

Changes in a summer bat community in southeastern Pennsylvania

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Abstract: Bat population changes are poorly understood, making it difficult to establish management priorities. In 2017, a summer mist-netting survey previously conducted in 2004 at Fort Indiantown Gap was replicated to evaluate temporal changes in the local bat community. The authors hypothesized that captures of species most affected by white-nose syndrome (WNS) would decline between survey periods, and that community structure would shift. The results showed a 100% decline in captures of northern long-eared *Myotis* (*Myotis septentrionalis*) and little brown *Myotis* (*M. lucifugus*), no change in captures of eastern red bats (*Lasiurus borealis*), a 276% increase in captures of big brown bats (*Eptesicus fuscus*), and a considerable shift in community structure. These results are consistent with expected effects of WNS on *Myotis* populations. Increases in big brown bat populations may result from ecological release after the decline of *Myotis* species, or from local or large-scale habitat change over time.

Keywords: bat community, capture rates, mist-netting, Pennsylvania, white-nose syndrome

North American bats have faced a number of severe threats in recent years including the rapid expansion of commercial wind energy (Arnett et al. 2008,

2016; Drake et al. 2015; Hein and Schirmacher 2016; O'Shea et al. 2016), climate change (Humphries et al. 2002; Sherwin et al. 2013), the loss and modification of critical roosting and foraging habitats (Pierson 1998; Racey and Entwistle 2003), and toxicity from pesticides and other environmental contaminants (Clark 1988; O'Shea et al. 2016). In addition to these threats, interannual variation in environmental conditions and changes in land use (Hayes and Loeb 2007; Law et al. 2016) may have affected populations of several bat species, and ultimately the structure of entire bat communities.

Over the past decade, white-nose syndrome (WNS) has caused significant declines in populations of several cave-hibernating bat species in much of the eastern United States and Canada (Thogmartin et al. 2012; Frick et al. 2015; Ingersoll et al. 2016). WNS, caused by the psychrophilic fungal pathogen *Pseudogymnoascus destructans* (Pd; Lorch et al. 2011; Warnecke et al. 2012), was first documented in Howe Caverns, NY, during the winter of 2006–07 (Blehert et al. 2009) and has since spread to 33 U.S. states and 7 Canadian provinces (U.S. Fish and Wildlife Service 2018b). A total of 12 North American bat species have been confirmed to have WNS (U.S. Fish and Wildlife Service 2018a), including all 6 cave-hibernating bat species found in Pennsylvania (Turner et al. 2011).

While some cave-hibernating bat species have been severely impacted by WNS, others have felt little or no negative impact. For example, the northern long-eared myotis (*Myotis septentrionalis*) has experienced significant population declines throughout the eastern portion of its range (Turner et al. 2011; Frick et al. 2015) and is the first bat species to be federally listed as Threatened primarily due to WNS (U.S. Department of the Interior 2015). Population declines exceeding 70% have also been documented for little brown myotis (*M. lucifugus*; Dzal et al. 2011; Ingersoll et al. 2013; Frick et al. 2015), threatening this species with regional extirpation (Frick et al. 2010). Conversely, big brown bats (*Eptesicus fuscus*) remain relatively unaffected by WNS (Frank et al. 2014) despite being susceptible to Pd infection and having been found within WNS-affected hibernacula (Blehert et al. 2009).

Population changes have often been determined through repeated surveys of winter hibernacula (e.g., Ingersoll et al. 2016). However, changes in populations of individual species and in bat communities can also be assessed through changes in capture rates during summer mist-netting surveys. This approach has the advantage of also documenting changes in migratory bat species, which are not included in hibernacula surveys. Several recent studies have found significant declines in summer captures (Francl et al. 2012; Moosman et al. 2013; Hauer et al. 2016; Reynolds et al. 2016; Pettit and O'Keefe 2017; Thalken et al. 2018) or activity (Brooks 2011; Ford et al. 2011; Jachowski et al. 2014) of *Myotis* species and tri-colored bats (*Perimyotis subflavus*) following the onset of WNS. Summer

patterns in species less affected by WNS, such as big brown bats, and species unaffected by WNS, such as eastern red bats (*Lasiurus borealis*), are less clear. Several summer studies found that numbers of these species remained the same after WNS (Brooks 2011; Ford et al. 2011; Francl et al. 2012; Pettit and O'Keefe 2017), while one study found that big brown bats increased (Hauer et al. 2016).

