



Original Research Article

Patterns of acoustical activity of bats prior to and 10 years after WNS on Fort Drum Army Installation, New York

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ABSTRACT

Previous acoustic surveys, netting, and count data have shown that overall bat activity patterns have shifted among most species between pre- and post-white-nose syndrome (WNS) years in much of North America where WNS has occurred. However, the significance of these changes is based on the species-specific susceptibility to WNS. We used acoustically recorded echolocation passes obtained at Fort Drum, New York to describe changes in bat activity pre-WNS (2004–2007) to post-WNS (2008–2018). We examined seasonal and yearly changes in bat activity as they relate to the presence of WNS at hibernacula near (<25 km) Fort Drum. *A priori*, we expected that overall activity for communal hibernating species would be less in years following WNS, and migratory bats or those hibernating bats that are less affected by WNS would show no response or a positive response, due to niche relaxation/competitive release. Our results indicated both an overall and seasonal decrease in activity for *Myotis* spp. post-WNS. For WNS-susceptible species, our results reflect the high level of mortality in regional winter hibernacula post-WNS and possibly variable reproductive effort and recruitment thereafter. Although migratory bats did show increases in post-WNS activity throughout the summer, we found little evidence that community displacement was occurring on a nightly level by any species. The continuous spread of WNS across North America has had strong negative effects on bat populations of affected species, and our research identifies how individual species (both impacted and non-impacted) respond to WNS.

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1. Introduction

The emergence of the fungal pathogen, *Pseudogymnoascus destructans* (Pd), causative agent of White-nose Syndrome (WNS), was first documented in the United States in the winter of 2006 at Howe's Caverns, in eastern New York (Blehert et al., 2009). This disease agent has moved rapidly throughout the eastern and central regions of the United States as far west as the state of Washington, and into several provinces in Canada (U.S. Geological Survey, 2018). To date, Pd has been found to infect

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eight species of cave-dwelling bats in eastern North America: the federally-endangered Indiana bat (*Myotis sodalis*, MYSO), the federally-threatened northern long-eared bat (*Myotis septentrionalis*, MYSE), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), federally-endangered gray bat (*Myotis grisescens*, MYGR), Southeastern bat (*Myotis austroriparius*, MYAU), big brown bat (*Eptesicus fuscus*, EPFU), and tri-colored bat (*Perimyotis subflavus*, PESU). The fungus infects epithelial tissues of hibernating bats causing abnormally frequent arousal through winter leading to loss of fat reserves and water balance disruption (Cryan et al., 2010; Frick et al., 2010; Meteyer et al., 2012). Infected bats often die of starvation and dehydration or exposure during winter months.

Among impacted species, the most dramatic changes in activity patterns, abundance, and to some degree distribution have been observed for MYLU, MYSE, MYSO, and PESU (Bleher et al., 2009; Frick et al., 2010; Brooks, 2011; Ford et al., 2011). For example, prior to the onset of WNS, MYLU were either stable or increasing and were considered among the most abundant of bats in North America. Yet, since the discovery of WNS, winter populations have declined by 75–99%, as mirrored by acoustical sampling declines and low captures (Bleher et al., 2009; Frick et al., 2010; Dzal et al., 2011; Ingersoll et al., 2016). Although some MYLU survive winter infection and are able to reproduce (Dobony et al., 2011; Dobony and Johnson, 2018), overwintering mortality, poor female physiological condition, and energetic demands to repair dermal tissue have resulted in variable reproductive output and recruitment, limiting population recovery across the affected distribution (Dobony et al., 2011; Ford et al., 2011; Francl et al., 2012; Dobony and Johnson, 2018). As a result, pre-WNS trends of activity levels increasing in mid-summer, consistent with reproduction and summer recruitment of juveniles, has been reduced after the onset of WNS in northwestern New York and elsewhere (Ford et al., 2011; Francl et al., 2012; Reynolds et al., 2016).

