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Original investigation

White-nose syndrome dramatically altered the summer bat assemblage in a temperate Southern Appalachian forest

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ABSTRACT

White-nose syndrome (WNS), an epizootic disease caused by an invasive fungus, threatens bat populations across North America. WNS-induced changes in summer bat populations could impact functional diversity. We assessed the shift in relative abundance within an assemblage of bats in a temperate southern Appalachian forest in North Carolina and Tennessee from 2009 through 2016. We used mixed linear effects models to identify bat species significantly impacted by WNS and those showing resistance, and to determine effects on reproductive rates for WNS-affected species. Four once-common species — the little brown bat (*Myotis lucifugus*), Indiana bat (*M. sodalis*), northern long-eared bat (*M. septentrionalis*), and tri-colored bat (*Perimyotis subflavus*) — showed significant and dramatic declines (82–99%), while the big brown bat (*Eptesicus fuscus*), red bat (*Lasiurus borealis*), Rafinesque's big-eared bat (*Corynorhinus rafinesquii*), and small-footed bat (*M. leibii*) did not decline significantly after WNS was detected on the landscape. We detected no significant interactions between reproductive condition and WNS period (pre- and post-arrival of the disease). Declines in summer populations mirrored declines detected in nearby winter hibernacula. Because the loss of WNS-affected bat species could negatively impact ecosystem health, it is important to monitor bat, insect, and plant community responses wherever WNS threatens bats. We hypothesize that, in the absence of small-bodied bats, there might be increases in populations of small forest pests, such as defoliating moths, as larger WNS-resistant bats may avoid or miss these small prey.

Introduction

White-nose syndrome (WNS) is an epizootic, infectious disease caused by a fungal pathogen (*Pseudogymnoascus destructans*), which in 2011 was estimated to have killed at least 6 million bats since its discovery in North America in 2006 (US Fish and Wildlife Service, 2019a). White-nose syndrome, first observed via photographs of affected bats in a New York cave in 2006 (Coleman and Reichard, 2014), has spread across much of the U.S. and many Canadian provinces. By 2018, eight species in eastern North America were confirmed with WNS: big brown bats (*Eptesicus fuscus*), southeastern bats (*Myotis austroriparius*), eastern small-footed bats (*M. leibii*), gray bats (*M. grisescens*), Indiana bats (*M. sodalis*), little brown bats (*M. lucifugus*), northern long-eared bats (*M. septentrionalis*), and tri-colored bats (*Perimyotis subflavus*) (US Fish and Wildlife Service, 2019b); new species are affected as the disease spreads. Some cave-dwelling bats appear to resist *P. destructans* (e.g., Rafinesque's big-eared bats, *Corynorhinus rafinesquii*; Johnson et al., 2012) or are resistant to mass mortality (e.g., big brown bat; Frank et al., 2014). Others are more susceptible. For example, in hibernacula in western Virginia, hibernating populations of the little brown bat, northern long-eared bat, Indiana bat, and tri-colored bat have declined by 34–99% (Powers et al., 2015).

It is important to measure the magnitude of population declines post-WNS to assess impacts to bat assemblages. While many workers have measured declines in hibernating bats (e.g., Frick et al., 2010; Langwig et al., 2012; Powers et al., 2015), it is difficult to detect some species during winter hibernacula surveys (e.g., northern long-eared bat and eastern small-footed bat, Moosman et al., 2013). During summer, however, assemblage-level changes may be documented through presence or relative abundance data derived from capture or acoustic surveys. With multi-summer

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datasets pre- and post-WNS, Moosman et al. (2013) detected 68–98% declines in capture rates for three *Myotis* species in New Hampshire and Francl et al. (2012) detected 77–90% declines for four *Myotis* species and tri-colored bats in West Virginia. In central Indiana, two *Myotis* species declined by 59–79% and tri-colored bats declined by 12% based on summer captures pre-WNS (1998–2010) to post-WNS infection (2011–2014; Pettit and O'Keefe, 2017). With multi-summer acoustic data, Brooks (2011) detected a 72% reduction in *Myotis* echolocation activity four years after WNS arrived in central Massachusetts and Dzal et al. (2011) detected a one-year 78% decline in little brown bat echolocation activity near the cave where WNS was first detected in New York. With such significant declines, we might expect shifts in the structure of food webs among bats, insects, and plants. For example, WNS-related declines may relax spatial and temporal niche partitioning, allowing resistant species to forage in spaces formerly used by declining species (Jachowski et al., 2014). However, ecosystem processes may be affected if there is little dietary overlap between WNS-resistant species and WNS-sensitive species.

