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Strong geographic and temporal patterns in conservation status of North American bats

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ABSTRACT

Conservationists are increasingly concerned about North American bats due to the arrival and spread of the White-nose Syndrome (WNS) disease and mortality associated with wind turbine strikes. To place these novel threats in context for a group of mammals that provides important ecosystem services, we performed the first comprehensive conservation status assessment focusing exclusively on the 45 species occurring in North America north of Mexico. Although most North American bats have large range sizes and large populations, as of 2015, 18–31% of the species were at risk (categorized as having vulnerable, imperiled, or critically imperiled NatureServe conservation statuses) and therefore among the most imperiled terrestrial vertebrates on the continent. Species richness is greatest in the Southwest, but at-risk species were more concentrated in the East, and northern faunas had the highest proportion of at-risk species. Most ecological traits considered, including those characterizing body size, roosting habits, migratory behavior, range size, home range size, population density, and tendency to hibernate, were not strongly associated with conservation status. However, nectarivorous bats tended to be more at risk. The conservation status of bats improved from 1985 to 2000 as human disturbances to roosting sites were reduced, but then declined sharply (7%) by 2015 due principally to threats from WNS and wind energy. Although uncertainty about threats from pollution and climate change remain, past experience shows that when threats are clearly identified and management actions taken, populations can recover.

1. Introduction

Bats are one of the most diverse members of the North American mammal fauna, with 45 species occurring in the continental United States and Canada. They are also among the most locally abundant, with colonies numbering into the millions (e.g., Brazilian free-tailed bats, *Tadarida brasiliensis*) and representing some of the largest concentrations of mammals on earth. North American bats also play a role in insect control, providing ecosystem services valued in the millions of dollars annually to farmers and helping to sustain natural habitats (Pierson and Kunz, 1998; Jones et al., 2009a; Boyles et al., 2011; Kunz et al., 2011). Despite the importance of bats in temperate North America, relatively little attention has been focused on characterizing the conservation status of the fauna as a whole.

Concern about the conservation status of North American bats dates back decades. Initially, attention focused on disturbance and destruction of cave-dwelling bats and their habitats (Mohr, 1952, 1953; Humphrey, 1964; Barbour and Davis, 1969). In the 1970s, researchers first quantified the degree of decline for particular colonies of a few cave-dwelling species (Cope and Hendricks, 1970; Humphrey and Cope, 1976; Tuttle, 1979). Today, bats continue to experience threats from cave alteration and disturbance (Gore and Hovis, 1998), habitat loss (Racey and Entwistle, 2003), and forest management practices that are incompatible with tree-roosting species (Carter et al., 2003; Kunz and Lumsden, 2003; Barclay and Kurta, 2007; Carter and Menzel, 2007; Hayes and Loeb, 2007). Bats are also experiencing major novel threats and drastic rapid declines from disease and renewable energy development (O'Shea et al., 2016). White-nose Syndrome (WNS), an introduced and fast-spreading fungal pathogen, has killed several million cave-dwelling bats of multiple species in eastern North America over the past decade (Frick et al., 2010a; Langwig et al., 2012; Reeder and Moore, 2013; Frick et al., 2015; Langwig et al., 2015a, 2015b). During the same period, turbines at rapidly expanding wind energy facilities have killed hundreds of thousands of bats, mostly migratory species

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(Arnett and Baerwald, 2013; Hayes, 2013).

A number of factors may influence the susceptibility of bats to these threats. Long-distance migrants are more vulnerable to mortality from wind turbines and therefore may have less secure populations than non-migratory species. Only species that hibernate and cluster in caves are likely to succumb to WNS and are therefore more likely to have threatened statuses than species that follow other overwintering strategies. Body size has been associated with extinction risk in mammals (Davidson et al., 2009), although not in a global analysis of bats (Jones et al., 2003). North American bats are most diverse in the southwestern US (Hoffmeister, 1986; Frey et al., 2006; Ammerman et al., 2012), where, if all other factors are equal, the highest concentrations of threatened species would be expected to occur. However, WNS has so far been reported largely from colonies in the eastern portion of the continent (Maher et al., 2012; USFWS, 2016). If WNS is causing a significant decline in conservation status, then the eastern species should have a higher proportion of threatened species than elsewhere. Species with smaller range sizes tend to be more threatened with extinction (Böhm et al., 2016), so bats with smaller ranges should be more threatened than those with larger ranges. Finally, the recent nature of threats from disease and wind turbines suggests that the conservation status of North American bats may be declining relative to their status in the late twentieth century.

To explore the relative importance of these factors on bat conservation status, we conducted conservation status assessments of each species that regularly occurs in North America north of Mexico (hereafter referred to North America for simplicity) using a standard methodology. We used historical conservation status assessments spanning the past 30 years to determine how status has changed over time. The results provide a continent-wide snapshot of priorities for action and highlight gaps in our knowledge of bat conservation.

2. Methods

2.1. Geographic/taxonomic scope

We assessed the conservation status of 45 bat species regularly occurring in North America (English and scientific names listed in Table 1). We regarded the western small-footed myotis to include the form *melanorhinus* (following Holloway and Barclay, 2001, Reid, 2006, and Armstrong et al., 2011) and considered the Arizona bat as a distinct species following most authorities (Adams, 2003; Reid, 2006; Harvey et al., 2011; ITIS, 2016).