Land managers will need to understand how bat populations and communities have changed over time and assess possible causes of decline when making current and future management decisions. The objectives of this study, therefore, were to evaluate changes over time in local bat populations and in the local bat community and then to evaluate whether such changes are consistent with an important effect of WNS on hibernating bat species. To do this, we compared species-specific capture rates and similarity of the bat community during summer mist-netting surveys conducted at 12 sites in 2004 and 2017 at Fort Indiantown Gap National Guard Training Center (FIG-NGTC), a military training area in southeastern Pennsylvania. Because of the effects of WNS on affected species in this region, and because the disease was first recorded in Pennsylvania during the winter of 2008–09 and has since spread throughout the state (Sewall et al. 2016), we hypothesized that capture rates of northern long-eared myotis, little brown myotis, and tri-colored bats would decline from 2004 to 2017. In contrast, because species that are less affected or unaffected by WNS may not experience declines and could even expand to fill the niches of previously-common *Myotis* species (Ford et al. 2011), we also hypothesized that capture rates of big brown bats and eastern red bats would remain the same or increase from 2004 to 2017. Finally, we hypothesized that a shift in the overall composition and relative abundance of bat species would also be observed over this same time period.

MATERIALS AND METHODS

Mist-Netting Surveys

We designed our mist-netting in 2017 to replicate as closely as possible mist-netting surveys performed by Bat Conservation and Management, Inc. (BCM) in 2004 at Fort Indiantown Gap National Guard Training Center (FIG-NGTC), Lebanon and Dauphin counties, Pennsylvania. BCM surveyed 12 sites for two consecutive nights each from 19 to 30 June 2004 (J. Chengler, personal communication; figure 1). Sites in 2004 were selected based on their suitability for capturing the federally endangered Indiana myotis (*M. sodalis*) and included forested roads, trails, and streams that were surrounded by mature mixed-hardwood forest and located near or within the boundaries of five proposed military firing ranges (figure 1). At each site, BCM deployed two or three

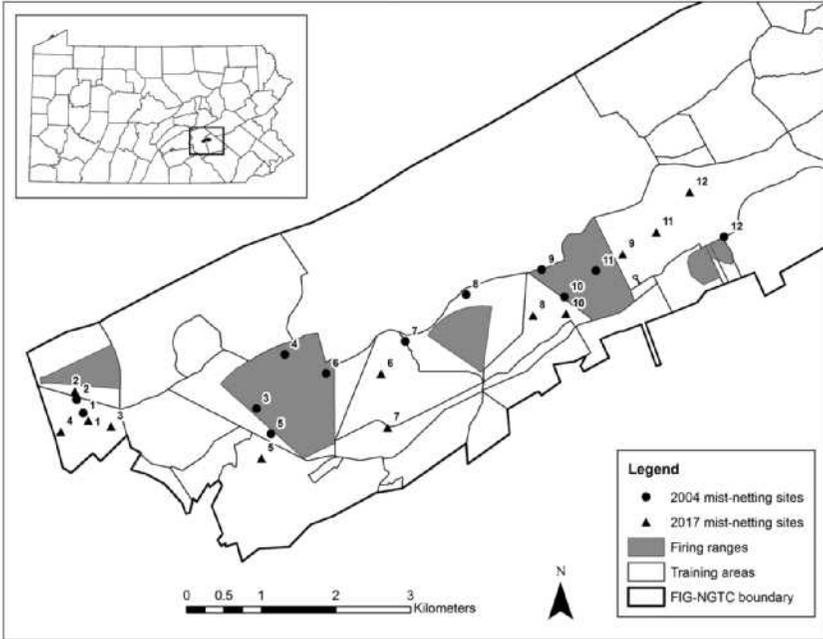


Figure 1. Mist-netting sites on Fort Indiantown Gap National Guard Training Center, PA, in 2004 and 2017. All sites were located in the western portion of the installation. Military firing ranges shown were constructed after 2004. Matching site numbers indicate paired, analogous sites.

triple high mist-nets consisting of three vertically stacked nets (Avinet, Dryden, NY, 7.8 m high, 6–12 m wide) along with up to two single high mist-nets. Mean \pm SE sampling intensity was 2.9 ± 0.1 nets per night. Nets were left open for 5 h after sunset with survey protocols following the guidelines in the Indiana Bat Revised Recovery Plan (U.S. Fish and Wildlife Service 1999).