Inter-specific population suppression or competitively-based habitat segregation occurs in bat communities, with relationships changing as community composition (richness and absolute numbers) changes (Haupt and Schmidt, 2007; Ford et al., 2011). For example, in Europe, expanding populations of pipistrelle bats (*Pipistrellus pipistrellus*) lead to suppression of the horseshoe bat (*Rhinolophus hipposideros*), which shares interspecific dietary requirements with the former bat species (Arlettaz et al., 2000). Due to the severity of WNS, research has shown changes in spatial and temporal niche partitioning among bat communities in the Northeast, whereby reduced numbers of MYLU has reduced the competitive suppression effect on other bat species (Jachowski et al., 2014a). Specifically, they showed that WNS has destabilized spatial and temporal niche partitioning in *Myotis* spp. by allowing the eastern red bat (*Lasiurus borealis*, LABO) and EPFU to increase foraging activity in areas formerly dominated by MYLU. This suggests that WNS has a cascading positive effect on behavior and interspecific interactions of species not directly impacted by WNS. Generally, it appears that sympatric species within the genus *Myotis*, i.e., MYLU, MYSE, and MYSO, appear to be increasingly restricted to smaller, isolated summer populations due to WNS and competitive release of other non-impacted species (Brooks, 2011; Jachowski et al., 2014a).

Nonetheless, there is limited data encompassing both pre-WNS and post-WNS years from the same location, which has made it difficult to compare the relative change in bat activity or to assess how population declines of WNS-affected species allow for competitive release of non-impacted species. An exception to this is the extensive long-term acoustic monitoring of bat distribution, activity, and occupancy at Fort Drum Military Installation (Fort Drum) in northern New York from 2003-present that followed the local discovery of summer maternity activity of MYSO (Jachowski et al., 2014a,b). Continuous acoustic monitoring and captures between 2003 and 2018 have documented changes in patterns of acoustical activity pre- and post- WNS and the effects WNS has had on bat community composition and structure at Fort Drum (Dobony et al., 2011; Ford et al., 2011; Coleman et al., 2014b; Jachowski et al., 2014a; Dobony and Johnson, 2018).

Overall activity patterns, as measured by acoustic surveys and mist-netting, shifted among all species between pre- and post- WNS years at Fort Drum (Ford et al., 2011). The significance of these changes was clearly linked to the species-specific susceptibility to WNS, with MYSE, MYSO, and MYLU bat activity patterns decreasing after WNS onset (Ford et al., 2011). This long-term monitoring program has provided a unique opportunity to observe the ecological dynamics of a novel, invasive disease with implications for understanding disease impacts to threatened and endangered species, how additional species might become imperiled, and how these changes manifest themselves at the landscape scale. To expand on the work of Ford et al. (2011), we used acoustically recorded echolocation passes obtained from Fort Drum to more fully describe changes in bat activity pre-WNS to post-WNS, 2004–2018. Accordingly, we hypothesized that overall activity for communal hibernating species, i.e., MYLU, MYSE, and MYSO, would be less in the years following WNS onset, reflective of their declining populations. Conversely, we hypothesized that activity of migratory bats, i.e., LABO and LANO, and/or resident hibernating species less affected by WNS, e.g., EPFU, would show a positive response due to competitive release and niche relaxation as posited by Jachowski et al. (2014a). Whereby these bats might better exploit foraging habitat vacated by MYLU within the constraints allowed by their morphological characteristics, i.e., echolocation type, body size and jaw morphology or overlapping habitat associations (Ford et al. 2005, 2011). Lastly, by examining the summer season partitioned by the pregnancy/juvenile pre-volancy period with the juvenile post-volancy period, we hypothesized that changed activity levels of WNS-affected bats could provide evidence to explain, in part, competitive release observations.

2. Methods

We conducted our study at the Fort Drum Military Installation in Jefferson and Lewis counties in northwestern New York, USA. Fort Drum is a 43,750 ha U.S. Army installation that contains a variety of habitat types and conditions. These include: mature northern hardwood forests, managed conifer plantations, emergent and shrub wetlands, riverine corridors and open/early successional habitat conditions resulting from forest harvesting of hardwood and conifer stands, previous agricultural

use or those maintained for military training. Limestone formations containing caves used by hibernating bats occurs 10–15 km west of the reservation (Ford et al., 2011). There are 9 extant bat species at Fort Drum: MYSE, MYSO, MYLU, EPFU, LABO, PESU, MYLE, hoary bat (*Lasiurus cinereus*, LACI), and silver haired bat (*Lasionycteris noctivagans*, LANO) (Coleman et al., 2014a). Of these, the endangered MYSO was specifically targeted during acoustic surveys since 2003, whereas, following the advent of WNS, interest in the threatened MYSE and declining MYLU increased.

