

## Mobile bat acoustic routes indicate cavity-roosting species undergo compensatory changes in community composition following white-nose syndrome

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Emerging pathogens can cause mass mortalities in susceptible species. High host mortality, in turn, can alter species composition, community structure and function. White-nose syndrome (WNS) is an emerging wildlife disease introduced to North America that has decimated millions of cave-dependent bats. For areas affected by WNS, there have been reports of community compositional changes, but compensatory changes to species composition following WNS has only been suggested, not reported. To determine if compensatory changes to species composition occur following WNS, we used seven years of data from statewide citizen science mobile bat acoustic routes initiated by the Ohio Division of Wildlife in 2011. We hypothesized that migratory bat abundance increased and cave-dependent bat abundance decreased following the emergence of WNS in the study period (2011–2017). Our hypothesis was based on the higher susceptibility of cave-dependent bats than migratory bats to infection and WNS mortality. We used two sets of models to identify abundance trends of each species found in Ohio and species grouped by wintering and roosting behaviors that are putatively important to changes in species composition post-WNS. Following WNS, we found a compensatory change in species in summer months from cave-dependent, cavity-roosting species (*Myotis* species and *Eptesicus fuscus*) to migratory, cavity-roosting species (*Nycticeius humeralis* and *Lasionycteris noctivagans*). However, for species that roost in foliage in the summer, we did not detect an increase in migratory species (*Lasiurus borealis* and *Lasiurus cinereus*) paired with a decrease in cave-dependent species (*Perimyotis subflavus*). The observed post-WNS trends in bat populations could suggest shifts in bat species composition in other areas where WNS is established.

**Key words:** white-nose syndrome, bat species composition, bat abundance, bat acoustics, mobile acoustic route

### INTRODUCTION

High host mortality due to emerging pathogens may alter species composition (Van Riper *et al.*, 1986), community structure and function (Holdo *et al.*, 2009; Pettit and O’Keefe, 2017). Emerging infectious diseases can also cause drastic declines in host species at community and regional levels (Lips *et al.*, 2006; Frick *et al.*, 2010), as well as across species ranges (Frick *et al.*, 2015). At the community level, pathogens can eradicate sensitive species and reduce competition for other sympatric species (Tompkins *et al.*, 2003; Jachowski *et al.*, 2014). For example, when introduced gray squirrels (*Sciurus carolinensis*) with squirrel pox virus (*Parapoxvirus* spp.) caused mortality in the susceptible red squirrel (*Sciurus vulgaris*) in England, the less susceptible invasive gray squirrel populations benefited due to

a reduction in competition from native red squirrels (Tompkins *et al.*, 2003). Here, we investigate changes in bat species composition due to severe population declines caused by white-nose syndrome (WNS) following the introduction of its causative agent, the fungal pathogen *Pseudogymnoascus destructans*.

WNS is a devastating wildlife disease that is causing rapid declines in temperate, insectivorous bat populations in North America (Blehert *et al.*, 2008; Frick *et al.*, 2015). The fungal pathogen, *P. destructans*, originated from Europe (Puechmaille *et al.*, 2011, Leopardi *et al.*, 2015, Davy *et al.*, 2017) and was first discovered in New York in 2006 (Blehert *et al.*, 2008). It has since spread across North America. *Pseudogymnoascus destructans* infects hibernating bats that occupy caves by embedding in epithelial wing tissues (Meteyer *et al.*,

2009) and causing fatal physiological effects such as electrolyte depletion (Cryan *et al.*, 2013; Warnecke *et al.*, 2013; Verant *et al.*, 2014), acidosis (Warnecke *et al.*, 2013; Verant *et al.*, 2014), and increases to torpid metabolic rate and evaporative water loss (McGuire *et al.*, 2017). North American migratory tree bat species in temperate climates can also carry the fungus (Bernard *et al.*, 2015), but have yet to be reported with WNS. This is likely due to their long distance migrations during winter months (Cryan, 2003), their brief hibernating patterns (Saughey *et al.*, 1998; Mormann and Robbins, 2007) and lack of cave-dependency for hibernating (Perry *et al.*, 2010). Although cave-dependent and migratory species typically do not share wintering roosts due to interspecific differences in seasonal movements, both groups spread *P. destructans* and share summer foraging habitats in temperate regions (Timpone *et al.*, 2006; Jachowski *et al.*, 2014). Thus, it is likely the introduction and epidemic of WNS is reshaping the composition of North American insectivorous bat communities in summer months.