2.2. Conservation status assessment categories and criteria

We used the NatureServe methodology to determine the conservation status of North American bats (Faber-Langendoen et al., 2012; Master et al., 2012). This method combines information on rarity (e.g., range extent, population size), trends, and threats to produce a global conservation status rank (G rank): G1 = Critically Imperiled; G2 = Imperiled; G3 = Vulnerable; G4 = Apparently Secure; G5 = Secure. Species assigned to the G1–G3 range are referred to as "at risk" and those in the G4–G5 range are here termed "more secure". In the NatureServe system, at-risk status is independent from designation under the US Endangered Species Act, as amended (ESA), or Canadian Species at Risk Act (SARA), but it is roughly equivalent to the term "Threatened" and "Near Threatened" used for the IUCN Red List, encompassing the Critically Endangered, Endangered, Vulnerable, and Near-Threatened categories (Mace et al., 2008). In addition to overall conservation status, the methodology assigns an impact category (from "negligible" to "very high") for each threat as well as an overall threat impact score. We assessed these factors rangewide, including the Mexican and Central American portions of the ranges for the species that occur there.

The NatureServe methodology uses generation time (mean age of the breeding cohort) in calculating short-term trend and threat severity (a contributor to threat impact), which is estimated over 10 years or 3 generations, whichever is longer. Generation time for most North American bat species is unknown (Barclay and Harder, 2003), but likely ranges from 2 to several years (Humphrey and Cope, 1976, Frick et al., 2010b, Russell et al., 2011). We therefore estimated the appropriate time frame for short-term trend and threat severity as 10–15 years.

Table 1
Variation in global conservation status ranks of North American bats over 30 years.

Scientific name	English common name	Global conservation status rank		
		1985	2000	2015
Phyllostomidae				
Choeronycteris mexicana	Mexican long-tongued bat	G3G4	G3G4	G3G4
Leptonycteris nivalis	Mexican long-nosed bat	G3	G3	G3
Leptonycteris yerbabuenae	Lesser long-nosed bat	G3	G3	G3
Macrotus californicus	California Leaf-nosed bat	G3G4	G3G4	G3G4
Molossidae				
Eumops floridanus	Florida bonneted bat	G1	G1	G1
Eumops perotis	Greater bonneted bat	G4G5	G4G5	G4G5
Eumops underwoodi	Underwood's bonneted bat	G4	G4	G4
Molossus molossus	Pallas's mastiff bat	G5	G5	G5
Nyctinomops femorosaccus	Pocketed free-tailed bat	G5	G5	G5
Nyctinomops macrotis	Big free-tailed bat	G5	G5	G5
Tadarida brasiliensis	Brazilian free-tailed bat	G5	G5	G5
Mormoopidae				
Mormoops megalophylla	Ghost-faced bat	G5	G5	G5
Vespertilionidae				
Antrozous pallidus	Pallid bat	G4	G4	G4
Corynorhinus rafinesquii	Rafinesque's big-eared bat	G3G4	G3G4	G3G4
Corynorhinus townsendii	Townsend's big-eared bat	G3G4	G3G4	G4
Eptesicus fuscus	Big brown bat	G5	G5	G5
Euderma maculatum	Spotted bat	G4	G4	G4
Idionycteris phyllotis	Allen's big-eared Bat	G4	G4	G4
Lasionycteris noctivagans	Silver-haired Bat	G5	G5	G3G4
Lasiurus blossevillii	Western red bat	G4	G4	G4
Lasiurus borealis	Eastern red bat	G5	G5	G3G4
Lasiurus cinereus	Hoary bat	G5	G5	G3G4
Lasiurus ega	Southern yellow bat	G5	G5	G5
Lasiurus intermedius	Northern yellow bat	G5	G5	G5
Lasiurus seminolus	Seminole bat	G5	G5	G5
Lasiurus xanthinus	Western yellow bat	G4G5	G4G5	G4G5
Myotis auriculus	Southwestern myotis	G5	G5	G5
Myotis austroriparius	Southeastern myotis	G4	G4	G4
Myotis californicus	California myotis	G5	G5	G5
Myotis ciliolabrum	Western small-footed myotis	G5	G5	G5
Myotis evotis	Long-eared myotis	G5	G5	G5
Myotis grisescens	Gray myotis	G2	G3	G4
Myotis keenii	Keen's myotis	G3	G3	G3
Myotis leibii	Eastern small-footed myotis	G4	G4	G4
Myotis lucifugus	Little brown myotis	G5	G5	G3
Myotis occultus	Arizona myotis	G4G5	G4G5	G4G5
Myotis septentrionalis	Northern myotis	G4	G4	G1G2
Myotis sodalis	Indiana myotis	G1G2	G2	G2
Myotis thysanodes	Fringed myotis	G4	G4	G4
Myotis velifer	Cave myotis	G4G5	G4G5	G4G5
Myotis volans	Long-legged myotis	G4G5	G4G5	G4G5
Myotis yumanensis	Yuma myotis	G5	G5	G5
Nycticeius humeralis	Evening bat	G5	G5	G5
Parastrellus hesperus	Canyon bat	G5	G5	G5
Perimyotis subflavus	Tricolored bat	G5	G5	G2G3

When ranges of possible values are used for rarity, trend, or threat factors, the NatureServe method produces a compound rank such as G3G4, indicating in this case that available information does not clearly indicate whether the species is Vulnerable (G3) or Apparently Secure (G4). In most analyses we use "rounded ranks", a simplification that reflects the more conservative part of the rank (e.g., G3G4 rounds to a more precautionary G3). The information used to support our categorizations is summarized in the Supplementary material (Appendix A) and NatureServe (2016).