We know little about bat population responses to WNS in southeastern North America where shorter, warmer winters presumably afford higher survival rates for hibernating bats in general (Ehlman et al., 2013). We conducted our study in Great Smoky Mountains National Park (GRSM) in the Southern Appalachian Mountains. GRSM and the surrounding area hosted a diverse community of ≥11 bat species, with high relative abundance for *Myotis* bats pre-WNS (Rojas et al., 2017). White-nose syndrome or the *P. destructans* fungus was first detected in various counties in close proximity to GRSM from 2010 to 2014 (Janicki et al., 2015). In this region, Bernard and McCracken (2017) observed significant declines in captures and acoustic activity for cave-hibernating bats during winter and spring (Oct.–May, 2011–2012 through 2013–2014), including one cave in GRSM. In the same area, fungal loads on WNS-affected bats were lower in the second winter (2013–2014) of a two-year study, suggesting the potential for persistence of WNS-affected bat populations (Bernard et al., 2017). Bats hibernating in southern caves experience milder winter temperatures and shorter winters, which should give WNS-infected bats more opportunities to replenish fat stores via foraging (Bernard et al., 2017) and higher survival rates (Ehlman et al., 2013) compared to bats in colder climates. However, warmer caves may provide optimal temperatures for faster fungal growth (*P. destructans* exhibits highest growth rates at 12.5–15.8 °C; Verant et al., 2012), negating the potential advantages of shorter winters. Further, bats adapted to warmer climates with short (<150 days) winters may enter hibernation with insufficient fat stores for surviving a winter that is longer than usual; e.g., bats in the South experienced an unusually long winter in 2013–2014 (Reynolds et al., 2015).

We collected data from 2009 to 2016, using data from long-term mist-net sites established prior to the onset of WNS effects in this region. Our goal was to determine which members of the summer bat assemblage were impacted by WNS and which species showed resistance to the disease. Specifically, we assessed changes in capture rates over time and looked for changes in reproductive rates for WNS-affected bats.

Material and methods

Study area

GRSM occurs in Haywood and Swain counties, North Carolina, and Blount, Cocke, and Sevier counties, Tennessee. This 211,000 ha area, where elevation ranged from 258 to 2019 m (Linzey, 1995), is a World Heritage site renowned for its biodiversity. Conifer-mixed hardwood forests dominated the landscape at lower and middle elevations, succeeded by northern hardwoods and spruce (*Picea*)-fir (*Abies fraseri*) forests at the highest elevations. Early successional patches (e.g., open fields and high-elevation balds) were a small part of the landscape. Prescribed fire, used on a small scale, was the primary forest management tool in GRSM (Schwartz et al., 2016). Most available water was in the form of streams and rivers, typically perennial only at lower slopes and elevations. Impoundments along rivers formed lakes on the south and west sides of GRSM. All roads inside GRSM were two lanes or smaller. From 2009 to 2016, May to August temperatures averaged 19.2 °C, ranging from −5.6 to 39.4 °C, and rainfall averaged 55.6 cm across four local weather stations (State Climate Office of NC, www.nc-climate.ncsu.edu). During the hibernation season, November to February 2009–2016, temperatures at the same stations averaged 3.1 °C, ranging from −30.6 to 26.7 °C.

Several significant caves are found on the north side of GRSM in Blount County, TN. One WNS-affected cave in GRSM ("Blount Cave" in Bernard and McCracken, 2017) is designated critical habitat for the largest known hibernating colony of endangered Indiana bats in Tennessee. Abandoned mines in Swain County, NC were significant hibernation sites for Rafinesque's big-eared bats (Linzey, 1995).

Survey periods and methods

We conducted mistnet surveys to capture bats between late April and early September 2009–2016; due to funding constraints, we did not conduct surveys in 2013. The *P. destructans* fungus was first detected on a bat hibernating in a GRSM cave in 2010 and bats in GRSM were confirmed positive for WNS in 2011 (Carr et al., 2014). GRSM biologists and visitors noticed unusual flight activity for wintering bats in late 2012 (Carr et al., 2014), and significant declines were first detected during hibernacula surveys in Jan.–Feb. 2013. Daytime acoustic activity increased at Blount Cave in 2012–2013, and then overall activity declined in 2013–2014 (Bernard and McCracken, 2017). Thus, we classified capture data into two periods: pre-WNS (2009–2012) and WNS (2014–2016). We assumed most populations of hibernating bats in GRSM were exposed to *P. destructans* by the WNS period. With no other obvious disturbances to the protected GRSM landscape during the study period, we hypothesized that any detected declines were the result of WNS-induced mortality in wintering populations.

In 2009, we began establishing survey points along bat flyways (streams, trails). We surveyed 45 capture sites 1–16 times each over the eight years (mean = 3.3 nights/site); we placed a lower priority on resurveying sites that were unproductive or close to other net sites. We used mistnets to capture bats, erecting double and single-high 4–12 m nets (Avinet, Dryden, NY, USA) over trails, roads, and stream corridors (total net area/night ranged from 39–185 m^2; mean = 99.6 m^2/night). We checked mistnets every 8–10 min, keeping nets open 1–6 h each night (mean = 4.3 h/night; any <3 h due to thunderstorms). We surveyed on 148 nights, 53 nights pre-WNS (2009–2012) and 95 nights during WNS (2014–2016). Thirteen sites were sampled pre- and during WNS, nine sites were sampled only pre-WNS, and 23 sites were sampled only during WNS. We present capture data for all sites in Table S1.