Compositional changes in bat communities are occurring post-WNS from the Northeast across the Midwest, US with relative bat activity and captures showing overall declines in *Myotis* spp. and *E. fuscus* following initial mortalities from WNS and *P. destructans* establishment (Brooks, 2011; Ford *et al.*, 2011; Jachowski *et al.*, 2014; Pettit and O’Keefe, 2017; Nocera *et al.*, 2019). In New York, just three years after the discovery of WNS, activity of the temperate migratory bat, *Lasionycteris noctivagans*, increased and continued increasing long-term after *P. destructans* establishment (Ford *et al.*, 2011; Nocera *et al.*, 2019). In Indiana, captures of another migratory species, *Nycticeius humeralis*, also increased three years after the state’s confirmation of WNS (Pettit and O’Keefe, 2017). Of course, other factors than WNS also influence bat abundances. For example, *N. humeralis* has been expanding its range in the midwestern United States prior to WNS due to changes in land use (Whitaker and Gummer, 2003; Sparks *et al.*, 2012). Taken together, it would appear that winter cave-dependent bats could become replaced by migrating bats within a few short years following *P. destructans* introduction and initial WNS mortality. We suggest that, in areas of *P. destructans* establishment, this cave-dependent-to-migrator shift in bat communities observed in site-specific studies could combine to cause larger scale population changes. Alternatively, if migratory bats do not take advantage of foraging resources made available from cave-dependent

species declines over time, we expected to see abundance declines across cave-dependent species and no change in migratory bat species abundance.

To determine if bat community composition had changed on a larger spatiotemporal scale, we analyzed acoustic transect data from the Ohio Division of Wildlife from 2011–2017. Although bat capture studies are useful for exact species identification and reproductive status information, mobile acoustic monitoring methods are non-invasive and can provide large amounts of information in less time compared to capture methods. Mobile acoustic transects provide greater landscape coverage in shorter time frames for estimating relative abundance of bats and their activity compared to capture methods (Roche *et al.*, 2011). The lack of permitting needed to conduct mobile acoustic surveys and the increase of potential public engagement through the use of volunteers also make larger-scale acoustic survey efforts easier to accomplish than large scale mist-netting efforts. National programs such as the North American Bat Monitoring Program (Loeb *et al.*, 2015) are making headway for large-scale data collection of summer bat foraging activity through the creation of standardized protocols. With the inclusion of acoustic classification, it may be possible to detect compositional changes of bat diversity over space and time. Mobile acoustic route transects were implemented in Summer 2011 in parts of Ohio, after the state’s first detection of *P. destructans* and confirmed WNS in the preceding winter. We expected decreasing abundance in cave-dependent species (i.e., *E. fuscus*, *Myotis leibii*, *M. lucifugus*, *M. septentrionalis*, *M. sodalis*, and *Perimyotis subflavus*) due to WNS.

Our research question was whether the decline in cave-dependent species would lead to an overall decline in bat abundance or whether other bat species, less impacted by WNS, would increase in abundance in compensation. The rationale for an increase in some bat species is that they could make use of resources unused by species that declined in abundance. For example, some of the cave-dependent and migratory species overlap in food preference (Whitaker and Clem, 1992; Whitaker, 1995), roosting sites (Timpone *et al.*, 2006) or foraging niches (Jachowski *et al.*, 2014). Although quantifying this overlap in resource use is beyond the scope of this study, the limited availability of these resources suggests interspecific competition might be important and possibly increase under continued conservation threats (Kerth, 2008; Salinas-Ramos *et al.*, 2020). We therefore hypothesized that the emergence of

WNS led to a decrease in cave-dependent species abundance across Ohio, while allowing for an increase in migratory species abundance.

MATERIALS AND METHODS

*Mobile Bat Acoustic Routes Protocols*

The Ohio Division of Wildlife (ODOW) began conducting mobile bat acoustic routes in Summer 2011 after the first detection of white-nose syndrome (WNS) in the southern-most county (Lawrence County) during Winter 2011 (Ohio Department of Natural Resources, 2011). Ohio’s mobile acoustic routes are a volunteer-based citizen science program, which includes participation by civilians, certified naturalists, state and federal park and agency employees, and city metro park employees. Initially there were 10 driving routes with six of the 10 located in the Wayne National Forest in southeastern Ohio. By Summer 2017, participation expanded to 42 total driving routes spanning 51 of the 88 counties and over 100 participants (Fig. 1). Since participation was volunteer based, not every driving route was completed every year.

The Ohio Division of Wildlife created mobile acoustic route protocols adapted from previous acoustic guidelines (Britzke and Herzog, 2009). Participants annually completed each driving transect three times in the month of July. To ensure monitoring covered the entire month of July, reduce bias for time of month and lunar phase, and to ensure each monitoring event was an independent sample, each route was driven on non-consecutive nights (Gannon and Willig, 1997). Each transect consisted of a 48.3 km (30-mile) loop on roads with less traffic to

decrease noise interference. Driving transects began 30 minutes after sunset and volunteers drove between 24 km/h (15 mph) and 32 km/h (20 mph) to increase the likelihood that each bat detection was an individual bat without repeats (Roche *et al.*, 2011). Beginning in Summer 2014, ODOV started changing the direction of routes each time they were run (forward or reverse) to minimize temporal bias within individual acoustic transects (Skalak *et al.*, 2012). Since the forward route direction was typically driven twice there was still a bias towards the forward direction. However, each transect included at least one instance of driving the route in the opposite direction since 2014.