We determined threat impact by scoring the projected scope and severity of 11 major threat categories (level 1 threats in Salafsky et al., 2008: residential and commercial development, agriculture and aquaculture, energy production and mining, transportation and service corridors, biological resource use, human intrusions and disturbance, natural system modifications, invasives and other problematic species and genes, pollution, geological events, climate change and severe weather) over the next 10–15 years. These individual scores (Appendix B) combine to determine an overall threat used in the calculation of the status category.

Threat impact determinations involved uncertainty, as they required projections of future conditions and assumptions about how bats will respond. Some of this uncertainty is reflected in the threat impact scores that span 2 categories (e.g., high-medium).

2.3. Geographic patterns of imperilment

We used distribution maps from NatureServe (2016), which in turn were based on sources including Reid (2006) and the mammalian species accounts of the American Society of Mammalogists. We overlaid these maps to visually determine patterns in species richness, richness of at-risk species, richness of more secure species, and the proportion of species at risk.

2.4. Trends in imperilment

To characterize trends in conservation status, we examined change in G ranks for all bat species at 3 time intervals: 1985, 2000, and 2015. To eliminate methodological influences on temporal changes in conservation status, for 1985 and 2000 we "back-casted" ranks using current information about the sizes of populations, trends, and threats at those points in time (Butchart et al., 2007; Quayle et al., 2007; Teucher and Ramsay, 2013). For each of the 3 assessment years, we calculated a conservation status index (analogous to a Red List Index; Butchart et al., 2007) following the protocols described by Quayle et al. (2007). Briefly, we assigned species numerical weights from 0 to 5 according to their rounded rank in each time period and summed all ranks relative to the maximum possible rank weight (5) to derive a conservation status index score ranging from 1.0 (all species ranked G5) to 0.0 (all species extinct).

2.5. Ecological patterns of imperilment

To examine ecological correlates of conservation status, we used available life history and demographic information (Davidson et al., 2009; Jones et al., 2009b; NatureServe, 2016) for 8 binary and 6 continuous trait variables (Supplementary material: Appendix C). The binary variables were diet (primarily nectarivore or insectivore); roosting habitat (trees, caves or mines, cliffs or talus, buildings or bridges; species could be assigned to more than one category if they use more than one during the annual cycle; each roosting habitat treated as a binary variable); hibernation, colonial breeding, and long-distance migration (regular movements of greater than 200 km). The continuous variables were body mass, range size, home range size, population density, and latitude and longitude of the geographic centroid of the distributional range. To improve the normality of the variables, we log-transformed the continuous variables with the exception of latitude and longitude. We converted conservation status, the dependent variable, to a continuous variable using the same numerical scale as for the analysis of temporal patterns of imperilment.

To determine whether any ecological traits or geographical characteristics were associated with conservation status, we performed a multiple linear regression using the 14 variables. Although these variables were selected from a larger variable set in order to reduce collinearity, some collinearity still existed among them, reducing the interpretability of regression coefficients. To further explore the relative importance of these variables as conservation risk factors, we also performed variable selection using bidirectional stepwise regression (with AIC as the selection criterion). Stepwise regression can be useful in qualitatively identifying a subset comprising the most explanatory variables, but has been criticized for underestimating *P*-values (Wilkinson and Dallal, 1981) and therefore we interpret the results cautiously.

3. Results

3.1. Conservation status

The conservation status assessment revealed that, as of 2015, the available data suggest that 31 species (69%) of North American bat species are Secure (G5) or Apparently Secure (G4), whereas 8 species (18%) are at risk and an additional 6 species (13%) have data uncertainty that span the range between Vulnerable (G3) and Apparently Secure (G4) and so are possibly at risk (Table 1). Seven species have somewhat uncertain conservation status (calculated rank = G1G2, G2G3, or G4G5) but nevertheless are clearly either at risk or more secure. Using precautionary rounded ranks, 14 species (31%) are at risk (G1–G3, including G3G4).

3.2. Trend in imperilment

The conservation status of North American bats improved slightly between 1985 and 2000, but then declined by 7% between 2000 and 2015 (Fig. 1). The 1985–2000 change resulted from an improvement in the status of 2 species (*Myotis grisescens* and *M. sodalis*). Between 2000 and 2015, improvement in the status of 2 species (*Corynorhinus*

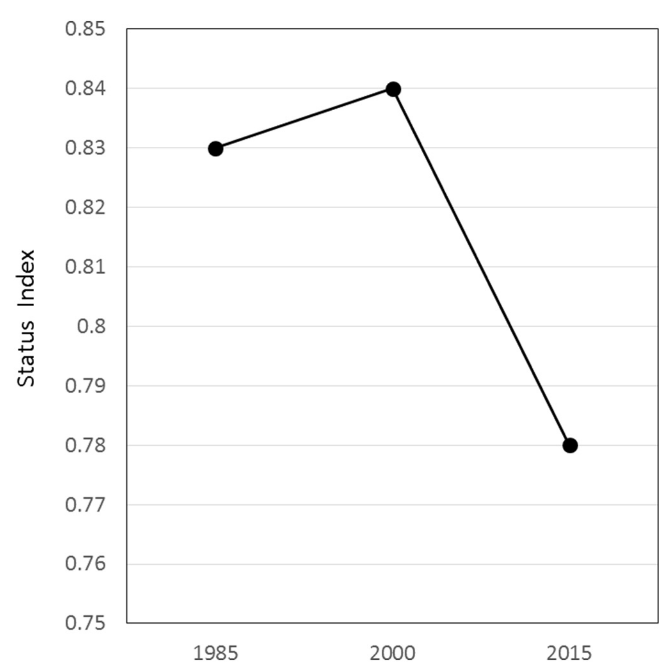

Fig. 1. Temporal change in an index of the conservation status of North American bats. Index values range from 1.0 (all species secure) to 0.0 (all species extinct).