From May 15 through August 15, 2004–2018, we deployed Anabat II detectors connected to a compact flash-storage zero-crossings analysis-interface module (ZCAIM), and SD1 and SD2 detectors using the same transducer model (Tittley Electronics, Ballina, NSW, Australia¹). Following Ford et al. (2011) and Coleman et al. (2014a,c), we placed each detector on a 1.5 m tripod and adjusted so that sound could enter the detector at an angle of 45° (Weller and Zabel, 2002). Our sample sites primarily included locations along roads and forest tracts where detectors were positioned to capture sound along the trail, forest canopy gaps with detectors pointed toward the gap, and emergent wetland sites where detectors were positioned towards open water. From 2004 to 2011, we initially placed Anabat units in weatherproof boxes, but left the microphone exposed, sampling only when there was a minimal chance of inclement weather. From 2012 onwards, we attached a PVC tube to protect the microphone from rain and to aid in funneling sound into the microphone to the weatherproofing boxes. Though variability between weatherproofing methods occurred throughout the years, differences in detection and recording are thought to be minimal (Britzke et al., 2013). Acoustic data were only retained for analyses if the detector unit was operable over the entire sunset to sunrise period.

Following acoustic data acquisition, we visually assessed recorded echolocation passes and then scanned in Analook W (Tittley Scientific Inc., Columbia MO) compatible filters for extraneous non-bat noise. Echolocation files were then analyzed using Kaleidoscope Pro classifier 4.2.0 (Wildlife Acoustics Inc., Maynard MA), under the recommended settings of the U.S. Fish and Wildlife Service using 0 for the program sensitivity setting, and 3 pulse minimum (U.S. Fish and Wildlife Service, 2017). Prior to statistical analysis, we assigned activity counts for each site-night and species to pre-WNS years (2004–2007) or post-WNS years (2008–2017) groups. Using over 10 years of demographic information collected at Fort Drum, we modified methods originally outlined by Ford et al. (2011), and divided the summer into two periods, early (15 May–29 June) representing pregnancy and parturition, and late (30 June–15 August), representing volancy, when juvenile bats begin to be incorporated into the population (Anthony et al., 1981). We used nonparametric Mann-Whitney-Wilcoxon tests in program R (R Core Team, 2018) to determine if ranked mean activity levels through the night significantly differed between early summer (pre-WNS) and early summer (post-WNS) and then late summer (pre-WNS) and late summer (post-WNS), for each bat species. We repeated these analysis to account for the relative change among the two periods of summer for each species by testing whether activity levels through the night differed between early summer (pre-WNS) and late summer (pre-WNS) as well as early summer (post-WNS) and late summer (post-WNS).

We then compared rates of change in bat activity across sites sampled in both pre- and post-WNS years. Out of 289 sites at Fort Drum, 71 were sampled in both pre-WNS years and post-WNS years. We used the ranked mean number of calls identified to a species by night for each site in both groups, to account for higher sampling effort post-WNS. We then assessed both the change in proportion and the directionality of change (either positive or negative) in activity between these same sites pre-WNS and post-WNS. For every individual site, we subtracted the ranked mean number of calls sampled during pre-WNS from the mean number of calls sampled during post-WNS. To correctly show directionality we then transformed the data with a -1 multiplication. We then used correlation coefficients and leverage plots in program R (R Core Team, 2018) to assess relationships between the change in activity between pre- and post-WNS for each species pair using package *corrplot* (Wei and Simko, 2017).