Prior to the 2017 field season, we examined aerial photographs and spatial data layers in ArcMap 10.4 (ESRI, Redlands, CA) and conducted site visits to determine the feasibility of conducting follow-up surveys. Due to the construction of firing ranges and roadways, as well as extensive forest management onsite, many of the 12 sites originally surveyed in 2004 were no longer suitable for mist-netting. Additionally, because sites in 2004 were intentionally selected within or near proposed firing ranges that are now actively used for military training, we were unable to gain access to most sites during the 2017 survey period. As a result, returning to the exact locations of the 2004 surveys would not have been possible or representative of the original habitat type. For this reason, and to control for changes in habitat quality across years, we selected 12 sites in 2017 that were paired with and analogous to those used in 2004. The 2017 sites we selected had similar habitat characteristics

(mean \pm SE difference between paired 2004 and 2017 sites: elevation = 22.8 ± 5.3 m, distance to nearest permanent water source = 116.7 ± 33.7 m) and were as close as possible to each 2004 site (mean \pm SE distance between paired 2004 and 2017 sites = 956.6 ± 252.3 m; figure 1). The 2017 mist-netting sites were again located on forested roads, trails, and streams within mature mixed-hardwood forest, and sampling was restricted to a 2-week period in the middle of the summer maternity season. The survey timing overlapped between years, but the start and end dates were 8–11 days later (27 June–11 July) in 2017. At each site, we deployed two or three triple high mist-nets (7.8 m high, 6–12 m wide) and up to one single high mist-net, with a mean \pm SE sampling intensity of 2.4 ± 0.1 nets per night. These mist-nets were again deployed and left open for 5 h after sunset. Sites were only surveyed for 1 night in 2017 due to access restrictions related to military training. Our protocols for mist-netting surveys followed guidelines (U.S. Fish and Wildlife Service 2017) similar to those used in 2004. Weather conditions were similar during each 2-week survey period in 2004 and 2017, with mean \pm SE temperatures at the start of the nightly survey period of $19.5 \pm 0.55^\circ\text{C}$ and $21.3 \pm 0.68^\circ\text{C}$, respectively. Additionally, all surveys in both years were conducted on nights with no wind or low wind speeds (Beaufort wind code = 0–3) and little to no precipitation.

For all captured bats, we recorded species, sex, age class (adult vs. juvenile; this was based on the degree of ossification of the epiphyseal joints in the phalanges, Anthony 1988), and reproductive status (males: scrotal, nonreproductive; females: pregnant, lactating, postlactating, nonreproductive). We also recorded morphometric data including mass (g) and length of the forearm (mm), ear (mm), tragus (mm), and hindfoot (mm). Bat capture and handling procedures followed the U.S. Fish and Wildlife Service's Range-Wide Indiana Bat Summer Survey Guidelines (U.S. Fish and Wildlife Service 2017) and decontamination protocols (U.S. Fish and Wildlife Service 2016), and all methods were reviewed and approved by the Institutional Animal Care and Use Committee of Temple University (Protocol No. 4587). Data collection was conducted under permits from the PA Game Commission (38004 and 40752, held by B.J. Sewall).

Data Analysis

We developed statistical models for each bat species and total bats (all species combined) with the survey night as the sampling unit ($n = 24$ in 2004, $n = 12$ in 2017). The number of adult bat captures per survey night was the response variable for each model. Because our later survey period in 2017 facilitated the capture of several juvenile bats (14 big brown bats and 3 eastern red bats), while no juveniles were captured in 2004, we excluded these 17 individuals from our analyses. We further excluded 5 bats (3 big brown bats and 2 eastern red bats)

captured in 2017 because they escaped from mist-nets before their age and sex could be determined. Categorical survey year (2004 vs. 2017) was the fixed main effect. We included \log_{10} of the unit of effort (UOE) as an offset variable to account for differences in sampling effort across nights and years. We set 1 UOE as equal to 1 m² net in place for 1 h (Pennsylvania Game Commission 2017). We also ran all models using an offset of net-night (no. nets/survey night), and results did not differ for any bat species (results not shown). A random effect of site was also employed to group repeated samples of 2004 sites and to group 2004 sites with the analogous sites in 2017 (figure 1). We then tested the data with Poisson and negative binomial generalized linear mixed models (GLMM) and compared models using Akaike's Information Criterion corrected for small sample sizes (AICc). For each species, negative binomial models generated lower AICc values and—unlike Poisson models—did not reveal overdispersion (i.e., values in negative binomial models were close to 1). Thus, we report only the negative binomial models. We also used chi-squared procedures to test for differences in the proportion of adult males and adult females of each species captured in 2004 and 2017. Statistical analyses were performed with JMP Pro version 13 (SAS Institute Inc. 2017) using $\alpha = 0.05$.