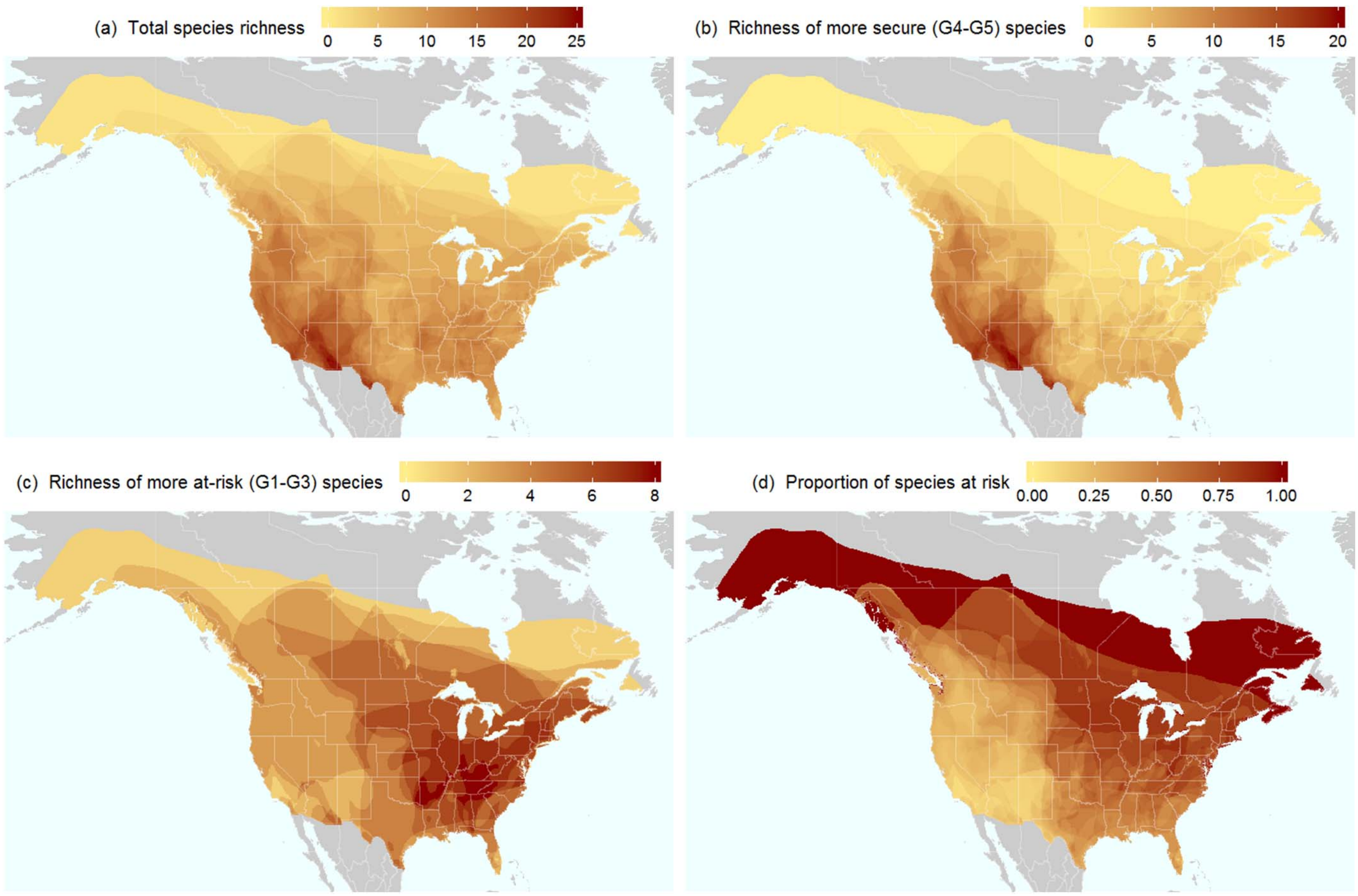

Fig. 2. Patterns of bat species richness in North America: (a) total species richness, (b) richness of more secure (rounded rank G4–G5) species, (c) richness of at-risk (rounded rank G1–G3) species, (d) proportion of species at risk.

townsendii and *M. grisescens*, again) was more than offset by the deterioration in the status of 6 species (*Lasionycteris noctivagans*, *Lasiurus borealis*, *Lasiurus cinereus*, *M. lucifugus*, *M. septentrionalis*) (Table 1). The magnitude of the 2000–2015 decline is equivalent to 13.5 species, or 30% of the fauna, qualifying for a one-category increase in imperilment.

3.3. Geographical patterns of imperilment

Bat species richness in North America is centered in the southwestern US and, to a lesser degree, in the southeastern US (Fig. 2a). The bat species composition of these 2 regions is largely different, with only 6 species occurring in both regions. Richness of secure (G4–G5) species largely reflects this same pattern, whereas most at-risk species are in the eastern part of the continent (Fig. 2b & c). Strikingly, the proportion of at-risk species occurring in a particular area is highest across eastern North America and in the northern part of the range of bats on the continent (Fig. 2d).