3. Results

From 2004 to 2018, we acoustically sampled 6986 detector-nights (Table 1) and recorded 442,200 bat passes from 9 bat species including MYLU ($n = 80,702$), EPFU ($n = 102,442$), LABO ($n = 41,315$), LACI ($n = 143,833$), MYSO ($n = 4593$), LANO ($n = 59,880$), MYSE ($n = 1243$), PESU ($n = 7658$), and MYLE ($n = 534$). A total of 105,294 files were not identified to the bat species level. When divided into pre-WNS early summer (31 nights), pre-WNS late summer (31 nights), post-WNS early summer (4080 nights), and post-WNS late summer (4152 nights), activity patterns varied among species (Fig. 1). Activity levels for EPFU, LACI, LANO, MYLE, MYLU, MYSE, MYSO, and PESU differed significantly between pre- and post-WNS periods, with overall activity levels declining from pre- to post-WNS for EPFU, MYLE, MYLU, MYSE, MYSO and PESU and increasing for LANO and LACI (Table 2, Fig. 1). However, no differences were observed for LABO (Table 2). Furthermore, activity levels for MYLU, MYSE, MYSO, and PESU significantly differed between pre-WNS early summer and post-WNS early summer, with fewer number of echolocation passes post-WNS (Table 2, Fig. 1). Activity between pre-WNS late summer and post-WNS late summer was significantly different for MYLU, MYLE, MYSE, MYSO and PESU, with reduced number of echolocation passes following WNS (Table 2, Fig. 1).

Prior to WNS, activity levels for all *Myotis* spp., except for MYLU, showed increasing but not significant trends between early summer and late summer. Following WNS, this trend, albeit at far lower levels, continued for these same species on Fort Drum, including MYLU, and was significant (Table 2, Fig. 1). Activity for both EPFU and PESU followed similar trends to that of

¹ Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Table 1

Minimum, maximum, and mean number of nights and total number of detector site locations on Fort Drum Military Installation, New York, 2004 to 2018, between May 15 and August 15. Total effort accounted for 6986 detector-nights, 2004–2018.

Year	Minimum number of detector nights/site	Maximum number of detector nights/site	Mean number of detector nights/site	Total number of detector sites	Total detector nights
2004	1	3	1.88	17	32
2005	1	2	1.76	13	23
2006	2	2	2.00	15	30
2007	2	2	2.00	3	6
2008	2	2	2.00	3	6
2009	2	2	2.00	11	22
2010	1	3	2.00	12	24
2011	1	68	12.68	57	723
2012	2	138	39.04	43	1679
2013	2	93	25.35	40	1014
2014	52	93	70.40	5	352
2015	2	89	9.79	129	1263
2016	8	28	14.98	81	1214
2017	44	63	58.40	5	292
2018	45	93	61.20	5	306