We also used relative abundance data (number of adult bat captures per survey night for each species) to construct a triangular resemblance matrix using the Bray–Curtis similarity measure. The resulting matrix was visually displayed by nonmetric multidimensional scaling (nMDS) ordination. To avoid bias in the ordination, one site from 2017 with no bat captures was removed from our analysis. We used a permutational multivariate analysis of variance (PERMANOVA) to test for differences in community structure between years, with the Bray–Curtis similarity values as the response variable, survey year (2004 vs. 2017) as the fixed effect, and site (nested within survey year) as the random effect. We then identified species with the greatest contribution to differences in community structure between years using a similarity percentages analysis (SIMPER). Analyses were performed in Primer version 6 (Clarke and Gorley 2006) and its PERMANOVA+ add-in package (Anderson et al. 2008).

RESULTS

We completed 10,541 UOE during 12 surveys at 12 analogous sites in 2017, which was nearly half the sampling effort of BCM's 19,734 UOE during 24 surveys at 12 sites in 2004. Mean \pm SE sampling effort per survey night, 822.25 \pm 40.2 UOE in 2004 and 878.42 \pm 33.9 UOE in 2017, did not differ between years ($t_{32} = -1.068$, $P = 0.293$).

Total bat capture rates did not differ between 2004 (mean = 0.011 bats/ UOE, $n = 195$) and 2017 (0.011 bats/UOE, $n = 121$; $\chi^2 = 1.716$, $P = 0.190$). In 2004, northern long-eared myotis were common (0.005 bats/UOE, $n = 98$) and little brown myotis were relatively common (0.002 bats/UOE, $n = 31$) at FIG-NGTC. However, in 2017, we failed to capture a single individual of either species (northern long-eared myotis: $\chi^2 = 7.32$, $P = 0.007$, figure 2A; little brown myotis: $\chi^2 = 5.02$, $P = 0.025$; figure 2B). A third species, the tri-colored bat, that was rare in 2004 (<0.001 bats/UOE, $n = 2$), was also not captured in 2017 (sample sizes too small for meaningful analysis). Two other species, big brown bats and eastern red bats, were captured in both years. Big brown bats were already relatively common in 2004 (0.003 bats/UOE, $n = 45$), but had become very common by 2017 (0.010 bats/UOE, $n = 117$), representing a substantial increase over time (276% increase, $\chi^2 = 15.15$, $P \leq 0.001$; figure 2C). Eastern red bats were relatively uncommon in both 2004 (0.001 bats/UOE, $n = 19$) and 2017 (0.0004 bats/UOE, $n = 4$) and there was no change in capture rates for this species over time ($\chi^2 = 0.02$, $P = 0.890$; figure 2D).