We recorded species, sex, age, mass (g), and forearm length (mm) of each bat captured in a mistnet. We determined age (juvenile or adult) by degree of ossification of the finger joints (Kunz and Anthony, 1982) and reproductive condition (pregnant, lactating, or non-reproductive for females and scrotal or non-reproductive for males; Racey, 1988). We banded bats with a unique aluminum forearm band (Porzana Ltd., East Sussex, UK) for individual identification. We recorded wing damage scores (0–3; Reichard and Kunz, 2009) as an index of WNS effects. We followed USFWS white-nose syndrome protocols (e.g., US Fish and Wildlife Service, 2018) and handling guidelines for bats (e.g., Sikes et al., 2016), Clemson Uni-

versity IACUC protocol 2009–16 and Indiana State University IACUC protocol 226895. Field work was conducted under permits held by JM O'Keefe: federal recovery permit TE206872, North Carolina permit ES261, Tennessee permit 3148, and National Park Service Permits GRSM-2009-SCI-0075, GRSM-2012-SCI-0085, and GRSM 2014 SCI-1179.

Analytical methods

To determine which species were experiencing significant declines coincident with the appearance of WNS, we analyzed captures across seven years of an eight-year period (2009–2016, no surveys in 2013). All analyses were performed in Program R (R Core Team, 2018). We used the lme4 package (Bates et al., 2015) to fit a generalized linear mixed model with a negative binomial distribution in a strictly hypothesis testing approach to identify factors affecting changes in captures over time. Prior to modeling, we culled the dataset to limit capture data to the most common species: big brown bats, eastern red bats, tri-colored bats, Rafinesque's big-eared bats, northern long-eared bats, Indiana bats, eastern small-footed bats, and little brown bats (>95% of dataset). The dataset was also limited to species-sex-age-reproductive status combinations where at least one bat of that combination was captured over the entire study period. To limit bias from sites visited only once, we applied two filters: first, when two net sites were <500 m apart, we collapsed them into one, yielding 37 sites. For modeling, we applied an additional filter, considering data only for net sites visited in more than one year (i.e., 26 sites).

Our model assessed changes in capture rates by species with WNS arrival by modeling number of bats per visit (the dependent variable) as a function of bat species, WNS status (pre-WNS or WNS), and the interaction between those two fixed effects. We accounted for demographic variation by including age, sex, and reproductive condition as random effects, and for spatial and temporal variation by including site and year as random effects. We accounted for variability in netting effort by offsetting captures in the model by the log of net effort (net area * hours). The log transformation matched the transformation of the response variable imposed by the generalized linear model. Eastern red bat was the reference or default species in the model because it was commonly captured and there is no evidence in the literature to suggest this species is directly affected by WNS; model estimates for other species were based on comparisons with the default species.

We modeled reproductive class interactions with WNS period in two additional models, one for big brown bats and another for pooled WNS-sensitive *Myotis* species (little brown bats, northern long-eared bats, and Indiana bats). We excluded tri-colored bats from this analysis, as we did not capture adult females pre-WNS. We tested for significant interactions between WNS period and reproductive condition of adult female bats of these species groups.

Results

Effort and captures

Survey effort was typically higher during WNS (2014–2016) than pre-WNS (2009–2012), but overall bat capture rates were highly variable, particularly in 2012 and 2014 (Fig. 1). In 2012, after WNS was detected in GRSM but before declines had been observed in hibernacula, capture rates were 50–60% of rates observed in 2009–2011. In 2014, two summers after observed declines in hibernacula, capture rates spiked to almost two times higher than in 2012.

GRSM hosted a diverse bat community. Both pre- and during WNS, we captured 11 species. The principal species (Table 1) comprised most of our sample, but we also captured hoary bats, silver-haired bats (*Lasionycteris noctivigans*), evening bats (*Nycticeius humeralis*). We captured one Seminole bat (*Lasiurus seminolus*) in 2014 (Table S1). Wing damage scores ranged from 0 to 3 for 1410 bats (of 1457 captures). Many bats showed signs of wing scarring, but we scored only eight bats with a 2 and one bat with a 3.

Trends for common bat species

Comparing captures per unit effort for pre-WNS to WNS (Table 1), we detected substantial declines for Indiana bats (–95%), northern long-eared bats (–94%), little brown bats (–99%), tri-colored bats (–82%), and Rafinesque's big-eared bats (–53%); we never caught many of the latter species, even pre-WNS (Table S1). We captured big brown bats and eastern small-footed bats at higher rates during WNS than pre-WNS (Table 1) and eastern red bats, which do not hibernate in caves, at a lower rate during WNS vs. pre-WNS (Table 1).

Little brown bats, Indiana bats, northern long-eared bats, and tri-colored bats showed significant declines during the WNS period ($p < 0.001$; Table S2, Fig. 2). Big brown bats and eastern small-footed bats showed non-significant increases during WNS ($p > 0.3$; Table S2), and red bats and Rafinesque's big-eared bats showed non-significant declines ($p > 0.1$; Table S2).