Seven transects did not follow ODOV’s standardized protocols: Wayne National Forest (Routes 1–6) and Kelly’s Island (Route 14). Transects completed in Wayne National Forest followed US Fish and Wildlife Service (USFWS) Acoustic Monitoring Protocols (US Fish and Wildlife Service, 2018) but contributed data to ODOV for annual analysis. USFWS Acoustic Monitoring Protocols differed from ODOV’s as follows: monitoring was not restricted to the month of July, routes were often linear as opposed to loops, and monitoring can be conducted on consecutive nights. Kelly’s Island (Route 14) located North of Sandusky, Ohio in Lake Erie, is not large enough for a 48.3 km loop so it is modified to an 18.66 km (11.6 mile) loop.

*Acoustic Equipment Protocols*

All volunteers conducting mobile acoustic transects used an Anabat™ SDII recording unit (Titley Scientific, Columbia, Missouri, USA). Each year prior to surveys, ODOV calibrated all Anabat™ SDII units with an Anabat™ Chirper MKII and Anabat™ Equalizer software. Anabat™ SDII unit recording

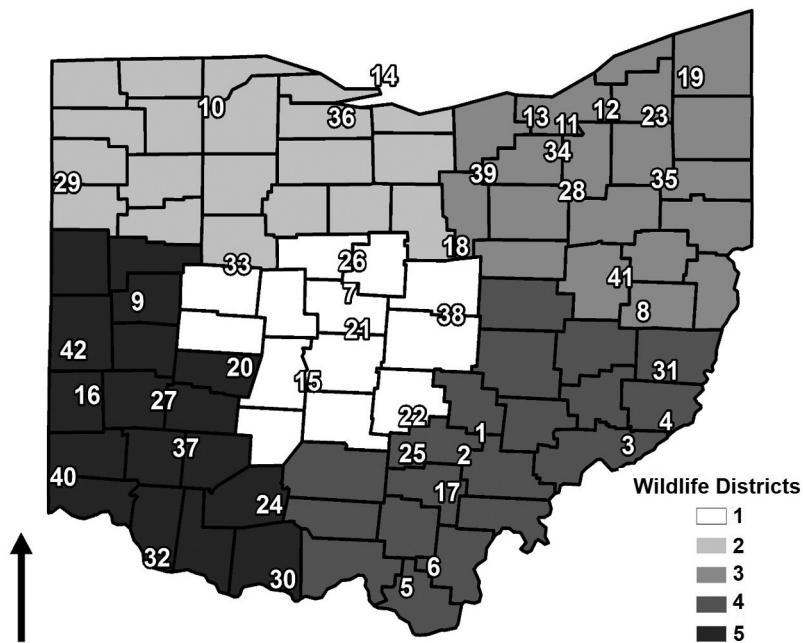


FIG. 1. Locations of all Ohio Division of Wildlife Mobile Bat Acoustic Routes and districts throughout Ohio. Transects are in white and numbered in the order they were added to the program. The colored polygons show Ohio counties within Ohio Division of Wildlife districts. With the exception of Routes 1, 2, 3, 4, 5, 6, and 14, all routes are 38.3 km (30 mile) loops. Districts were treated as a fixed effect and routes were treated as a random effect in all linear mixed effects models. This map was created in ArcMap™ version 10.0 (ESRI, Redlands, CA)

sensitivity settings were set to seven to reduce background noise, 16 for audio division ratio to set the tone heard while recording, and eight for data division ratio to reduce data storage by reducing the resolution of each call. We used directional microphones attached to the roof of vehicles and connected to the Anabat™ SDII, which rested inside the vehicle. To provide better aerodynamics and minimize wind interference during recordings, volunteers tilted microphones caudally during transect execution. Volunteers collected geographic locations through Personal Digital Assistants (PDA) included in the Anabat™ SDII units with Compact Flash GPS cards or GPS mouse units.

### Acoustic Classification Protocols

The data collected from each transect was provided to ODOW to analyze. To determine changes in abundance over time, ODOW employees classified bat detections to species identification in Bat Call ID© (BCID) East version 2.6a after completion of data collection. ODOW tailored classification settings within the software to account for known species within the state of Ohio. These classification settings were consistent every year and were in compliance with US Fish and Wildlife Service's Region 3 guidelines as follows. We manually added *M. leibii* to the species classification list and set a frequency range of 5–60 kHz, a smoothness setting of 30 percent, sweep range (bandwidth of acoustic waveform) of 1–70 kHz, and a duration range (length of time for a single pulse or full, continuous sound emission) of 1–30 ms. All other settings were set to default including classification recognition of five pulses. In 2017 only, we classified detections in Echoclass Version 3.1 (Eric Britzke, ERDC) along with BCID©. When classification did not agree between both acoustic software programs, we manually vetted calls and classified any unverifiable call as unknown. Due to their very high call frequencies and overlapping inter- and intraspecific variations in call frequency, we grouped *Myotis* species together (Thomas *et al.*, 1987; Hayes, 2000). Finally, we summarized detection data into counts of acoustic route detections by species for every route completed from 2011 through 2017. This summary data accounted for 4,651 samples (routes completed) and 38,230 total detections.