3.4. Ecological patterns of imperilment

The full model multiple regression analysis result indicated that at-risk status was not strongly associated with diet, any roosting habitat type, body mass, species distribution size, home range size, population density, or migratory habit (multiple $r^2 = 0.44$; Table 2). The only detectable pattern was geographic. Bats occurring further south were more likely to have greater imperilment status (Table 2). Also, bats occurring in the east were marginally more likely to have greater imperilment status (Table 2).

The stepwise regression resulted in a more nuanced view of the ecological variables. Although latitude and longitude were both included in the final model (multiple $r^2 = 0.39$), so was diet (nectarivores being more at-risk, $t = 1.978$, $P = 0.055$), cliff nesting ($t = 1.799$, $P = 0.08$), and population density ($t = 1.99$, $P = 0.054$).

Table 2
Results of a multiple linear regression of ecological traits and geographical characteristics on North American bat conservation status rank.

Factor	Coefficient estimate	Standard error	*P*
Diet*	1.092	0.857	0.212
Tree roosting	− 0.217	0.451	0.634
Cave/mine roosting	− 0.433	0.631	0.499
Cliff/talus roosting*	0.636	0.431	0.150
Building/bridge roosting	0.072	0.454	0.876
Hibernate	− 0.272	0.440	0.541
Migration	0.065	0.475	0.893
Colonial breeding	0.216	0.434	0.623
Body mass	− 1.132	1.166	0.339
Range size	0.489	1.062	0.339
Home range size	0.192	0.867	0.826
Population density*	1.161	1.145	0.319
Latitude (south to north)*	− 2.832	1.175	0.022
Longitude (east to west)*	− 1.646	0.847	0.061

*Variable included in final stepwise regression model ($F_{6,38} = 4.051$, $P = 0.003$).

3.5. Threats

Projections of threat impact indicate that nearly half (22 species) of the North American bat fauna faces substantial threats (threat impact medium to high) from one or more sources, and more than half of these (14 species, 64%) were in the high and high-medium categories (Fig. 3

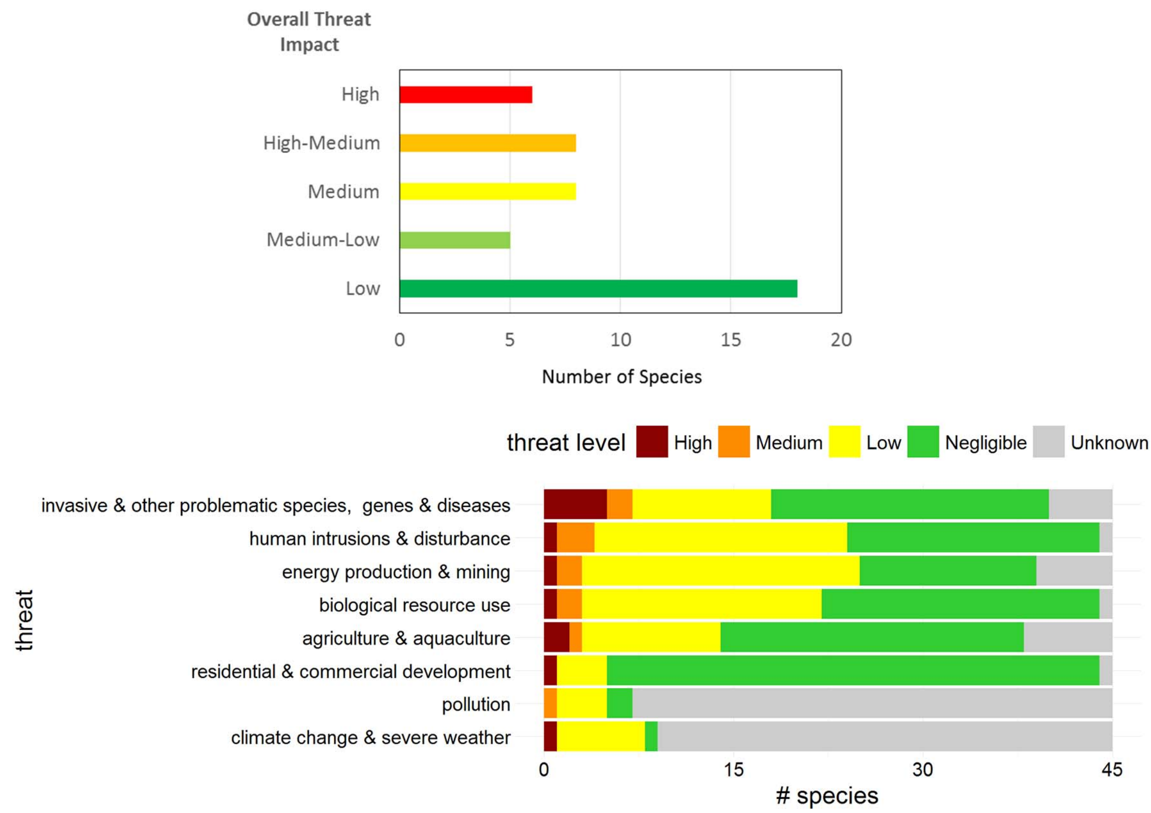

Fig. 3. Threats to North American bats: (top) overall threat impact (next 10–15 years); (bottom) estimated impact of major threat categories (residential and commercial development, transportation and service corridors, and natural system modification threats were low, negligible, or unknown and therefore not shown), listed in approximate order of impact.

top). A substantial minority of species (40%) are unlikely to be much affected by any threat over this time frame.