With respect to demographic interactions, we captured more post-lactating than lactating big brown bats (reference condition; $p = 0.01$; Table S3, Fig. 3A), but there were no significant interactions between reproductive condition and WNS period ($p > 0.07$), and the WNS period parameter alone was not significant ($p = 0.43$). For WNS-sensitive *Myotis*, WNS decreased prevalence of captures ($p < 0.001$, Table S4). For adult females, there were no significant interactions between WNS period and reproductive condition ($p > 0.1$, Table S4, but see negative slopes in Fig. 3B).

Discussion

We provide evidence for significant changes in the bat assemblage in GRSM. We conclude that declines were due to WNS and not confounding effects from land cover changes. We establish that, prior to the invasion of local hibernacula with *P. destructans*, at least 11 bat species inhabited this area during summer. With significant declines in four small, cave-hibernating bats—little brown bats, northern long-eared bats, Indiana bats, and tri-colored bats—functional diversity of bats has been altered in GRSM.

Little brown bats

We observed a staggering 99% decline in the little brown bat population. Soon after WNS began to impact bat populations in northeastern North America, a study predicted a regional collapse in the little brown bat population due to WNS (Frick et al., 2010). However, subsequent work demonstrates that hibernating populations of little brown bats stabilize within four years of WNS infection (Langwig et al., 2012). Further, the probability of extinction is greater for smaller hibernating colonies of little brown bats (Frick et al., 2015). The hibernating little brown bat population in Blount Cave, the major hibernaculum in GRSM, was only 574 bats in winter 2011 (Samoray, 2011). While this is a moderate population size, it is smaller than many known hibernating populations of little brown bats in the northeast, where summer and winter colonies are persisting post-WNS (Dobony et al., 2011; Maslo et al., 2015; Dobony and Johnson, 2018). In a New Jersey mine that housed ~27,000 little brown bats pre-WNS, little brown bats persisted at least four years after WNS infection and post-WNS survival rate was 0.70–0.75 (95% CI 0.50–0.89; Maslo et al.;, 2015). Declines in summer capture rates in GRSM are consistent with declines observed in regional winter hibernacula. Across Tennessee, cave-hibernating

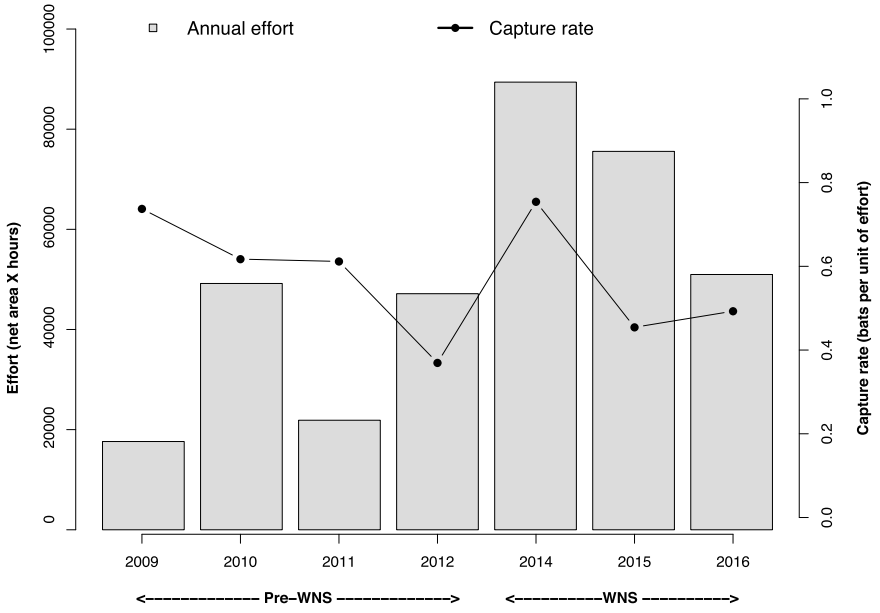

Fig. 1. Survey effort (net area * hours) and all bats captured per unit of effort for a long-term (Summers 2009–2016, 148 net nights) study of bats in Great Smoky Mountains National Park in North Carolina and Tennessee.

Table 1
Total bat captures per unit effort (net area × hours) for eight bat species in each WNS period, with percent change between the periods. Capture data are from a long-term (Summers 2009–2016, 148 net nights) study in Great Smoky Mountains National Park in North Carolina and Tennessee.