### Statistical Analysis

To determine if trends in foraging bat abundances indicated compensatory changes to species composition following confirmation of WNS, we fit two groups of linear mixed effects models (see Supplementary Table S1 for details) with maximum likelihood using 'lme4' (Bates *et al.*, 2015) in the statistical programming environment R (R Core Team, 2020). The first group of 14 models was based on species, whereas the second group of 94 models relied on functional groups of species based on wintering and roosting behavior (Davis and Mumford, 1962; Watkins, 1972; Fenton and Barclay, 1980; Shump and Shump, 1982a, 1982b; Thomson, 1982; Barclay *et al.*, 1988; Kurta and Baker, 1990; Caceres and Barclay, 2000). Since we determined roosting behavior by species, we did not include species identity and roosting behavior in the same models. Ideally, models with detection count data should be analyzed with a Poisson family generalized linear mixed model, but zero-inflation of the data prevented models from converging. Thus, we transformed detection counts using the equation  $\sqrt{(y + 3/8)}$  (Anscombe, 1948; Kihlberg *et al.*, 1972) to meet linear mixed model assumptions, which allowed model convergence despite zero-inflation.

The dependent variable in every created model was the sum of classified species detections of each individually completed transect from 2011–2017. The sum of classified species detections from each route is equivalent to the sum of individual bats because driving speed made it more likely that a single bat detection was an individual bat without repeats (Roche *et al.*, 2011). Therefore, we considered bat detection counts as indices of relative bat abundance.

Independent variables included year as a continuous fixed effect to test for temporal changes to indices of relative bat abundance following WNS in Ohio. For the species-specific models, we included species-specific classification (with *Myotis* species grouped) as a fixed effect. For the behavior models group, we used wintering behavior ('SppType' i.e., hibernating or migratory), and/or summer roosting behavior ('RoostType' i.e., cavity or foliage/tree). Within both model groups, we incorporated ODOW district (Fig. 1) as a categorical fixed effect to test for spatial trends in species composition across Ohio and to account for bat variability in these districts due to natural features. Although each individual transect is nested within ODOW wildlife district, we chose to use ODOW wildlife district as a fixed effect because of varying bat population baselines due to land-use history. For example, wildlife district four in southeastern Ohio is predominantly deciduous forest with rolling hills while wildlife district two in northwestern Ohio is flat and mostly agricultural lands. Thus, ODOW wildlife district was chosen as a land-use proxy. We chose individual transects as a random effect to eliminate bias for specific site variation across the state, account for repeated measures and difference in route completion each year since implementation. We used Akaike's Information Criterion (AIC) for selecting the best-fit model in each model group to determine which variables most influenced bat abundance across the state post-WNS.

Once AIC selection determined the best-fit model in each model group, we tested fixed effects with Satterthwaite's method implemented in 'lmerTest' (Kuznetsova *et al.*, 2017). We extracted bat abundance predictions for all combination of fixed effect categories for the two top models using package 'lme4' (Bates *et al.*, 2015). We bootstrapped these predictions 1,000 times to estimate 95 percent confidence intervals for all predicted bat abundances (species-specific and behavior models) for each year and ODOW wildlife district using the statistical package 'glmmTMB' (Brooks *et al.*, 2017; Magnusson *et al.*, 2017). We back-transformed predicted outcomes and plotted bat abundance for both top models with respective confidence intervals using 'ggplot2' (Wickham, 2009).

## RESULTS

The indices of relative bat abundance depended on species identity or the species traits of wintering and roosting behavior, ODOW wildlife district, and year. This result indicated that, following WNS emergence in Ohio, bat abundance varied by species or behavioral trait across time and space. The best-fit species-specific model included an interaction between species, year and wildlife district with an added random effect of each driving transect ( $F_{24, 41} = 3.67$ ,  $P < 0.001$ ,  $R^2 = 0.46$  — Table 1). Similar to the species-specific models, the best-fit



TABLE 1. Results for fixed effects variables within the top species-specific and behavior models subject to analysis of variance with Satterwhite's Method. The variable 'Spp' included all species detected (i.e. *E. fuscus*, *L. borealis*, *L. cinereus*, *L. noctivagans*, *Myotis* spp., *N. humeralis*, and *P. subflavus*). 'Year' was a continuous variable for all years of data collection spanning 2011 through 2017. 'District' included Ohio Division of Wildlife's five wildlife districts as a categorical variable. 'SppType' was a categorical variable for migratory behavior (cave-dependent or migratory) and 'RoostType' was a categorical variable for roosting behavior (cavity or foliage). Finally, 'Route' was a categorical variable for individual mobile acoustic transects. Significant values are denoted as follows: \* —  $P < 0.05$ , \*\* —  $P < 0.01$ , \*\*\* —  $P < 0.001$