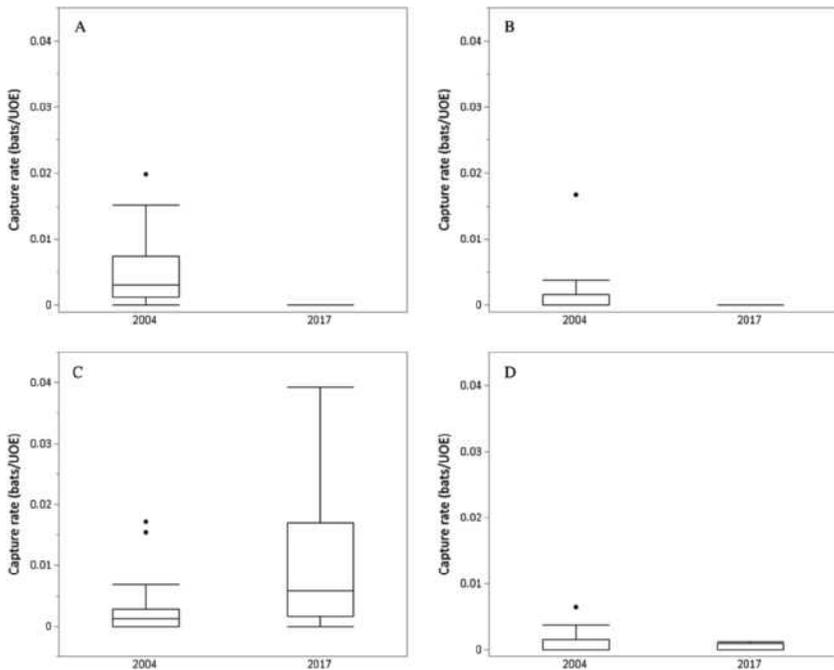


Figure 2. Mean \pm SE capture rates (bats/unit of net effort or UOE) of (A) northern long-eared myotis, (B) little brown myotis, (C) big brown bats, and (D) eastern red bats during summer mist-netting surveys conducted on Fort Indiantown Gap National Guard Training Center, PA, in 2004 and 2017.

There was a difference in the ratio of adult males and adult females captured in 2004 and 2017 for big brown bats (male-biased in 2004 and female-biased in 2017, $\chi^2 = 28.44$, $P \leq 0.001$), but not for eastern red bats ($\chi^2 = 2.27$, $P = 0.194$). In 2004, captures of northern long-eared myotis were strongly female-biased, whereas captures of little brown myotis were strongly male-biased. However, the lack of captures of these two species in 2017 prevented statistical comparison of adult sex ratios.

On a whole-community scale, sites in 2004 differed consistently from those in 2017 (PERMANOVA; $F_{1, 34} = 11.68$, $P \leq 0.001$), with sites clustered by survey year (figure 3). Differences in the bat community were largely attributable to changes in the relative abundance of two species: northern long-eared myotis, which were more abundant in 2004, and big brown bats, which were more abundant in 2017 (SIMPER; cumulative contribution = 83.9%).

DISCUSSION

In this study, we documented changes in capture rates of several bat species between 2004 and 2017, indicating that a restructuring of the bat community

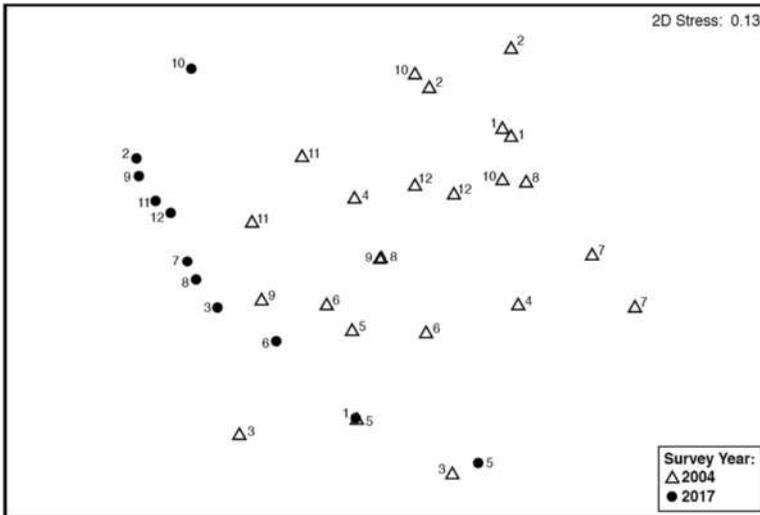


Figure 3. Two-dimensional nonmetric multidimensional scaling (nMDS) ordination plot of bat relative abundance data from summer mist-netting surveys conducted on Fort Indiantown Gap National Guard Training Center, PA, in 2004 and 2017. Each point represents a survey night (two nights in 2004, one in 2017) at each site, with matching point numbers indicating paired, analogous sites. Where points are closer together in the plot, the structure of the bat community is more similar.

had occurred at FIG-NGTC. Our findings are consistent with predictions that changes in capture rates would correspond to species-specific susceptibility to WNS. As predicted, we observed significant declines (-100%) in capture rates of both northern long-eared myotis and little brown myotis from 2004 to 2017. In 2004, northern long-eared myotis was the most common bat species captured in summer mist-netting surveys on the installation; this species was captured at 10 of 12 sites and comprised 50.3% of total bat captures (figure 4). Little brown myotis was the third most common bat species (behind northern long-eared myotis and big brown bats) in 2004; this species was captured at