Threats with the highest projected threat impact included invasive species and diseases (particularly WNS); energy production and mining, especially wind energy; human intrusions and disturbance of primarily cave- or mine-dwelling species; and biological resource use, such as tree cutting and forestry practices (Fig. 3 bottom). For most species, the impact of pollution and climate change is unknown due to a lack of sufficient study in these areas.

4. Discussion

This first-ever study focusing exclusively on the conservation status of the bats of North America demonstrates the imperiled nature of the fauna. As of 2015, from 18 to 31% of the 45 species are known to be at risk. Although diversity is greatest in the Southwest, at-risk species were more concentrated in the East. Conservation status overall has declined 7% during the 15 years prior to 2015. The major patterns of imperilment in this fauna are (1) threatened species are concentrated in eastern North America rather than in the typical hotspots of endangerment in California, Florida, and the southern Appalachians (Chaplin et al., 2000; Evans et al., 2016), (2) narrow-ranging species are no more threatened than wide-ranging species (Böhm et al., 2016), and (3) larger body mass is not associated with greater imperilment (Davidson et al., 2009). Below we discuss these findings and highlight gaps in our knowledge that hinder a more precise characterization of the conservation status of North American bats.

4.1. Conservation status

Our conservation status results differ somewhat from a previous assessment that formed part of the Global Mammal Assessment (Schipper et al., 2008) following the IUCN Red List criteria (IUCN, 2001). In that study, 4 species were assessed in one of the threatened categories (CR: Florida bonneted bat; EN: Mexican long-nosed bat, Indiana myotis; VU: Lesser long-nosed bat), 2 as Near Threatened (NT; Mexican long-tongued bat, gray myotis), and the rest as Least Concern (LC). A comparison of the NatureServe and IUCN assessment methodologies indicated that at-risk (G1–G3) species in the NatureServe system correspond to the threatened (CR, EN, VU) and NT categories in the IUCN system (Keith et al., 2004). Thus, the current Red List status for North American bat species indicates that only 9% of the 45 species are in one of the threatened categories, and an additional 5% are NT. This figure is lower than the number of at-risk species reported here (18%; exclusive of the G3G4 species). Although there are many similarities, the Red List assessment criteria place somewhat more emphasis on trend and less on rarity than the NatureServe criteria. However, the differences between our results and the Red List data have little to do with methodological differences. The most recent Red List assessment of North American bats was completed in 2008 (Schipper et al., 2008) based on data compiled a few years previously when species now known to have undergone recent severe declines were categorized as stable. The differences between our results and the Red List data most likely reflect assessment date and recent (post-mid 2000s) changes in bat status rather than differences in conclusions about bat rarity, trends, and threats.

Our findings do not completely mirror the way species are listed by the US Fish and Wildlife Service (USFWS) under the ESA. The USFWS has listed as endangered or threatened only 6 (13%) of the species that we assessed: lesser long-nosed bat (G3), Mexican long-nosed bat (G3), gray myotis (G4), northern myotis (G1G2), Indiana myotis (G2), and Florida bonneted bat (G1). Two subspecies of Townsend's big-eared bat (G3G4) are also listed under the ESA, but the species as a whole is not because the western subspecies appears to be secure. At-risk species that are not currently listed include Keen's myotis (G3), little brown myotis (G3), and tricolored bat (G2G3). Direct comparisons between species listed under the ESA and conservation status ranks are unlikely to match completely because the 2 processes have different objectives. Criteria for listing species under the ESA are heavily weighted by threat and are geared to identify priorities for management action. Conservation status ranks are designed to approximate extinction risk, just one factor to be considered when determining management priority (Mace et al., 2007, 2008). Nevertheless, we note that the USFWS is currently reviewing the status of the little brown myotis, a species that has declined precipitously in recent years; the agency should also review tricolored bat, which has also declined (Table 1; Frick et al., 2010a; Langwig et al., 2012).

The proportion of North American bat species that we assessed as at risk or possibly at risk (31%) is higher than that for several other groups of North American vertebrates, including birds (15% at risk; includes recently extinct species and those only known from historical records), squamate reptiles (16%), mammals overall (19%), but less than for amphibians (40%), turtles (41%), freshwater and anadromous fishes (41%), and crocodilians (50%) (NatureServe, 2016). Bats, therefore, are among the most threatened group of North American vertebrates not primarily associated with aquatic habitats.

With the arrival of WNS in the West (USFWS, 2016) and continued expansion of wind energy infrastructure, the conservation status of North American bats will likely continue to deteriorate. More monitoring of fatalities at wind facilities, particularly those located in the Midwest and West that are currently understudied, may reveal greater threats to a broader range of species than currently recognized (Arnett and Baerwald, 2013). Establishment of more wind energy facilities in Texas where Brazilian free-tailed bats, a species well-known to forage above the forest canopy at heights comparable to where turbines spin, could cause severe mortality in this species (Kunz et al., 2007; McCracken et al., 2008).

