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Shifts in Assemblage of Foraging Bats at Mammoth Cave National Park following Arrival of White-nose Syndrome

Marissa M. Thalcken¹, Michael J. Lacki^{1,*}, and Joseph S. Johnson²

Abstract - The arrival of white-nose syndrome (WNS) to North America in 2006, and the subsequent decline in populations of cave-hibernating bats have potential long-term implications for communities of forest-dwelling bats in affected regions. Severe declines in wintering populations of bats should lead to concomitant shifts in the composition and relative abundance of species during the staging, maternity, and swarming seasons in nearby forested habitats. We examined capture rates of bats collected in mist nets from 2009 to 2016 to evaluate summer patterns in abundance of species pre- and post-arrival of WNS to Mammoth Cave National Park, KY. The data demonstrated a significant change in overall relative abundances. *Myotis septentrionalis* (Northern Long-eared Myotis) was the most commonly captured species pre-WNS but declined to 18.5% of its original abundance. *Nycticeius humeralis* (Evening Bat), uncommonly caught in mist nets pre-WNS, demonstrated the largest increase in capture success following arrival of WNS to the Park, followed by *Eptesicus fuscus* (Big Brown Bat) and *Lasiurus borealis* (Eastern Red Bat). These data suggest that losses of cave-hibernating bats to WNS may be leading to a restructuring of foraging bat assemblages in nearby forested habitats, with species less affected by WNS potentially exploiting niche space vacated by bats succumbing to infection with WNS.

Introduction

Species are strongly influenced by environmental changes, including natural and anthropogenic disturbance. These events can act on a broad geographic scale (e.g., climate change), or on regional and local scales (e.g., habitat destruction, deforestation, and fragmentation) (Habel et al. 2015, Karl et al. 2009). Changes in land use have been a primary driver in the loss of biodiversity worldwide (Meyer and Kalko 2008); habitat generalists and highly mobile species are most likely to avoid extirpation after extensive environmental impacts (Habel et al. 2015). Shifts in species assemblages at the community level, however, have been more difficult to document, due to the lack of historical data and scarcity of information on entire communities.

Many bat species in eastern North America are facing threats from anthropogenic disturbances (e.g., habitat fragmentation, development of wind-power facilities, etc.) and the emerging disease white-nose syndrome (WNS). White-nose syndrome is caused by the fungus *Pseudogymnoascus destructans* (Gargas, Trest, Christensen, Volk, and Blehert) and is responsible for regional population collapses in many cave-hibernating species of bats in eastern North America (Hoyt et al. 2016, Ingersoll et al. 2016). Since WNS was discovered in 2006, losses of hibernating

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bats total in the millions, potentially restructuring summer communities of bats in affected regions (Jachowski et al. 2014).

Measurable shifts in community composition are usually precipitated by a disturbance that significantly alters existing habitats (Fukui et al. 2011, Habel et al. 2015, Johnston and Maceina 2008, Scott and Helfman 2001). However, declines in local bat populations due to WNS are not necessarily accompanied by loss or degradation of forested habitat. Non-impacted species likely experience reduced levels of interspecific competition for foraging and roosting resources, permitting them to occupy niches in forests vacated by WNS-affected bats (Jachowski et al. 2014).

Studies have documented declines in summer populations of several species in the eastern US due to WNS (Francel et al. 2012, Reynolds et al. 2016). For example, the arrival of WNS in New Hampshire resulted in significant declines in overall abundance of local bats during summer (Moosman et al. 2013). Reductions in capture rates varied by species, with *Myotis lucifugus* (Le Conte) (Little Brown Myotis) and *M. septentrionalis* (Trouessart) (Northern Long-eared Myotis) exhibiting the largest declines and *Eptesicus fuscus* (Palisot de Beauvois) (Big Brown Bat) showing the least amount of change (Moosman et al. 2013). Ultimately, the community of bats in New Hampshire was reduced from 7 species before the onset of WNS to effectively 4 species on the landscape after WNS. Francel et al. (2012) postulated that an ecological release due to the decline in species of *Myotis* could signal permanent shifts in local bat assemblages.

It is presently unclear how summer bat communities will reorganize in the post-WNS period in eastern North America. Populations of WNS-impacted species migrate from hibernacula in spring to maternity sites and foraging grounds, where they remain for the summer and early autumn. Their absence in forests has potential for long-term restructuring of bat assemblages during the summer maternity season, especially in severely affected areas. We hypothesized that the decline of wintering bat populations in Mammoth Cave National Park, KY, particularly species of *Myotis* (Lacki et al. 2015), should lead to shifts in the composition and relative abundance of bat species in forests in the park during the active season. Species with similar ecological requirements, but not affected by WNS, should find foraging and roosting resources more readily available following collapse of WNS-affected populations. We used data from mist-netting captures, collected before and after arrival of WNS in the park, to assess temporal changes in the bat assemblage.

Study Area and Methods

Mammoth Cave National Park (MCNP) is about 212 km² in extent and is situated within the Green River Valley in south-central Kentucky (37°11'N, 86°6'W). The park lies on karst topography, with much of the terrain in and around the park pitted by depressions or sinkholes. Thus, despite an average rainfall of about 130 cm annually, few surface streams exist, other than the Green and Nolin rivers, and most water drains beneath the ground (Livesay 1953). Mammoth Cave National Park varies in elevation from 128 m to 281 m above sea level and has a mean temperature from April to August of 21.5 °C (Weather Underground 2016).