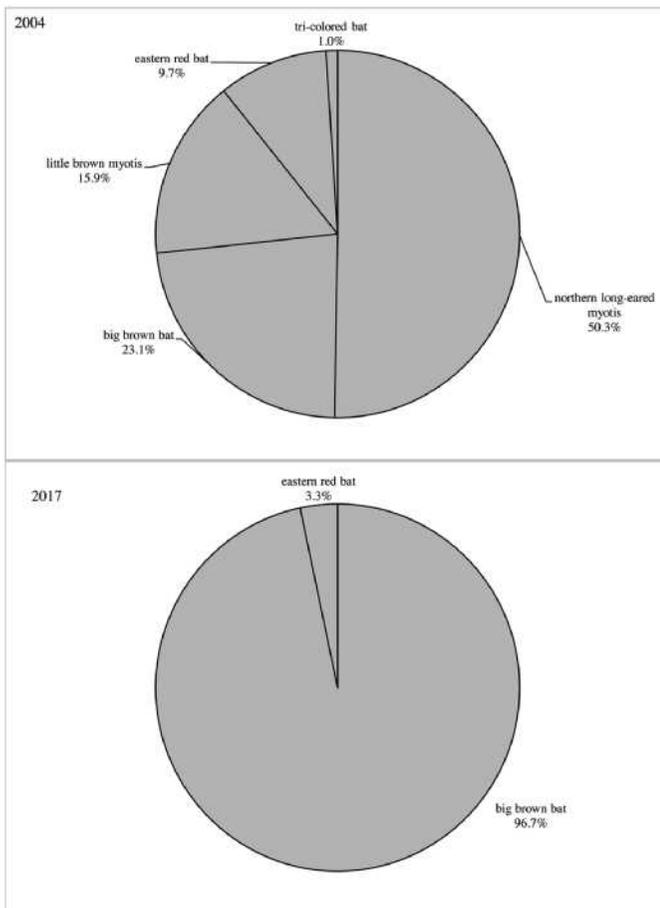


Figure 4. Species composition of bats captured during mist-netting surveys conducted on Fort Indiantown Gap National Guard Training Center, PA, in 2004 (top) and 2017 (bottom).

9 of 12 sites and comprised 15.9% of total bat captures (figure 4). However, in 2017, we failed to capture a single individual of either formerly common species (or of tri-colored bats, which were rare in 2004) at the 12 analogous sites, suggesting severe population decline of each species over time (figure 4).

The decline in capture rates of northern long-eared myotis and little brown myotis that we observed in this study support findings from previous studies indicating dramatic declines in these species in the eastern United States. The Pennsylvania Game Commission has documented a statewide decline in summer captures of these two species since 2001, with capture rates of northern long-eared myotis and little brown myotis declining from 2.28 to 1.17 captures/1000 UOE (-48.7%) and from 3.24 to 1.28 captures/1000 UOE (-60.5%), respectively (Butchkoski and Bearer 2016). Summer captures of northern long-eared myotis and little brown myotis declined by 77.1% and 79.9% in West Virginia following the occurrence of WNS (Francl et al. 2012). Moosman et al. (2013) found a 98% decline in summer captures of both species in New Hampshire. Similarly, Reynolds et al. (2016) found a 95.1% decline in summer capture rates of northern long-eared myotis in western Virginia. Captures of northern long-eared myotis declined by 81.5% at sites surveyed before (2009–2011) and after (2014–2016) the initial detection of WNS in Mammoth Cave National Park, KY (Thalken et al. 2018).

In contrast to these dramatic declines in *Myotis* capture rates, we documented a significant increase (+276%) in capture rates of big brown bats and no change in capture rates of eastern red bats from 2004 to 2017. These two species comprised 100% of total bat captures in 2017 (figure 4). Big brown bats are only moderately affected by WNS, possibly due to their more solitary roosting habits (Merritt 1987; Raesly and Gates 1987), which could decrease transmission of Pd; their ability to hibernate in anthropogenic structures (Whitaker and Gummer 2000) that are away from large bat aggregations and therefore may be less likely to be contaminated with Pd; their greater tolerance of colder temperatures near the entrances of hibernacula (Raesly and Gates 1987; Johnson et al. 2016), where temperatures may be below thermal optima for Pd growth (Verant et al. 2012); and their larger body size, which may reduce overwinter mortality from premature fat depletion (Frank et al. 2014). As a migratory, nonhibernating species, eastern red bats are not believed to be affected by WNS (Ford et al. 2011).