Species	Pre-WNS 2009–2012	WNS 2014–2016	Percent rate change [(WNS−Pre)/Pre] × 100
Rafinesque's big-eared bat, *Corynorhinus rafinesquii* (CORA)	0.000884734	0.000412721	−53.4
Big brown bat, *Eptesicus fuscus* (EPFU)	0.006900923	0.007594066	10.0
Eastern red bat, *Lasiurus borealis* (LABO)	0.005721278	0.004478023	−21.7
Eastern small-footed bat, *Myotis leibii* (MYLE)	0.000766769	0.000804806	5.0
Little brown bat, *Myotis lucifugus* (MYLU)	0.006075172	6.19081E-05	−99.0
Northern long-eared bat, *Myotis septentrionalis* (MYSE)	0.008965302	0.000536537	−94.0
Indiana bat, *Myotis sodalis* (MYSO)	0.003067077	0.000144452	−95.3
Tri-colored bat, *Perimyotis subflavus* (PESU)	0.002949112	0.000536537	−81.8

populations of little brown bats declined by 97% from 2010 to 2016 in 61 hibernacula where there were <750 little brown bats pre-WNS (Tennessee Wildlife Resources Agency, 2016; Samoray, 2011). In North Carolina hibernacula, 20–30 years of winter survey data show the hibernating population of little brown bats has declined by 93.5% (North Carolina Wildlife Resources Commission, 2017).

Indiana bats

The >95% decline we observed for Indiana bats suggests the species may experience local extinction at GRSM due to WNS. Like little brown bats, Indiana bats hibernate in large, tight clusters, which may increase *P. destructans* transmission rates (Langwig et al., 2012). While some little brown bats switch to roosting alone post-WNS and thus may be less susceptible to *P. destructans*, Indiana bats are less likely to exhibit this behavior (Langwig et al., 2012). Caves in GRSM were significant Indiana bat hibernation sites for the southeastern U.S., hosting 89% of the known Indiana bat winter population in Tennessee in early 2011 (Samoray, 2011). However, in 2014–2015 winter surveys, biologists observed a dramatic two-year decline of 87% in the Indiana bat population hibernating in Blount Cave (Tennessee Wildlife Resources Agency, 2016). Almost 750 Indiana bats were observed in Blount Cave in Winter 2016–2017 (Tennessee Wildlife Resources Agency, 2017), but this population could continue to decline at a slow rate due to phased exposure of survivors to the *P. destructans* fungus (Maslo et al., 2017). Indiana bats were rarely observed in North Carolina hibernacula prior to WNS and not at all since 2010 (Katherine Caldwell, NC Wildlife Resources Commission, personal communication).

Northern long-eared bats

Northern long-eared bat captures also dropped in an alarming fashion (94%). In 2009, northern long-eared bats were the most commonly captured species in GRSM and surrounding areas (Rojas et al., 2017). By 2016, these bats were so rare locally that we did not encounter any during 21 survey nights in GRSM. The US Fish and Wildlife was compelled to list northern long-eared bats as threatened under a 4(d) rule after determining WNS was a critical threat (US Fish and Wildlife Service, 2016). Unfortunately, the precipitous decline in GRSM had already begun prior to this listing. Langwig et al. (2012) observed local extinctions of hibernating populations of northern long-eared bats in hibernacula in four northeastern U.S. states surveyed pre- and post-WNS detection; 14 hibernating populations became extinct ≤2 years after WNS detection, with the remainder extinct at five years after detection. Early and late hibernation loads of *P. destructans* strongly predict declines for hibernating populations; of six species examined, northern long-eared bats exhibited the highest fungal loads and the greatest population declines in 21 winter sites (Langwig et al., 2016). In WNS-infected hibernacula, northern long-eared bats tend to have higher fungal loads and more visible evidence of infection compared to congeners (Janicki et al., 2015). Northern long-eared bats were rarely observed or counted in Tennessee hibernacula prior to