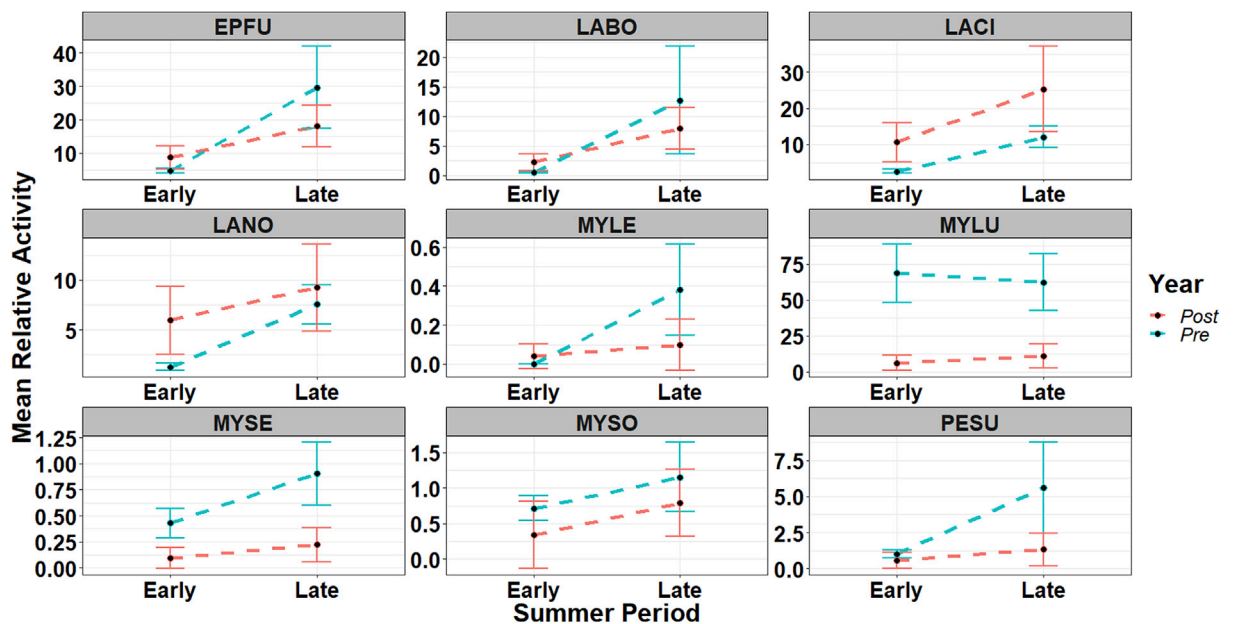


Fig. 1. Mean number of echolocation passes per hour, standard error for the nine bat species on Fort Drum Military Installation, New York in pre-White-nose Syndrome (WNS) years, 2004–2007 and post-WNS years, 2008–2018 for early summer (≤ 15 July) and late summer (> 15 July). Species include: big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), and tri-colored bat (*Perimyotis subflavus*, PESU). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Myotis spp. with no significant difference between early and late summer pre-WNS, but a significant increase between early and late summer post-WNS (Table 2). Significant increases between early and late summer both prior to WNS and following WNS were observed for LABO, LACI and LANO (Table 2).

Of the 71 sites sampled prior to and following WNS, there was an overall increase in activity for EPFU, LACI, and LANO (Table 3). We observed a decrease in LABO, MYLU, MYLE, MYSE, MYSO, and PESU activity following WNS at these sites (Table 3). However, based on correlation coefficients, there were no highly significant relationships between the changes in activity between any given species pairs except within *Myotis* spp. (Table 4).

4. Discussion

The extensive long term acoustic monitoring program on Fort Drum, spanning 15 years and encompassing both pre- and post-WNS periods, has provided a unique opportunity to assess changes and trends in bat activity and community structure

Table 2

Changes in echolocation activity pre-White-nose Syndrome (WNS) and post-WNS overall; early summer, pre-WNS and early summer, post-WNS; late summer, pre-WNS and late summer, post-WNS; early summer, pre-WNS and late summer, pre-WNS; and early summer, post-WNS and late summer, post-WNS for each species extant at Fort Drum Military Installation, New York between 2004 and 2017. Pre-WNS period includes years from 2004 to 2007, post-WNS period include years from 2008 to 2017. Summer periods included: early (15 May–15 July) and late (16 July onwards) representing parturition and then volancy when juvenile bats begin to be incorporated into the population. With (μ) mean estimate of activity, and $p < 0.05$ are significantly different (*). Species include: big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), and tri-colored bat (*Perimyotis subflavus*, PESU).

