artificial lighting on bats: a review of challenges and solutions. *Mamm. Biol.* **80:** 213–219.
137. Bunkley, J.P., C.J.W. McClure, A.Y. Kawahara, *et al.* 2017. Anthropogenic noise changes arthropod abundances. *Ecol. Evol.* **7:** 2977–2985.
138. Fensome, A.G. & F. Mathews. 2016. Roads and bats: a meta-analysis and review of the evidence on vehicle collisions and barrier effects. *Mamm. Rev.* **46:** 311–323.
139. Altringham, J. & G. Kerth. 2016. Bats and roads. *In Bats in the Anthropocene: Conservation of Bats in a Changing World.* C.C. Voigt & T. Kingston, Eds.: 35–62. Springer.
140. Abbott, I.M., A. Berthinussen, E. Stone, *et al.* 2015. Bats and roads. In *Handbook of Road Ecology*. R. van der Ree, D.J. Smith & C. Grilo, Eds.: 290–299. Chichester: John Wiley & Sons, Ltd.
141. Novaes, R.L.M., R.S. Laurindo, R.A.P. Dornas, *et al.* 2018. On a collision course: the vulnerability of bats to roadkills in Brazil. *Mastozool. Neotrop.* **25:** 115–128.
142. Berthinussen, A. & J. Altringham. 2011. The effect of a major road on bat activity and diversity. *J. Appl. Ecol.* **49:** 82–89.
143. Kerth, G. & M. Melber. 2009. Species-specific barrier effects of a motorway on the habitat use of two threatened forest-living bat species. *Biol. Conserv.* **142:** 270–279.
144. Myers, N., R.A. Mittermeier, C.G. Mittermeier, *et al.* 2000. Biodiversity hotspots for conservation priorities. *Nature* **403:** 853–858.
145. Tershy, B.R., K.-W. Shen, K.M. Newton, *et al.* 2015. The importance of islands for the protection of biological and linguistic diversity. *Bioscience* **65:** 592–597.
146. Fleming, T.H. & P.A. Racey. 2010. *Island Bats: Evolution, Ecology, and Conservation.* University of Chicago Press.
147. Shilton, L.A. & R.H. Whittaker. 2009. The role of Pteropodid bats in reestablishing tropical forests on Krakatau. In *Island Bats: Evolution, Ecology and Conservation.* T.H. Fleming & P.A. Racey, Eds.: 176–215. Chicago, IL: University of Chicago Press.
148. Conenna, I., R. Rocha, D. Russo, *et al.* 2017. Insular bats and research effort: a review of global patterns and priorities. *Mamm. Rev.* **47:** 169–182.
149. IUCN Red List of Threatened Species. Accessed October 10, 2018. http://www.iucnredlist.org.
150. Knutson, T.R., J.L. McBride, J. Chan, *et al.* 2010. Tropical cyclones and climate change. *Nat. Geosci.* **3:** 157–163.
151. Helgen, K.M., L.E. Helgen & D.E. Wilson. 2009. Pacific flying foxes (Mammalia: Chiroptera): two new species of *Pteropus* from Samoa, probably extinct. *Am. Mus. Novit.* **3646:** 1–37.
152. Jones, K.E., S.P. Mickleburgh, W. Sechrest, *et al.* 2009. Global overview of the conservation of island bats: importance, challenges and opportunities. In *Island Bats: Evolution, Ecology, and Conservation.* T.H. Fleming & P.A. Racey, Eds.: 496–530. Chicago, IL: University of Chicago Press.
153. Deharveng, L. & A. Bedos. 2012. Diversity patterns in the tropics. In *Encyclopedia of Caves.* W.B. White & D.C Culver, Eds.: 238–250.
154. Hunter, M.L., V. Acuña, D.M. Bauer, *et al.* 2017. Conserving small natural features with large ecological roles: a synthetic overview. *Biol. Conserv.* **211:** 88–95.
155. Gnaspini, P. & E. Trajano. 2000. Guano communities in tropical caves. In *Ecosystems of the World: Subterranean Ecosystems.* W.F. Humphreys, Ed.: 251–268. New York, NY: Elsevier Science.

156. Kunz, T.H., E. Braun de Torrez, D. Bauer, *et al.* 2011. Ecosystem services provided by bats. *Ann. N.Y. Acad. Sci.* **1223:** 1–38.
157. Medellin, R.A., R. Wiederholt & L. Lopez-Hoffman. 2017. Conservation relevance of bat caves for biodiversity and ecosystem services. *Biol. Conserv.* **211:** 45–50.
158. Urich, P.B., M.J. Day & F. Lynagh. 2001. Policy and practice in karst landscape protection: Bohol, the Philippines. *Geogr. J.* **167:** 305–323.