Model group	Fixed effects	<i>d.f.</i> fixed	<i>d.f.</i> random	<i>F</i> -value	<i>P</i> -value
Species	Spp	6	41	18.33	< 0.001***
	District	4	41	11.67	< 0.001***
	Year	6	41	1.36	0.24
	Spp * District	24	41	3.68	< 0.001***
	Spp * Year	6	41	21.61	< 0.001***
	Year * District	4	41	8.26	< 0.001***
	Spp * District * Year	24	41	3.67	< 0.001***
	Behaviors	SppType	1	41	27.37
RoostType		1	41	12.26	< 0.001***
District		4	41	8.80	< 0.001***
Year		1	41	2.06	0.15
SppType * RoostType		1	41	10.37	0.001**
SppType * District		4	41	2.61	0.03*
SppType * Year		1	41	30.31	< 0.001***
RoostType * District		4	41	4.38	0.002**
RoostType * Year		1	41	9.66	0.002**
District * Year		4	41	7.18	< 0.001***
SppType * RoostType * District		4	41	3.12	0.01*
SppType * RoostType * Year		1	41	15.38	< 0.001***
SppType * District * Year		4	41	2.77	0.03*
RoostType * District * Year		4	41	4.20	0.002**
SppType * RoostType * District * Year		4	41	3.13	0.01*

roosting behavior model included an interaction of all possible fixed effects with the random effect, driving transects ( $F_{24, 41} = 3.13$ ,  $P = 0.014$ ,  $R^2 = 0.25$  — Table 1). All other linear mixed models, regardless of species-specific or behavior models group, were not supported by AIC selection ( $\Delta AIC > 10$  — Burnham and Anderson, 1998).

Predicted values with 95% confidence intervals from our top species-specific model indicated species-specific changes to relative bat abundance in Ohio from 2011–2017 (Fig. 2). *Eptesicus fuscus*, *L. borealis*, and *P. subflavus* abundances decreased across ODOW districts in every year since WNS was confirmed in Ohio. *Myotis* spp. detections decreased across every district since WNS confirmation but not as drastically as *E. fuscus*, *L. borealis*, and *P. subflavus* (Table 2). In contrast, we found an overall increase in *N. humeralis* and *L. noctivagans* across Ohio since 2011 (Fig. 2 and Table 2). *Lasiurus cinereus* abundance varied across space and time, with declines in ODOW District 1 and District 4 and increases in Districts 3 and 5 (Fig. 2). Within the summer months of 2011–2017, the best-fit species-specific model indicated a species

compositional change from *E. fuscus* and *Myotis* spp. to *L. noctivagans* and *N. humeralis*.

Predicted values with 95% confidence intervals from our top wintering and roosting behavior model also indicated compositional changes to relative bat abundance in Ohio from 2011–2017 based on bat natural history. Cave-dependent, cavity-roosting bat abundances decreased across all ODOW districts in every year since WNS was confirmed in Ohio (Fig 3). Cave-dependent, foliage-roosting species declined in ODOW Districts 1, 3 and 5. These prediction trends were similar to the *P. subflavus* prediction in the species-specific model, as it is the only species in Ohio with this combination of behavioral traits. In contrast, we found an overall increase in migratory, cavity-roosting species across all ODOW districts but not to migratory foliage-roosting species (Table 2). Migratory foliage-roosting species declined in all ODOW districts except for District 5. Within the summer months of 2011–2017, the top wintering and roosting behavior model indicated a compositional change from cave dwelling, cavity-roosting species to migratory cavity-roosting species.

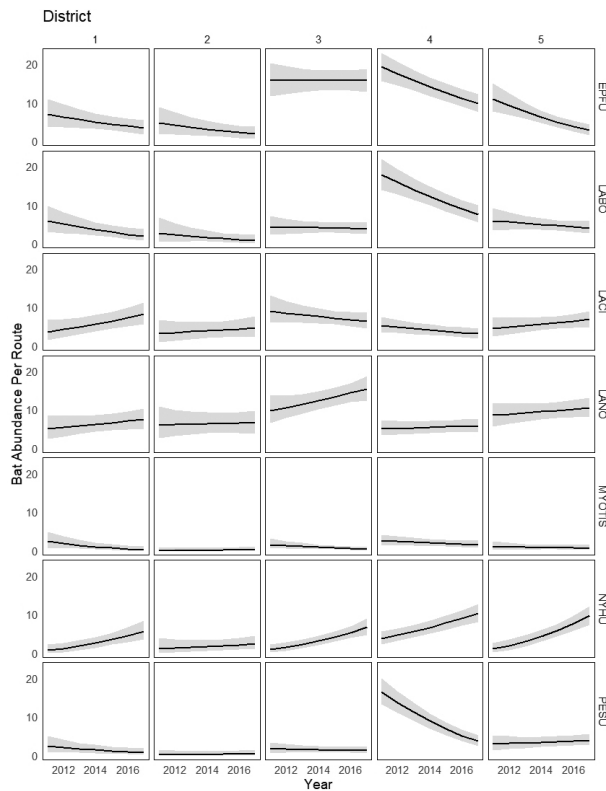


FIG. 2. Predicted bat species abundance from 2011–2017 per individual transect across Ohio Division of Wildlife districts. Gray shaded areas represent 95% confidence intervals. Species abbreviations: EPFU, *E. fuscus*; LABO, *L. borealis*; LACI, *L. cinereus*; LANO, *L. noctivagans*; MYOTIS, *Myotis* spp.; NYHU, *N. humeralis*; and PESU, *P. subflavus*