Activity between pre-WNS and post-WNS			
Species	μ Pre-WNS	μ Post-WNS	p-value
EPFU	27.70	14.40	<0.05*
LABO	11.77	5.69	0.58
LACI	11.25	19.45	<0.05*
LANO	7.09	7.96	<0.05*
MYLE	0.35	0.07	<0.0001*
MYLU	62.77	9.22	<0.0001*
MYSE	0.87	0.17	<0.0001*
MYSO	1.12	0.62	<0.0001*
PESU	5.24	1.02	<0.0001*
Activity between early summer (pre-WNS) and early summer (post-WNS)			
Species	μ Early Summer (pre-WNS)	μ Early Summer (post-WNS)	p-value
EPFU	4.71	8.67	0.43
LABO	0.57	2.24	0.56
LACI	2.57	10.55	0.65
LANO	1.29	5.96	0.31
MYLE	0.00	0.04	0.65
MYLU	68.57	6.22	<0.05*
MYSE	0.43	0.09	<0.05*
MYSO	0.71	0.34	<0.05*
PESU	1.00	0.56	<0.05*
Activity between late summer (pre-WNS) and late summer (post-WNS)			
Species	μ Late Summer (pre-WNS)	μ Late Summer (post-WNS)	p-value
EPFU	29.62	18.07	0.27
LABO	12.70	7.94	0.15
LACI	11.98	25.21	0.22
LANO	7.57	9.25	0.06
MYLE	0.38	0.10	<0.0001*
MYLU	62.29	11.14	<0.0001*
MYSE	0.90	0.22	<0.0001*
MYSO	1.15	0.79	<0.05*
PESU	5.60	1.32	<0.0001*
Activity between early summer (pre-WNS) and late summer (pre-WNS)			
Species	μ Early Summer (pre-WNS)	μ Late Summer (pre-WNS)	p-value
EPFU	4.71	29.62	0.10
LABO	0.57	12.70	<0.05*
LACI	2.57	11.98	<0.05*
LANO	1.29	7.57	<0.05*
MYLE	0.00	0.38	0.21
MYLU	68.57	62.29	0.28
MYSE	0.43	0.90	0.43
MYSO	0.71	1.15	0.96
PESU	1.00	5.60	0.39
Activity between early summer (post-WNS) and late summer (post-WNS)			
Species	μ Early Summer (post-WNS)	μ Late Summer (post-WNS)	p-value
EPFU	8.67	18.07	<0.0001*
LABO	2.24	7.94	<0.0001*
LACI	10.55	25.21	<0.0001*
LANO	5.96	9.25	<0.0001*
MYLE	0.04	0.10	<0.0001*
MYLU	6.22	11.14	<0.0001*
MYSE	0.09	0.22	<0.0001*
MYSO	0.34	0.79	<0.0001*
PESU	0.56	1.32	<0.0001*

Table 3

Change in activity between pre-White-nose Syndrome (WNS) and post-WNS at 71 sites sampled both in years prior to WNS (2004–2007) and years following WNS (2008–2017) at Fort Drum Military Installation, New York. Decrease in activity for a given species is represented by “-”. Species include: big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), and tri-colored bat (*Perimyotis subflavus*, PESU).

Species	Change in Activity by Site Night
EPFU	169.64
LABO	-93.47
LACI	908.30
LANO	643.28
MYLE	-19.08
MYLU	-3024.62
MYSE	-535.72
MYSO	-154.74
PESU	-164.48

Table 4

Correlation matrix of change in activity between pre-White-nose Syndrome (WNS) and post-WNS at 71 sites sampled both in years prior to WNS (2004–2007) and years following WNS (2008–2017) at Fort Drum Military Installation, New York. Species include: big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-ered bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), and tri-colored bat (*Perimyotis subflavus*, PESU).

	EPFU	LABO	LACI	LANO	MYLE	MYLU	MYSE	MYSO	PESU
EPFU	1.00
LABO	0.18	1.00
LACI	0.23	0.27	1.00
LANO	0.07	0.24	0.06	1.00
MYLE	.	0.06	-0.06	.	1.00
MYLU	.	0.29	-0.17	.	0.49	1.00	.	.	.
MYSE	.	.	-0.14	.	0.41	.	1.00	.	.
MYSO	0.06	.	.	.	0.66	0.53	0.30	1.00	.
PESU	.	0.13	0.14	-0.12	0.17	0.18	.	.	1.00

on a WNS-positive landscape. Moreover, these data can provide insight into how WNS may impact bats in the Midwest and the West, as WNS spreads. Although many studies have now documented the overarching effects of WNS on individual bat species (Frick et al., 2010; Dobony et al., 2011; Francl et al., 2012; Coleman et al., 2014a; Jachowski et al., 2014a; Powers et al., 2015; Ingersoll et al., 2016; Silvis et al., 2016; Langwig et al., 2017; Dobony and Johnson, 2018), few have examined trends in activity following disease outbreak and expansion onto the landscape over a similar duration or spatial scope (Brooks, 2011; Dzal et al., 2011). Our study, expanded on the initial work of Ford et al. (2011) and Jachowski et al. (2014a) that described the initial changes in activity both within species and among species, by looking at 10 years of acoustic data following WNS. Our results were consistent with our prediction and findings of others in the Northeast (Brooks, 2011; Dzal et al., 2011; Ford et al., 2011) that relative bat activity, based on species susceptibility to WNS, and overwintering strategies, i.e., hibernation or migration, would change between pre- and post-WNS years.