The increase in captures of big brown bats observed in this study contradicts previously documented statewide declines in summer captures of this species in years following the appearance of WNS. Big brown bat capture rates declined slightly from 2.87 to 2.27 bats/1000 UOE between pre- (2001–2008) and post-WNS (2009–2013) years, with the greatest decline occurring in the

southeastern region of the state, where FIG-NGTC is located (Butchkoski and Bearer 2016). We cannot rule out the possibility that slight differences in netting protocols between years could have affected these results, but most of these differences were slight and unlikely to account for the large differences in big brown bat captures. In particular, the increase we observed is unlikely to be due to the different number of survey nights per site in the two years (two survey nights in 2004 vs. one in 2017). While bat capture rates are known to decline on the second consecutive night of netting at a site (Robbins et al. 2008; Winhold and Kurta 2008), our results are robust to this difference in netting protocol; when the analysis was run without the second survey night from 2004, an increase in big brown bat captures was still observed ($\chi^2 = 9.379$, $P = 0.002$). Stochastic events, such as the relocation of a maternity colony closer to or further from one of the 2017 sites, also cannot be ruled out. However, the results are robust to the effects of such a maternity colony formation or relocation; when the analysis was run without the site with the greatest increase in big brown bat captures between years (site 10, which had two big brown bat captures in 2004 and 46 in 2017), an increase in capture rates was still observed (results not shown). While we controlled for habitat structure between years, changes in land management practices (e.g., increased use of prescribed fire and mechanical thinning) since 2004 or disturbances caused by military training may also have affected bat habitat use on site. However, the increase in captures of big brown bats we observed in this study was particularly pronounced and is supported by recent evidence from studies conducted in other areas of eastern Pennsylvania and nearby states, which found a significant increase (Hauer et al. 2016) or a trend to increasing summer captures of big brown bats after WNS (Francl et al. 2012; Pettit and O'Keefe 2017).

The results of our PERMANOVA analysis provide further empirical evidence of a restructuring of the bat community at FIG-NGTC following WNS, from one formerly dominated by northern long-eared myotis (and to a lesser extent little brown myotis) to one now dominated by big brown bats and eastern red bats. This shift in community structure may represent the impact of WNS on susceptible species. Reasons for the increase in big brown bats are less clear, but could be due in part to an ecological release of big brown bats, which may be exploiting available niche space vacated by declining *Myotis* species (Ford et al. 2011). While big brown bats have different diets (Agosta 2002, Whitaker 2004) and foraging strategies (Norberg and Rayner 1987) than the *Myotis* species, Jachowski et al. (2014) showed relaxed interspecific competition within the bat community at Fort Drum, NY following severe WNS-induced declines of previously abundant little brown myotis. Alternatively, other factors unrelated

to WNS-induced declines of *Myotis* species, such as local or large-scale land use change or different forest management practices on the installation, may be driving the increase in big brown bat abundance we observed.

In conclusion, our data indicate that populations of northern long-eared myotis and little brown myotis at FIG-NGTC have undergone severe declines since 2004, while the big brown bat population has increased, and the eastern red bat population has remained constant. These results are consistent with WNS having an important effect on bats since its arrival in Pennsylvania and lend support to the prediction of a restructuring of communities of forest-dwelling bats in WNS-affected areas (Jachowski et al. 2014). However, as is the case with changes at a regional scale (Ingersoll et al. 2013, 2016), local-scale changes in the relative abundance of bat species cannot be attributed to WNS alone. Threats such as climate change and wind energy development may have also affected local populations of particular bat species or the community as a whole. It is also difficult to assess whether changes in relative species abundance were due to changes in reproduction, emigration, or immigration; our brief sampling duration and small scale of study precluded our assessing changes in rates of pregnancy or juvenile recruitment or tracking large-scale movements. Nonetheless, our study adds to accumulating evidence indicating that important recent changes have occurred in bat populations of several species and in bat community structure, and that these changes are consistent with an important effect of WNS. This study also highlights the value of repeated sampling, such as via long-term monitoring programs, to document changes in bat communities over time.

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