## DISCUSSION

To the best of our knowledge, we are the first to show systematic and compensatory changes to species specific and behavioral indices of relative bat abundance using mobile acoustic route detections following WNS. Our results are consistent with compositional changes in stationary acoustic activity for *Myotis* spp. and *L. noctivagans* in New York as well as *N. humeralis* captures in Indiana following WNS (Ford *et al.*, 2011; Pettit and O’Keefe, 2017). It is unclear if a more complete replacement from cave-dependent, cavity-roosting bats to migratory, cavity-roosting bats will occur in the future, particularly since susceptibility to WNS and infected population persistence is currently species-specific (Langwig *et al.*, 2017; Moore *et al.*, 2018). Therefore, highly susceptible species will take a long time to recover (Russell *et al.*, 2015), especially with the additional external pressure of increased competition from other species that increased and use available food and roosting resources.

Bat abundance shifts from cave-dependent to migratory species during summer months was confirmed in summer cavity-roosting species but not in summer foliage-roosting species. It is possible migratory cavity-roosting bats are experiencing competitive release such that, the decline of cave-dependent, cavity-roosting species allowed for more summer roosting and foraging habitat availability for migratory cavity-roosting bats where both species groups overlapped. Within these data, this pattern is also more likely to occur within cavity-roosting species, as the only cave-dependent foliage-roosting species in Ohio is *P. subflavus*. All other cave-dependent bats in Ohio are cavity-roosters. Additionally, Ohio’s migratory foliage-roosting species populations (i.e. *L. borealis* and *L. cinereus*) are likely to be negatively impacted by wind turbine collisions, another threat to bat populations in Ohio (Frick *et al.*, 2017). Therefore, it is likely the lack of compensatory change in foliage roosting species is due to the limited number of cave-dependent, migratory species in Ohio and that migratory, foliage species face additional conservation threats.

Increases in *N. humeralis* and *L. noctivagans* from 2011–2017, both of which are migratory, cavity-roosting species (Barclay *et al.*, 1988; Boyles and Robbins, 2006), support our hypothesis of

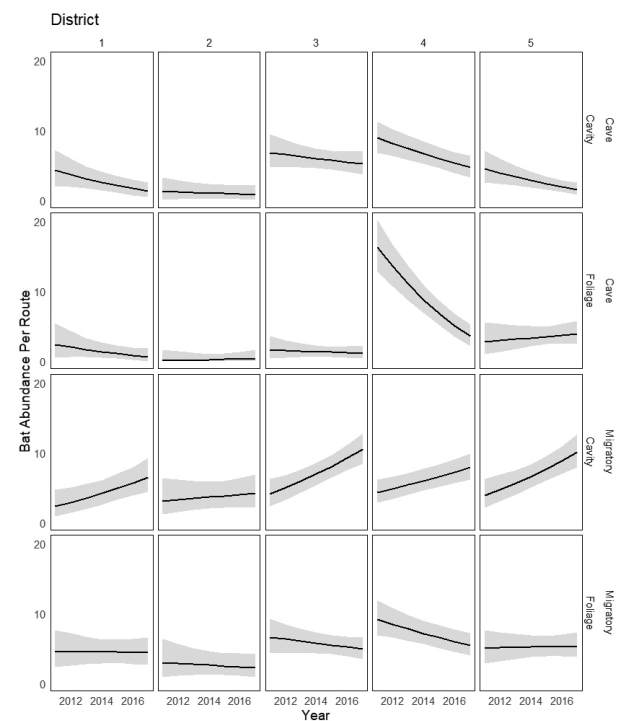
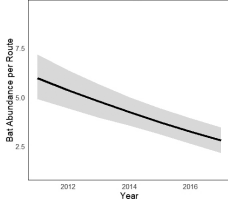
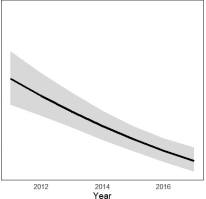
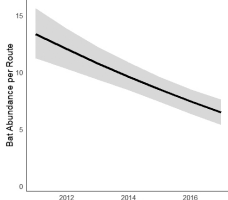
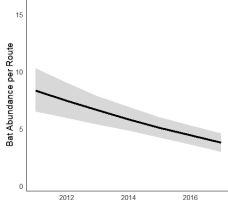
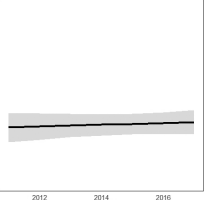
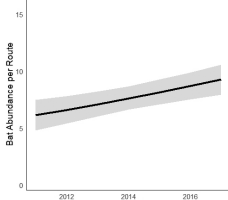
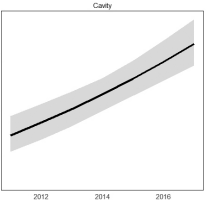
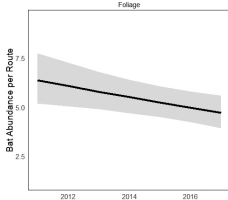
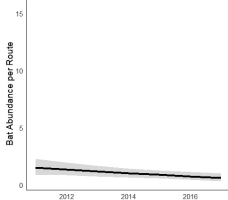
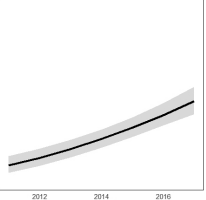
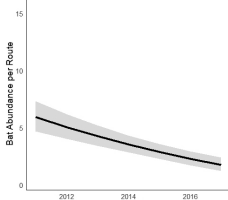