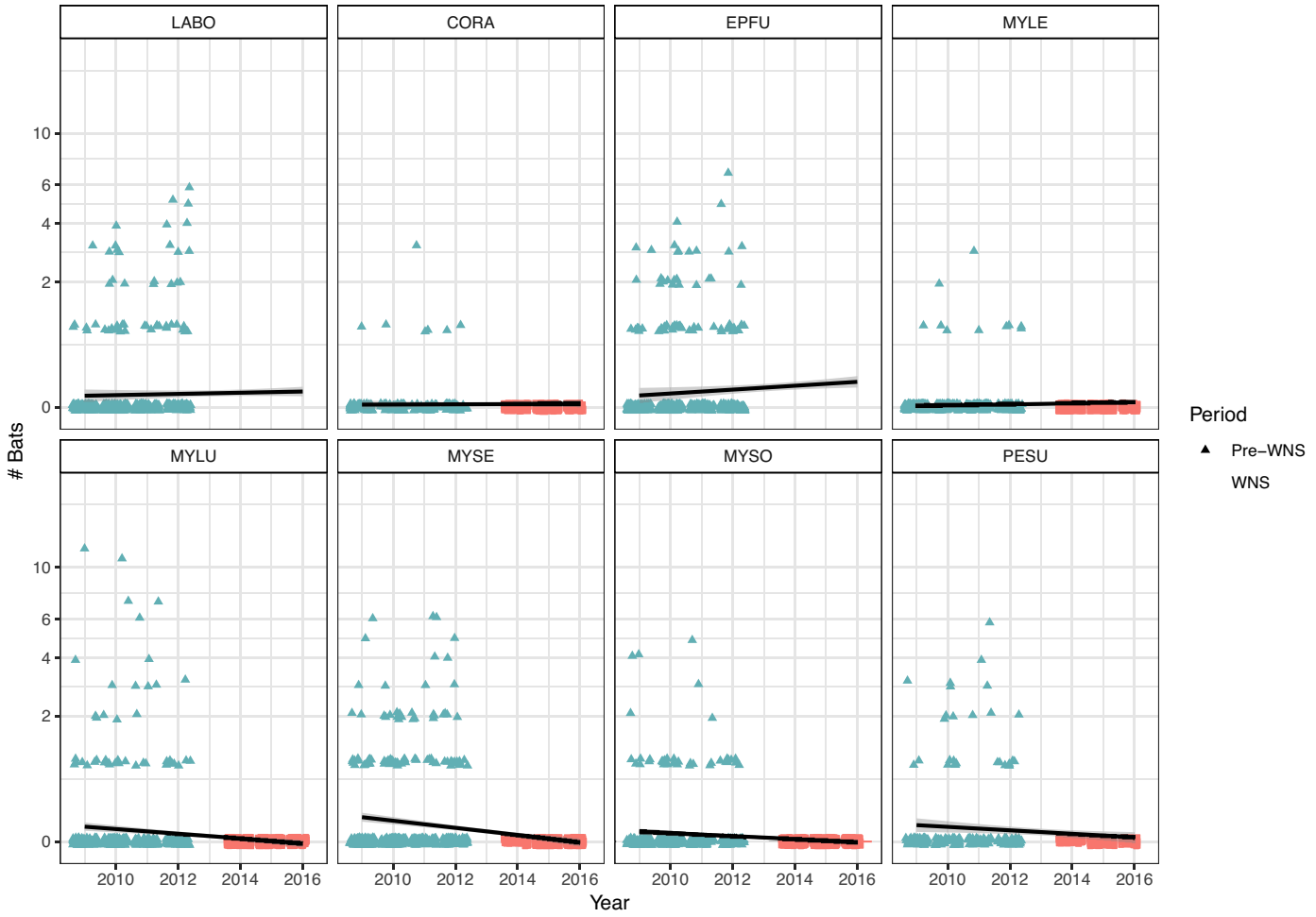

Fig. 2. Capture data for the 8 most-captured bat species, with data delineated by pre-WNS (blue; 2009–2012) and WNS (red; 2014–2016) periods. Trendlines show the change in captures across periods—declines were significant for MYLU, MYSE, MYSO, and PESU. See Table 1 for species code definitions. Data collected during summer mistnet surveys of Great Smoky Mountains National Park in North Carolina and Tennessee, at 26 sites visited in >1 year, in 2009–2012 and 2014–2016. We used a jitter function to disperse overlapping values and a log10 y-axis scale to make data patterns more clear. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

WNS, but by 2016 had declined by 100% in eight winter sites monitored 4–6 years between 2009 and 2016 in TN (Tennessee Wildlife Resources Agency, 2016) and 100% in North Carolina hibernacula (North Carolina Wildlife Resources Commission, 2017).

Tri-colored bats

With an 82% decline in capture rates, tri-colored bats have a slightly more promising outlook in GRSM than the WNS-affected *Myotis*. Around 90% of the tri-colored bats we captured were adult males (Table S1), indicating GRSM mainly harbors males in summer; females likely use lower elevation sites and may not have experienced the same rate of decline. In hibernacula, tri-colored bats tend to roost solitarily in moist conditions (Raesly and Gates, 1987); however, extinction risk is highest in hibernacula with larger numbers in winter (Langwig et al., 2012; Frick et al., 2015). In 2011, prior to the onset of significant WNS impacts, nine GRSM caves hosted moderate winter populations of tri-colored bats—283 bats on average (range 2–1365 bats; Carpenter, 2017). By 2016, this species had declined by 85% in those same nine caves (Carpenter, 2017) and 66% overall in 22 winter sites in Tennessee (Tennessee Wildlife Resources Agency, 2016); North Carolina observed an even greater decline, 96.3% (North Carolina Wildlife Resources Commission, 2017).

Other bat species

Our model showed no significant change in capture rates for Rafinesque's big-eared bats, eastern small-footed bats, big brown bats, or eastern red bats. In other regions, eastern small-footed bat and big brown bat populations have declined due to WNS. As WNS progressed through New Hampshire, Moosman et al. (2013) detected a significant decline in eastern small-footed bat captures. In contrast, we caught more eastern small-footed bats during WNS (Table 1). While big brown bat populations increased in many winter sites in the Northeast in the five years after WNS arrived, Turner et al. (2011) detected an overall 41% decline. Subsequently, Frank et al. (2014) concluded that in New York big brown bats are resistant to the fungus, as they do not show interruptions in torpor bout length, body fat declines, or significant fungal growth from infection by *P. destructans*. Moore et al. (2018) also found that only 30% of big brown bats exposed to *P. destructans* were histologically positive for WNS compared to 100% of little brown bats and concluded their apparent resistance may have been due to physiological and behavioral differences. We captured big brown bats at higher rates during WNS (Table 1) and WNS period did not affect reproduction (Table S3). Bernard et al. (2015) detected *P. destructans* on Rafinesque's big-eared bats and eastern red bats captured at Tennessee hibernacula during WNS. Rafinesque's big-eared bat