159. Rojas-Martínez, A., A. Valiente-Banuet, M. del Coro Arizmendi, *et al.* 1999. Seasonal distribution of the long-nosed bat (*Leptonycteris curasoae*) in North America: does a generalized migration pattern really exist? *J. Biogeogr.* **26:** 1065–1077.
160. Medellin, R.A., M. Rivero, A. Ibarra, *et al.* 2018. Follow me: foraging distances of *Leptonycteris yerbabuenae* (Chiroptera: Phyllostomidae) in Sonora determined by fluorescent powder. *J. Mammal.* **99:** 306–311.
161. Frick, W.F., P.A. Heady, A.D. Earl, *et al.* 2018. Seasonal ecology of a migratory nectar-feeding bat at the edge of its range. *J. Mammal.* **99:** 1072–1081.
162. USFWS. 2018. Endangered and threatened wildlife and plants; removal of the lesser long-nosed bat from the federal list of endangered and threatened wildlife. *Fed. Reg.* **83:** 17093–17110.
163. Conservation of key underground sites: the database | UNEP/EUROBATS. Accessed February 4, 2019. http://www.eurobats.org/activities/intersessional_working_groups/underground_sites.
164. Phelps, K., R. Jose, M. Labonite, *et al.* 2016. Correlates of cave-roosting bat diversity as an effective tool to identify priority caves. *Biol. Conserv.* **201:** 201–209.
165. IUCN. 2016. *A global standard for the identification of key biodiversity areas, version 1.0.* First Gland, Switzerland: IUCN.
166. Phelps, K.L. & T. Kingston. 2018. Environmental and biological context modulates the physiological stress response of bats to human disturbance. *Oecologia* **188:** 41–52.
167. International Union for the Conservation of Nature Species Survival Commission. 2014. Guidelines for minimizing the negative impact to bats and other cave organisms from guano harvesting.
168. Maas, B., D.S. Karp, S. Bumrungsri, *et al.* 2016. Bird and bat predation services in tropical forests and agroforestry landscapes. *Biol. Rev. Camb. Philos. Soc.* **91:** 1081–1101.
169. Boyles, J.G., P.M. Cryan, G.F. McCracken, *et al.* 2011. Economic importance of bats in agriculture. *Science* **332:** 41–42.
170. Cleveland, C.J., M. Betke, P. Federico, *et al.* 2006. Economic value of the pest control service provided by Brazilian free-tailed bats in south-central Texas. *Front. Ecol. Environ.* **4:** 238–243.
171. Maine, J.J. & J.G. Boyles. 2015. Bats initiate vital agroecological interactions in corn. *Proc. Natl. Acad. Sci. USA* **112:** 12438–12443.
172. Williams-Guillen, K., I. Perfecto & J. Vandermeer. 2008. Bats limit insects in a neotropical agroforestry system. *Science* **320:** 70.
173. Kunz, T.H., E. Braun de Torrez, D. Bauer, *et al.* 2011. Ecosystem services provided by bats. *Ann. N.Y. Acad. Sci.* **1223:** 1–38.
174. Lobova, T.A., C.K. Geiselman & S.A. Mori. 2009. *Seed Dispersal by Bats in the Neotropics.* New York, NY: Botanical Garden Press.
175. Seltzer, C.E., H.J. Ndangalasi & N.J. Cordeiro. 2013. Seed dispersal in the dark: shedding light on the role of fruit bats in Africa. *Biotropica* **45:** 450–456.
176. Muscarella, R. & T.H. Fleming. 2007. The role of frugivorous bats in tropical forest succession. *Biol. Rev. Camb. Philos. Soc.* **82:** 573–590.
177. Kelm, D.H., K.R. Wiesner & O. von Helversen. 2008. Effects of artificial roosts for frugivorous bats on seed dispersal in a neotropical forest pasture mosaic. *Conserv. Biol.* **22:** 733–741.
178. Sritongchuay, T., G.A. Gale, A. Stewart, *et al.* 2014. Seed rain in abandoned clearings in a lowland evergreen rain forest in southern Thailand. *Trop. Conserv. Sci.* **7:** 572–585.
179. Reid, J.L., J. Leighton Reid, E.K. Holste, *et al.* 2013. Artificial bat roosts did not accelerate forest regeneration in abandoned pastures in southern Costa Rica. *Biol. Conserv.* **167:** 9–16.
180. McConkey, K.R. & D.R. Drake. 2015. Low redundancy in seed dispersal within an island frugivore community. *AoB Plants* **7:** plv088.
181. Baum, D.A. 1995. The comparative pollination and floral biology of Baobabs (Adansonia-Bombacaceae). *Ann. Missouri Bot. Gard.* **82:** 322.
182. Bumrungsri, S., A. Harbit, C. Benzie, *et al.* 2008. The pollination ecology of two species of *Parkia* (Mimosaceae) in southern Thailand. *J. Trop. Ecol.* **24:** 467–475.