4.2. Temporal changes in status

An index derived from conservation status ranks is a blunt tool to measure changes in population status, especially in abundant species (Butchart et al., 2007), but nonetheless was able to show that the status of the North American bat fauna improved somewhat between 1985 and 2000 and then declined through 2015. The small change from 1985 to 2000 primarily reflected improved cave protection and associated increases in bat populations, especially for Indiana myotis and gray myotis (Table 1; USFWS, 2009a, 2009b). The subsequent deterioration was caused mainly by the impacts of novel and expanding threats, primarily wind energy (causing greater imperilment in silver-haired, eastern red, and hoary bats; Arnett et al., 2008) and the WNS disease (causing declines in little brown myotis, northern myotis, and tricolored bat; Frick et al., 2015; Langwig et al., 2015a, 2015b). The overall decline in 2015 masks the improvement in the status of Townsend's big-eared bat (Stihler, 2011) and the continued improvement in the status of gray myotis.

4.3. Ecological and geographic patterns

None of the ecological traits examined was strongly associated with conservation status. Although many traits have been associated with extinction risk in mammals globally (Davidson et al., 2009), this was not the case for North American bats. For example, body size is a major predictor of extinction risk in mammals overall (Davidson et al., 2009), but not in bats globally (Jones et al., 2003) or for the North American bat fauna (this study). Limited variation in body size and major threats, such as diseases, energy infrastructure, and disturbance, that act independently of body size may have led to this result.

Diet was marginally associated with conservation status, with a significant relationship in the stepwise regression but not in the full regression analysis. Only 3 species of North American bats are primarily nectarivores whereas the remaining species are insectivores. An additional species, the pallid bat, visits and pollinates agaves and cacti at least in part of its range (Frick et al., 2014), but it primarily feeds on terrestrial arthropods. Although all 3 nectarivorous species are either at risk or possibly at risk primarily due to disturbance of roosting caves and reductions in food resources such as *Agave* spp. (USFWS, 1994; USFWS, 2007, 2013a), the sample size is small and the species are not sufficiently imperiled to strongly associate diet with conservation status.

Migration, hibernation, and roosting site also were not strongly related to conservation status. Although migrating species are more likely to suffer mortality from wind energy installations, only 3 of the 18 species classed as migratory have sufficient documentation of declines to qualify for an at-risk conservation status. Although WNS has caused conservation status declines in hibernating species, the highest proportion of at-risk species occurs among nonhibernators. The major threats to North American bats (WNS, energy infrastructure, and disturbance) affect bats when they are hibernating or migrating, which may explain why roosting site was not associated with conservation status.

The major association we found with conservation status was geographic. Overall, bat species richness in North America does not reflect a primarily latitudinal or elevational pattern characteristic of broader or local scales (compare Willig et al., 2003) but rather is centered in the Southwest, as previously indicated in the well-documented bat faunas of this region (Hoffmeister, 1986; Frey et al., 2006; Ammerman et al., 2012). The relatively high concentration of at-risk bat species in the eastern US is counter to the overall pattern of imperilment of plants and animals, in which California, Florida, and the southern Appalachian Mountains harbor the greatest numbers of threatened species (Chaplin et al., 2000; Evans et al., 2016). The distribution of threatened bats primarily reflects the geography of cave availability, forest cover, disease, and wind energy development relative to cave-roosting bats and migratory tree-roosting bats. Few bat species occur in Canada, but a large proportion of these species are threatened (except in southern British Columbia). In contrast, the California, Florida and southern Appalachian foci of endangered species (across all taxa) result from a combination of small range size, rampant habitat loss, and alteration of aquatic habitats (Chaplin et al., 2000).

4.4. Contributors to imperilment

Two aspects of rarity—range extent and population size—are important criteria for conservation status determinations (Mace et al., 2008; Master et al., 2012). The range extent of nearly all North American bat species is relatively large. Although overall population sizes of North American bats are poorly known, the available data suggest that most species are represented by large populations (hundreds of thousands to millions of individuals; see Supplemental material). Even some species listed as Endangered under the US Endangered Species Act (gray and Indiana myotis) have populations exceeding 500,000 individuals (Martin, 2007; USFWS, 2013b). Despite the large ranges and large population sizes, the North American bat fauna includes a surprisingly high proportion of at-risk species. Aside from the Florida bonneted bat, which has a small population confined to a restricted geographic area in southern Florida (Marks and Marks, 2006), at-risk status among North American bat species is an indication of recent strong declines and ongoing serious threats. This pattern is in contrast to global studies of bats (Jones et al., 2003), mammals (Davidson et al., 2009), amphibians (Stuart et al., 2004), and birds (Manne et al., 1999; Manne and Pimm, 2001).

4.5. Population trend

Among North American bats, population trends are well documented at only a few localities of some cave-dwelling species (e.g., Mohr, 1972; Gore and Hovis, 1992; Martin, 2007; Frick et al., 2010a, 2015; Langwig et al., 2012). Species-wide populations and trends are poorly quantified for nearly all species (Pierson and Kunz, 1998; O'Shea and Bogan, 2003; Racey and Entwistle, 2003; Weller, 2007; Racey, 2013; Meyer, 2015), although new survey methods (Cryan and Gorresen, 2014) and recently established monitoring protocols (Loeb et al., 2015) eventually should improve the situation. Whereas population trajectories are often clear, the specific rate of change is uncertain. The available information indicated that most species have declined in distribution and/or abundance over the long and short term, even if the specific rate of decline is uncertain. The dearth of trend data led to uncertainty in the status ranks assigned, and highlights an area where more research emphasis is needed (O'Grady et al., 2004).