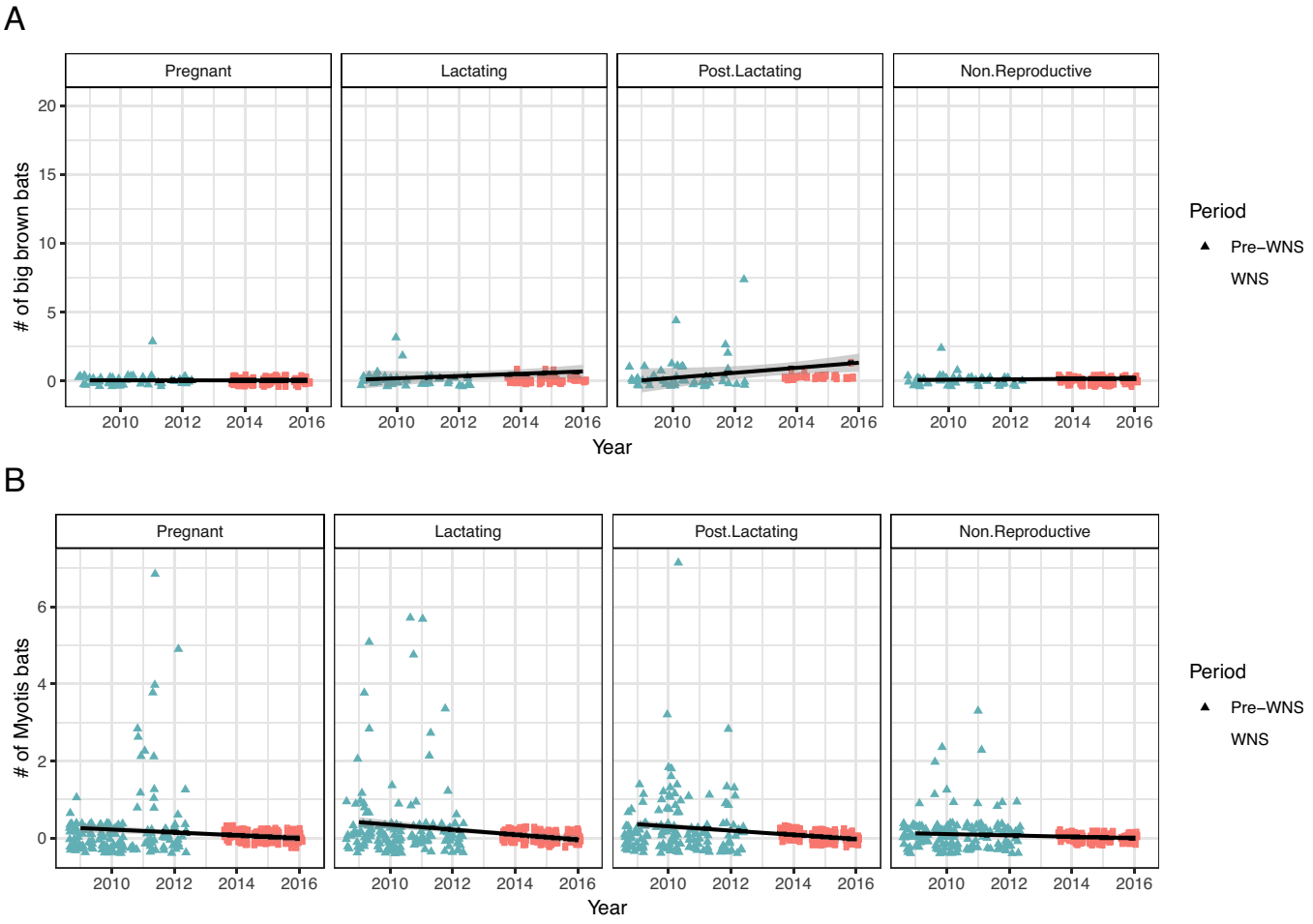

Fig. 3. Demographic patterns for captures of adult female (A) big brown bats and (B) WNS-sensitive *Myotis* (little brown bats, northern long-eared bats, Indiana bats) from pre-WNS (blue; 2009–2012) to WNS (red; 2014–2016) in Great Smoky Mountains National Park. For WNS-sensitive M*yotis*, we saw an overall decrease in all reproductive conditions but these trends were not statistically significant. Data collected during summer mistnet surveys of Great Smoky Mountains National Park, at 26 sites visited in >1 year, 2009–2012 and 2014–2016. We used a jitter function to disperse overlapping values to make data patterns more clear. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

winter populations were stable in Tennessee hibernacula as of 2016 (Tennessee Wildlife Resources Agency, 2016), but declined 56% in North Carolina hibernacula since WNS arrived (North Carolina Wildlife Resources Commission, 2017), similar to the 53% decline we observed. We detected a 22% decrease in capture rates of eastern red bats (Table 1); this species may be declining due to other factors, such as wind energy development (Arnett and Baerwald, 2013). Because eastern red bats do not hibernate in caves or mines where *P. destructans* experiences optimal growth, it is unlikely that WNS will negatively affect this species (see also Francl et al., 2012; Pettit and O'Keefe, 2017).