FIG. 3. Predicted wintering and roosting behavior bat abundance from 2011–2017 per individual transect across Ohio Division of Wildlife districts. Gray shaded areas represent 95% confidence intervals

TABLE 2. Species and behavioral groupings of bats detected from 2011 through 2017 during Ohio Division of Wildlife Mobile Bat Acoustic Routes. Visualizations of general compensatory changes are presented as statewide trends for each species and their combined wintering and roosting behaviors. Scales for bat abundance per route differ between species and behavioral groups

Species	Wintering behavior ('SppType')	Roosting behavior ('RoostType')	Species statewide trend	Behavioral statewide trend
<i>E. fuscus</i>	Cave-dependent	Cavity		
<i>Myotis</i> spp.				
<i>P. subflavus</i>	Cave-dependent	Foliage		
<i>L. borealis</i>	Migratory	Foliage		
<i>L. cinereus</i>				
<i>L. noctivagans</i>	Migratory	Cavity		
<i>N. humeralis</i>				

compositional changes driven by increases in migratory species, but only in cavity-roosting species. A reasonable ecological hypothesis could be that *N. humeralis* and *L. noctivagans* are filling habitat and using resources vacated by *Myotis* spp. and *E. fuscus*. Other studies have reported similar findings. For example, Pettit and O’Keefe (2017) reported increased capture rates of *N. humeralis* post-WNS, and *L. noctivagans* also showed post-WNS increases in activity in New York (Ford *et al.*, 2011).

Some reports of niche overlaps between *N. humeralis*, *L. noctivagans*, and *E. fuscus* support the ecological speculation that declines in *E. fuscus* could have allowed *N. humeralis* and *L. noctivagans* to increase in abundance by using vacated resources. *Nycticeius humeralis* and *E. fuscus* are recorded roosting and foraging within forested and urban habitats (Whitaker and Gummer, 2003; Duchamp *et al.*, 2004; Timpone *et al.*, 2006). Further, *N. humeralis* and *E. fuscus* have similar diets, preferring agricultural beetle pests (Whitaker and Clem, 1992; Whitaker, 1995). An increase in *N. humeralis* due to a rise in these available habitats and resources in the Eastern US could be contributing to the range expansion of *N. humeralis* across the Great Plains, where they are beginning to inhabit non-forested areas (Andersen *et al.*, 2017). Although it has been suggested that *E. fuscus* could outcompete *N. humeralis* when they co-occur due to their adaptability to urban environments (Timpone *et al.*, 2006), *N. humeralis* has been found to roost in man-made structures prior to confirmation of WNS in North America (Whitaker and Gummer, 2003). Additionally, *L. noctivagans* were reported to temporarily roost in buildings in late summer (McGuire *et al.*, 2012), making them likely to overlap in roosting niche with *E. fuscus*, which are regular found roosting in man-made structures (Rysgaard, 1942; Whitaker and Gummer, 1992; Whitaker, 1995; Whitaker and Gummer, 2000; Boyles *et al.*, 2007; Mills *et al.*, 1975). *Lasionycteris noctivagans* and *E. fuscus* were also found to overlap in foraging habitat (Jachowski *et al.*, 2014). Therefore, the decline in *E. fuscus* and the increase in *N. humeralis* and *L. noctivagans* following emergence of WNS within Ohio could reasonably be compensatory compositional change, although we have no direct evidence for this.

*Perimyotis subflavus* abundance consistently declined from 2011–2017 across all districts which is also seen regionally in winter hibernacula (Frick *et al.*, 2015). This species winters in caves and roosts

in foliage in the summer (Findley, 1954; Carter *et al.*, 1999; Kurta *et al.*, 1999; Veilleux *et al.*, 2003). The data did not portray potential replacement by *L. borealis* or *L. cinereus*, Ohio’s two migratory, foliage-roosting species (Shump and Shump, 1982a, 1982b; Mager and Nelson, 2001; Willis and Brigham, 2005). Our findings support decreases in overall summer acoustic activity post-WNS for *L. borealis*, but not *L. cinereus* (Ford *et al.*, 2011; Johnson *et al.*, 2013). *Lasiurus cinereus* actually had a constant abundance across the project. These trends in *L. borealis* and *L. cinereus* are unlikely due to WNS because while migratory species are found to carry *P. destructans* (Bernard *et al.*, 2015), they have not been reported as showing signs of infection. We suspect that the lack of compensatory change from *P. subflavus* to *Lasiurus* spp. could be due to declines in migratory species by mortality suffered in wind energy farms, also present in Ohio. Between 2011 and 2017, wind energy production increased in Ohio by 1,390 thousand MWh, yielding eight times greater wind energy production in 2017 compared to 2011 (US Energy Information Administration, 2019). Thus, it is likely *Lasiurus* spp. declines are consistent with increased wind energy production as seen throughout North America (Arnett *et al.*, 2008; Frick *et al.*, 2017).