Our results show that *Myotis* spp., except MYLE, and also PESU at Fort Drum, had significant lower levels of activity at the beginning of the summer post-WNS as compared to pre-WNS. For WNS susceptible species, our results reflect the high level of mortality in winter hibernacula reported by Blehert et al. (2009) and Frick et al. (2010). Whereas activity increased between early and late summer prior to WNS for these species, following WNS, overall there was a reduction in number of calls between early and later summer pre-WNS for EPFU, MYLE, MYSE and PESU, a factor possibly associated with variable reproductive output and lowered recruitment observed for WNS-impacted species (Francl et al., 2012; Powers et al., 2015; Reynolds et al., 2016; Dobony and Johnson, 2018). Consistent with the findings of Ford et al. (2011) at Fort Drum, MYLU and MYSE, both overall activity and in pre- and post-volancy periods, was less in our study, reflecting the decreased population in the region and lower rates of juvenile volancy. Similarly, MYSO also showed an overall decline in activity although activity rates did not decrease through the summer season, perhaps indicating a higher level of reproductive success than MYLU and MYSE post-WNS at Fort Drum. Nonetheless, activity of MYLU did increase between early and late summers post-WNS towards the latter portion of our post-WNS sample years. We limited analysis to data collected only from the U.S. Fish and Wildlife Service suggested survey period and by also setting the end of June as our transition period between early and late summer. This is in contrast to Ford et al. (2011), where analyses included from late summer and early fall along with a mid-July volancy date may

have conflated posited reductions or stability in recruitment with the beginning of fall migration off the installation towards winter hibernacula or inclusion of migrants staging at Fort Drum prior to using nearby hibernacula. Although the overall decrease in activity between pre- and post-WNS years may indicate that reproduction and recruitment have been impacted (Frick et al., 2010; Dobony et al., 2011; Ford et al., 2011; Francl et al., 2012); the small increases between early and late summer post-WNS activity does confirm some occurrence of successful reproduction on the Fort Drum landscape. Moreover, of the MYLU monitored at an artificial roost structure on the installation, returning adults have improved in their physiological condition since 2010 and successful reproduction and recruitment (although variable) has been apparent there and other areas of the Northeast (Dobony and Johnson, 2018). It remains to be determined whether this represents some level of population stability that may facilitate population growth or is a limited site-occurrence and therefore warrants continued monitoring.

As predicted, we saw lower levels of activity across the summer for LANO and LACI prior to WNS than observed with the other species. We believe this is attributable to the combination of a lower sampling effort pre-WNS and also a lower detection probability for LANO and LACI (Ford et al., 2011). Although these species are present on Fort Drum, they may not actively use the landscape in a fashion analogous to *Myotis* spp. that these acoustic samples originally were designed to target (Cryan, 2003; Ford et al. 2005, 2011). Following WNS, sampling effort across Fort Drum increased to more effectively and efficiently monitor for declining species, such as MYLU, MYSE and MYSO (Coleman et al., 2014a, b). Coincidentally, this increase in sampling effort could have allowed for greater detection of LANO and LACI post-WNS as more upland, open habitats such as open fields and newly regenerating forest harvest areas favored by these species (Ford et al., 2005) were surveyed than in the initial pre-WNS surveys. As a result, we observed that activity levels for LANO, LACI increased throughout the whole summer and between the early and late summer periods and post-WNS. Activity levels for PESU mirrored the same patterns elsewhere in the East where populations have declined precipitously (Pettit and O'Keefe, 2017; Powers et al., 2015).