Ecological implications

Because bats likely play a critical role in controlling insect populations (Boyles et al., 2011; Kunz et al., 2011), we may see a significant loss of ecosystem services where bat functional diversity has been altered due to WNS. Due to small body size and resultant high metabolic rates, bats consume large numbers of insects; e.g., little brown bats consume 140 tiny insects in the first 20 min of feeding per night (Anthony and Kunz, 1977); however, we need more data on the biomass of insects consumed by bats. Plant-damaging insects, including defoliating moths (Lepidoptera), scarab beetles (Coleoptera: Scarabeaidae), and sap-eating leafhoppers (Hemiptera: Cicadellidae) are major components of *Myotis* and tri-colored bat diets (Whitaker, 2004). Bats may be drawn to and decrease populations of irruptive defoliators (Charbonnier et al., 2014), which stress forests, causing reduced growth and tree mortality (Day and Leather, 1997; Davidson et al., 1999; Man and Rice, 2010). While there are no estimates of the economic impacts of bats in forested ecosystems like GRSM, agricultural pest control by bats is valued at billions of dollars annually (Boyles et al., 2011).

We hypothesize that there may be significant differences in the diets of WNS-imperiled bats versus the remaining WNS-resistant species. Differences in ecomorphology (body size, shape, and echolocation call structure; Norberg and Rayner, 1987) should lead to differences in dietary choices for the smaller *Myotis* and tri-colored bat when compared to the larger big brown bats and eastern red bats remaining in GRSM. For example, the 6–8 g northern long-eared bat, with low wing loading and high-frequency calls (Norberg and Rayner, 1987), consumes mainly small moths in Kentucky (93% of identified prey, average moth wingspan = 24.2 mm; Dodd et al., 2012), whereas eastern red bats, with higher wing loading/wing aspect ratio and lower frequency calls (Norberg and Rayner, 1987), consume larger moths in Ontario, Canada (average wingspan = 34.1 mm, calculated by Dodd et al., 2012 from data in Clare et al., 2009). Small *Myotis* bats often consume small prey; for example, over one-third of prey items identified for 7–9 g little brown bats were 4-mm long midgeflies (Diptera, e.g., *Chironomus decorus*) and mayflies (Ephemeroptera, e.g., *Caenis youngi*) (Clare et al., 2011) and

little brown bats consume two times more mosquitoes compared to sympatric big brown bats (Wray et al., 2018).

Future directions

Could WNS-imperiled bat species recover or persist in the southern Appalachian Mountains? Long-term data from other portions of North America are promising. A summer population of little brown bats in New York declined by 88%, but survivors healed from WNS-related wing damage and showed evidence of reproduction (Dobony et al., 2011). The same population increased by 76% from 2010 to 2017 and mean survival rate for adults and juveniles was 59%, indicating potential for population growth (Dobony and Johnson, 2018). Little brown bats repeatedly exposed to *P. destructans* during winter may be developing resistance and, thus, surviving to reproduce (Langwig et al., 2017). We saw some evidence of reproduction for WNS-sensitive *Myotis* (Table S1), but captures of reproductive females were relatively low during WNS compared to pre-WNS.

Environmental conditions predict risk of WNS infection (Lilley et al., 2018) and decline severity (Frick et al., 2015); thus, when compared to the Northeast, recovery and survival rates may differ for WNS-affected bats hibernating in the warmer southern Appalachian Mountains. A dynamic model shows that increasing mean temperatures in hibernacula to a value closer to *P. destructans*'s optimal growth temperature results in a shorter time to *P. destructans* invasion and a higher level of disease prevalence (Lilley et al., 2018); thus, bat populations may be more susceptible in warmer hibernacula. Ability to tolerate conditions near or below freezing in hibernacula, sometimes near cave entrances, may explain persistence of big brown bats and eastern small-footed bats in Pennsylvania hibernacula (Johnson et al., 2016). WNS-affected species tend to shift to colder parts of hibernacula after WNS infection, which could improve survival rates (Johnson et al., 2016); however, shifting to colder microclimates may be less feasible for bats hibernating in the warmer southern Appalachian climate.

Given the slow reproductive rates and long life spans of most WNS-imperiled bats, it is unlikely most populations will ever recover to pre-WNS levels; thus, we should assume much diminished populations of the four WNS-imperiled species in GRSM. As WNS marches westward in North America, we urge biologists to use standardized procedures to gather baseline data on bat populations in unaffected areas (i.e., per the North American Bat Monitoring Program; Loeb et al., 2015). We suggest continued monitoring of bat assemblages in WNS-affected areas, but also monitoring of insect and plant populations to assess responses to bat declines.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.mambio.2019.09.005.

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