Indices of *E. fuscus* relative abundance indicate declines from 2011–2017. Previous work comparing pre- and post-WNS community composition across the Northeast and Midwestern US demonstrated increased *E. fuscus* in hibernacula (Frank *et al.*, 2014), capture rates (Pettit and O’Keefe, 2017) and foraging activity (Brooks, 2011; Ford *et al.*, 2011) post-WNS. However, in areas with long-term establishment of *P. destructans* (as in Ohio), *E. fuscus* foraging activity declines (Nocera *et al.*, 2019). The documented declines could be due to: 1) a general decline in *E. fuscus* populations caused by other factors than *P. destructans* and WNS, or 2) ongoing host-pathogen pressures. *E. fuscus* is less-susceptible to *P. destructans* infection compared to highly susceptible species such as *M. lucifugus* (Moore *et al.*, 2018), but could be experiencing long-term effects such as a reduction of reproductive success due to increased cortisol levels (Davy *et al.*, 2016) or ongoing metabolic constraints (McGuire *et al.*, 2017; Meierhofer *et al.*, 2018). *Eptesicus fuscus* has also been reported to contract *P. destructans* in Ohio and show typical signs of wing damage from infection (necrotic holes and receding wing tissue) (Simonis *et al.*, 2018). Thus, the declines in *E. fuscus* populations could be due to repeated interactions with



*P. destructans* and may be slower in comparison to highly susceptible *Myotis* spp.

*Myotis* spp. declines from WNS are not well documented in this study. We likely failed to record the decline of the once common *M. lucifugus*, and therefore the bulk of the *Myotis* spp. decline. It is more likely that mobile transects missed interior species detections (Berthinussen and Altringham, 2012) such as *Myotis* spp., missed rare species altogether (Braun de Torrez *et al.*, 2017) or missed *Myotis* spp. declines due to driving routes beginning the summer following *P. destructans* and WNS confirmation in the state. Regardless, it is evident across the literature that all *Myotis* spp. occurring in Ohio (i.e. *M. leibii*, *M. lucifugus*, *M. septentrionalis*, *M. sodalis*) have experienced population declines from WNS (Frick *et al.*, 2010, 2015; Brooks, 2011; Dzal *et al.*, 2011; Ford *et al.*, 2011; US Fish and Wildlife Service, 2016; Pettit and O’Keefe, 2017).

Although acoustic classification suffers from substantial levels of classification error (Lemen *et al.*, 2015; Russo and Voigt, 2016), there is no evidence that mobile acoustic surveys systematically bias the tracking of compositional changes in bat communities and populations. Mobile acoustic transects provide reliable richness estimates as validated by comparison to stationary acoustics (Whitby *et al.*, 2014) and are able to specify bat abundances due to the speed transects are driven. Analyses of mobile acoustic surveys such as ODOW’s can detect distributional species trends (Jones *et al.*, 2013) and changes in populations. Manual vetting of 2017 classification data (approximately 40% of 2017 classified detections were vetted) indicated no consistent bias in misclassifications, which only adds random noise to our large dataset. For example, as previously mentioned, *E. fuscus* and *L. noctivagans* have similar waveforms and call frequencies and can be misclassified for one another. The addition of manual vetting for 2017 data supported proportional increases to *L. noctivagans* relative abundance and *E. fuscus* declines in relative abundance. Therefore, we trust that our results are a reliable portrayal of species-specific and roosting behavior abundance and demonstrate the compensatory changes in species composition of summer bat populations since disease introduction.

To conclude, we detailed species-specific and roosting behavior compositional changes at a state scale likely due to WNS affecting bat communities and populations. Large-scale programs for mobile bat acoustic surveys can document these changes

over time and can expand the range of population monitoring throughout summer months. We would suggest a meta-analysis of regional published findings and state and federal data for capture rates pre- and post-WNS to evaluate potential for complete species turnover in summer months by increases in *N. humeralis* and/or numbers with paired declines in *Myotis* spp. and *E. fuscus* numbers. We would also recommend further investigation of regional capture rates of *P. subflavus*, *L. borealis*, and *L. cinereus* to confirm that our predictions from mobile acoustic route data reflect a lack of potential turnover within our summer, foliage-roosting species. Finally, our results suggest that citizen science and mobile acoustic surveys can be used to determine trends statewide and nationwide, providing further use of the data that is collected by most states.

#### SUPPLEMENTARY INFORMATION

Contents: Supplementary Table S1. Models created and used for AIC selection. Supplementary Information is available exclusively on BioOne.

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