Our results were partially consistent with our second hypothesis, whereby we predicted that migratory bats, and those minimally impacted by WNS, might show a positive response post-WNS. Both LACI and LANO showed higher levels of activity post-WNS compared to pre-WNS. Although EPFU are less susceptible to WNS, as a minimal communal hibernator and larger body size (Frank et al., 2014), this species showed signs of negative impacts across the landscape of Fort Drum within the context of this study more than observed elsewhere in the East (Agosta, 2002; Foley et al., 2011; Frick et al., 2015; Silvis et al., 2016). Conversely, LANO and LACI are migratory species and not known to be impacted by WNS. Despite their increase at Fort Drum, these species have been shown to be highly susceptible to wind-energy related mortality along their Appalachian Mountain migratory flyways to the south and locally near Fort Drum (Arnett et al., 2008; Cryan and Barclay, 2009; Arnett and Baerwald, 2013). If wind-energy production did not occur in a post-WNS landscape as it did pre-WNS, it is possible we might have observed larger increases for these particular species (Ford et al., 2011; Arnett and Baerwald, 2013). Also owing to being unaffected by WNS, LABO activity between pre-WNS and post-WNS was not significantly different, and we posit that post-WNS, the species' detection probability has increased as populations of competing species have declined (Ford et al., 2011; Jachowski et al., 2014a; Turner et al., 2015).

In addition to mortality and population reduction of affected species, WNS may indirectly affect the broader bat community structure (Jachowski et al., 2014a; Turner et al., 2015). Consequently, the location of a study area and the extant bat community is an important consideration in the role in which WNS impacts lead to changes in community structure, as the assemblage of bat species and community composition changes both across latitudinal and longitudinal gradients. Individual bat species can become suppressed by the rapid increase of other bat species (Haupt and Schmidt, 2007; Ford et al., 2011), and although our results show an overall increase in the activity for both EPFU and LABO, there does not seem to be any indication of community displacement between *Myotis* spp. and non WNS-impacted species, such as LABO, relative to trends in nightly activity. At sites sampled both pre- and post-WNS, our results point to an increase in activity of EPFU, LACI, and LANO, however, the increase in activity for these species was not related to the decrease in other species. Post-WNS niche partitioning has been suggested at both Fort Drum and other areas in the Northeast (Frick et al., 2010; Jachowski et al., 2014a; Turner et al., 2015). Our results do not fully support this in the context of our analysis using nightly data identified with automated software rather than hourly and habitat specific data that was analyzed using visual vetting (Jachowski et al., 2014a). Additionally, it is important to note that the inclusion of nights with inclement weather in the later years (2012–2017) in conjunction with WNS, could have resulted in causing further negative bias in recording echolocation passes, though not biologically meaningful relative to WNS impact. At our installation-wide analysis that mirrors the scale that managers and regulators use for their decision-making, we could not discern the same patterns of niche partitioning or community displacement that have been shown with similar bat communities (Frick et al., 2010; Jachowski et al., 2014a; Turner et al., 2015). Still, this is not to imply that within the nightly period, WNS-induced temporal niche relaxation as described by Jachowski et al. (2014a) is not occurring. At present, the impacts of WNS, when extended to community composition at the landscape level, may still be too subtle to detect widespread bat species displacement or niche use change on a nightly level. However, further monitoring and analysis seems prudent, as WNS persists on the landscape causing evermore increasing and notable changes to bat community structure.

5. Conclusion

By comparing distribution and activity trends of bat species pre- and post- WNS, researchers have been able to document how once common species of bats have become functionally extirpated from the landscape due to WNS (Frick et al., 2010;

Brooks, 2011), with resulting changes and impacts on bat community structure through time (Jachowski et al., 2014a). Our work, over a longer duration provides greater insights into the impacts of WNS on the Fort Drum bat community that is typical of much of the northeastern USA. Whereas several common WNS-susceptible species have been greatly reduced in numbers, acoustic evidence has documented their persistence in the landscape. Further, at the landscape-scale of our study, conclusive evidence in niche space-use change was equivocal at the nightly level even with the drastic decreases of these once common and numerous species. Moreover, efforts to better calibrate acoustic data with assessments of MYLU productivity at Fort Drum (Dobony and Johnson, 2018), as well as local and regional netting data to develop species-specific periods of pre- and post-volancy enhance the utility of acoustic data for understanding potential changes in species' status and productivity.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00633>.

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