4.6. Threats

Disease was the most pervasive threat to North American bats. The ongoing spread of WNS is well known (Frick et al., 2010a). Major declines due to WNS are expected to occur in the near future in the Indiana myotis (Thogmartin et al., 2013). Major uncertainties relate to how much farther WNS will spread and to what degree it will affect populations in western North America. For example, the little brown myotis, with a range that spans the continent, has been particularly hard hit by WNS in the East (Frick et al., 2010a). The threat posed by WNS to the species was an important element contributing to the Vulnerable (G3) rank. Recent genetic studies question whether WNS threatens the entire range as severely as it does eastern populations (Vonhof et al., 2015; Davy et al., 2015). This new information and the rapidly expanding literature on the disease indicates that the conservation status of all WNS-affected species should be reevaluated at frequent intervals. We note that the gray myotis, which had an improved conservation status between 1985 and 2015, now faces potentially severe threats from WNS (Alves et al., 2014).

Wind energy development was the second most serious threat for North American bats. Three species (eastern red bat, little brown myotis, and Mexican long-nosed bat) face substantial impacts from renewable energy. For an additional 3 species (silver-haired bat, hoary bat, and tricolored bat), wind energy is a potentially important threat but whether measurable population declines will result is unclear due to the difficulty in measuring population sizes in these species. Clearly, mitigation measures such as increasing the cut-in speed of turbines and further study of the effects of wind energy facilities on bat populations are needed (Arnett et al., 2008; Hayes, 2013). These results are counter to a recent global study, which found collisions with wind turbines to be a more pervasive source of bat mortality than disease (O'Shea et al., 2016). The differing results are likely due to cases of disease mortality being concentrated in North America, the focus of our study, whereas mortality from turbine strikes are reported from many parts of the world.

Human intrusions, mostly through disturbances at underground roosting sites, have historically been important and continue to threaten numerous species (Tuttle, 1979; Furey and Racey, 2015). Disturbances to caves take many forms, including vandalism, recreational caving, commercialization of hibernacula, banding and monitoring activities, and flooding of caves by reservoir creation (USFWS, 2009a, 2009b; Furey and Racey, 2015). Bats that roost in abandoned mine lands (e.g., adits, shafts) are additionally threatened by hard closures to address human safety issues as well as renewed mining activities caused by increased commodity prices. Threats from human intrusions can usually be ameliorated through appropriate management actions, such as restricting access to cave entrances through gating (USFWS, 2009b; but see Crimmins et al., 2014 and Diamond and Diamond, 2014 for potential negative effects of gates).

The effects of pollution and climate change on North American bats are largely unknown. For example, we were unable to ascertain the effect of pollution on 37 species. Environmental pollution is widely thought to have detrimental impacts on bats (Clark and Shore, 2001; Bayat et al., 2014; Zukal et al., 2015). Polybrominated diphenyl ethers (PBDEs), as well as pharmaceuticals and chemicals in personal care products, have been found in recent samples of bat tissues from the northeastern US, and these potentially affect several physiological systems in bats including hibernation, immune function, and response to White-nose Syndrome (Secord et al., 2015). Bats occurring near rivers that are contaminated by mercury can suffer genetic damage (Karouna-Renier et al., 2014). Pesticides potentially reduce bat food resources and thereby negatively affect populations in some areas (Pierson and Kunz, 1998). Nevertheless—despite various known pollution-related mortality events (O'Shea et al., 2016)—the degree of impact of environmental pollution on bat populations (and their insect food resources) is not well understood, especially with regard to effects of chronic sublethal exposure (Bayat et al., 2014; Zukal et al., 2015).

The impact of climate change on populations is unknown for most species. Climate change-induced drought in western North America will likely be detrimental to reproduction and may result in large declines (Adams and Hayes, 2008; Adams, 2010; Hayes, 2011). Warming climates in the northeast may further restrict the range of Indiana myotis (Loeb and Winters, 2013). However, the full range of bat responses to climate change remain poorly known (Jones and Rebelo, 2013; Sherwin et al., 2013). Questions about the degree to which negative effects of climate change will be offset by positive effects on other life history features, whether population losses in one part of a species' range will be offset by gains in other regions, and the degree to which bats can adapt by adjusting their ecological and phenological characteristics remain largely unanswered.

4.7. Conservation successes

Our study also serves to highlight conservation successes. The most dramatic status improvement over the 30 years covered by the study was with the gray myotis (change from Imperiled to Apparently Secure). This cave-dwelling species has benefited from effective efforts to protect caves across its range, making it the least threatened bat currently listed under the ESA. However, the species would likely decline rapidly if current protection measures were relaxed. WNS unfortunately now looms as an additional threat.

The status of 2 additional species, Townsend's big-eared bat and Indiana myotis, also improved due to targeted conservation efforts. Threats from human disturbance at Indiana myotis cave hibernacula, scientific collecting and banding, commercialization of hibernacula, and poorly designed cave gates have been largely addressed (USFWS, 2009b). Protection of caves has also helped improve the status of Townsend's big-eared bat and other cavernicolous species, and ongoing improvements in forest management policies have likely helped populations of several tree-associated species. However, as with the gray myotis, WNS now threatens Indiana myotis (Thogmartin et al., 2013) and other species that have benefited from improved cave protection. Despite the large ranges and populations that characterize North American bats, our results show that a substantial proportion of the fauna warrants continued or increased conservation attention, including measures such as those highlighted here to prevent further biodiversity loss.

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