183. Bumrungsri, S., E. Sripaoraya, T. Chongsiri, *et al.* 2008. The pollination ecology of durian (*Durio zibethinus*, Bombacaceae) in southern Thailand. *J. Trop. Ecol.* **25:** 85–92.
184. Bumrungsri, S., D. Lang, C. Harrower, *et al.* 2013. The dawn bat, *Eonycteris spelaea* Dobson (Chiroptera: Pteropodidae), feeds mainly on pollen of economically important food plants in Thailand. *Acta Chiropt.* **15:** 95–104.
185. Trejo-Salazar, R.-E., L.E. Eguiarte, D. Suro-Piñera, *et al.* 2016. Save our bats, save our tequila: industry and science join forces to help bats and agaves. *Nat. Areas J.* **36:** 523–530.
186. Fleming, T.H., C.T. Sahley, J. Nathaniel Holland, *et al.* 2001. Sonoran desert columnar cacti and the evolution of generalized pollination systems. *Ecol. Monogr.* **71:** 511–530.
187. Ratto, F., B.I. Simmons, R. Spake, *et al.* 2018. Global importance of vertebrate pollinators for plant reproductive success: a meta-analysis. *Front. Ecol. Environ.* **16:** 82–90.
188. Sheherazade & S.M. Tsang. 2018. Roost of gray flying foxes (*Pteropus griseus*) in Indonesia and records of a new hunting threat. *Diversity* **10:** 102.
189. Russo, D., L. Ancillotto, A.C. Hughes, *et al.* 2017. Collection of voucher specimens for bat research: conservation, ethical implications, reduction, and alternatives. *Mamm. Rev.* **47:** 237–246.
190. Young, C.C.W. & K.J. Olival. 2016. Optimizing viral discovery in bats. *PLoS One* **11:** e0149237.
191. Hill, A.P., P. Prince, E.P. Covarrubias, *et al.* 2018. AudioMoth: evaluation of a smart open acoustic device

for monitoring biodiversity and the environment. *Methods Ecol. Evol.* **9:** 1199–1211.

192. Frick, W.F. 2013. Acoustic monitoring of bats, considerations of options for long-term monitoring. *Therya* **4:** 69–78.
193. Mac Aodha, O., R. Gibb, K.E. Barlow, *et al.* 2018. Bat detective—deep learning tools for bat acoustic signal detection. *PLoS Comput. Biol.* **14:** e1005995.
194. Banner, K.M., K.M. Irvine, T.J. Rodhouse, *et al.* 2018. Improving geographically extensive acoustic survey designs for modeling species occurrence with imperfect detection and misidentification. *Ecol. Evol.* **8:** 6144–6156.
195. Jones, K.E., J.A. Russ, A.-T. Bashta, *et al.* 2013. Indicator bats program: a system for the global acoustic monitoring of bats. In *Biodiversity Monitoring and Conservation: Bridging the Gaps between Global Commitment and Local Action.* B. Collen, N. Pettorelli, J.E.M. Baillie & S. Durant, Eds.: 211–247. Wiley.
196. Loeb, S.C., T.J. Rodhouse, L.E. Ellison, *et al.* 2015. *A plan for the North American Bat Monitoring Program (NABat).* Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station.
197. Zamora-Gutierrez, V., C. Lopez-Gonzalez, M. Cristina MacSwiney Gonzalez, *et al.* 2016. Acoustic identification of Mexican bats based on taxonomic and ecological constraints on call design. *Methods Ecol. Evol.* **7:** 1082–1091.
198. Boyles, J.G. 2017. Benefits of knowing the costs of disturbance to hibernating bats. *Wildl. Soc. Bull.* **41:** 388–392.
199. White-nose syndrome. Accessed November 30, 2018. https://www.whitenosesyndrome.org/mmedia-education/united-states-national-white-nose-syndrome-decontamination-protocol-april-2016-2.
200. Hayes, J.P. & H.K. Ober. 2009. Survey and monitoring of bats. *In Ecological and Behavioral Methods for the Study of Bats.* T.H. Kunz & S. Parsons, Eds.: 112–129. The Jones Hopkins University Press.
201. Fahr, J., M. Abedi-Lartey, T. Esch, *et al.* 2015. Pronounced seasonal changes in the movement ecology of a highly gregarious central-place forager, the African straw-coloured fruit bat (*Eidolon helvum*). *PLoS One* **10:** e0138985.
202. Conservation Measures Partnership. 2013. Open standards for the practice of conservation.
203. Sutherland, W.J. & C.F.R. Wordley. 2017. Evidence complacency hampers conservation. *Nat. Ecol. Evol.* **1:** 1215–1216.
204. Kingston, T., L. Aguirre, K. Armstrong, et al. 2016. Networking networks for global bat conservation. In *Bats in the Anthropocene: Conservation of Bats in a Changing World.* C.C. Voigt & T. Kingston, Eds.: 539–569. Springer International Publishing.