Vegetation on MCNP is dominated by second-growth *Quercus* (oak)–*Carya* (hickory) forest (USNPS 2016). The area is a transitional zone between open grasslands and oak–hickory forests to the west and mesophytic forests to the east. The park is situated between colder northern climates and sub-tropical climates to the south. The different vegetation types create a mosaic of habitats across the park that support an array of flora and fauna (USNPS 2016). In 2002, a management plan involving prescribed fire was established to reduce fuel loads and restore the forest to pre-settlement conditions. Since then, over 25% of the park has been burned using prescribed fires during the non-growing season (Lacki et al. 2014).

Mammoth Cave National Park is home to 8 species of bats year-round: *Corynorhinus rafinesquii* (Lesson) (Rafinesque’s Big-eared Bat), Big Brown Bat, *Myotis grisescens* (A.H. Howell) (Gray Bat), *M. leibii* (Audubon and Bachman) (Eastern Small-footed Myotis), Little Brown Myotis, Northern Long-eared Myotis, *M. sodalis* (Miller and G.M. Allen) (Indiana Bat), and *Perimyotis subflavus* (F. Cuvier) (Tricolored Bat). During the migratory or summer seasons, the park is home to 5 other species of tree-roosting bats: *Lasiurus borealis* (Müller) (Eastern Red Bat), *L. cinereus* (Palisot de Beauvois) (Hoary Bat), *L. seminolus* (Rhoads) (Seminole Bat), *Lasionycteris noctivagans* (Le Conte) (Silver-haired Bat), and *Nycticeius humeralis* (Rafinesque) (Evening Bat).

We conducted bat surveys on 78 nights from 2009 through 2016, except 2012, when no netting took place. We collected data 25 July–27 August 2009, 10 June–25 July 2010, 10 May–29 June 2011, 19 May–28 July 2013, 21–27 May 2014, 8 May–22 September 2015, and 10 April–14 July 2016. We captured bats, for subsequent identification to species, using mist-nets that were 6–18 m in length and 6–9 m in height (Avinet, Dryden, NY). Field methods included adherence to decontamination protocols prescribed by the US Fish and Wildlife Service (USFWF 2016).

We placed mist nets at 25 sites located throughout the park. Overall sampling intensity was 2.7 ± 0.2 (SE) nets per night. Netting frequencies were 1–3 times per year per site, except 2 ephemeral ponds at which netting occurred either 5 or 6 times in 2016. To minimize the potential of bats becoming net averse, no netting occurred on consecutive nights at any site (Winhold and Kurta 2008).

For our first comparison, 6 of the 25 locations provided a set of focal sites that were sampled both pre- (9 nights) and post-WNS (33 nights). We included these data in direct comparisons of change in relative abundance of species due to the disease. The focal sites comprised 2 upland ephemeral ponds, a permanent mid-slope pond, a back-country road intersection, and the vicinity of 2 cave entrances. All focal sites were surrounded by mature hardwood forest. Three of the locations were impacted by prescribed fire—Temple Hill Pond (2009), Crystal Cave Pond (2011), and the road crossing (2008).

We used a chi-square test of independence to compare the pre-WNS (2009–2011) and post-WNS (2014–2016) relative abundance of bat species at the focal sites, and relied on the relative contribution (%) to the chi-square score, to identify which species were likely driving the overall changes (Daniel and Cross 2013, The Pennsylvania State University 2017). We did not include data for 2013 in this

analysis because they were collected the summer immediately following discovery of WNS in the park, and the extent of WNS effects was unclear at that time (Lacki et al. 2015). Due to the number of years involved and inherent differences in mist-netting protocols used over time, we calculated expected capture probabilities for the pre- and post-WNS periods based on the level of netting effort that took place, which allowed us to account for both hours sampled and total net-surface area deployed each night (i.e., $m^2 \cdot h$ = square meters of net x number of hours left open). We summed these data across sampling nights pre- and post-WNS, and used the percentage of total sampling effort by period to calculate expected capture probabilities for the chi-square analysis.

For our second comparison, we added data from the remaining 19 sites to those from the 6 focal sites, to obtain 36 more nights of netting from 2013 to 2016. These 19 sites included an additional 11 ephemeral ponds, 5 back-country roads or trails, the vicinity of 1 cave entrance, and 2 natural springs. From these data, collected at 25 total sites, we calculated capture rates using a more traditional method, based on captures per net-night. We examined data for 8 species of bats and tested for change in intraspecific capture rates over the 7 y of sampling using single-factor ANOVAs (PROC GLM; SAS 9.4, SAS Inc., Cary, NC). We employed a Fisher's LSD multiple-comparison procedure to identify specific differences among years.

We also combined all captures, excluding 2013, into pre-WNS (2009–2011) and post-WNS (2014–2016) groupings. We qualitatively compared species totals between these 2 periods as a final metric to assess possible changes in the assemblage of bat species in the park resulting from WNS.

Results

During the pre-WNS period (2009–2011), overall capture rate at the 6 focal sites was 1.7 bats/net-night on 9 calendar nights of netting, whereas the overall rate of capture after WNS reached the park (2014–2016) at these same sites was 1.54 bats/net-night on 33 nights of netting. The number of bats captured for these comparisons was 390 (Table 1). Netting from focal sites in 2013 and the additional 19 capture sites from all years, produced another 284 bats collected over 36 nights of netting.

At the 6 focal sites, the effect of WNS-period on relative species abundance was significant ($\chi^2 = 337$, $P < 0.001$, $df = 7$; Table 1). Our analysis was based on a total netting effort of 2892.8 $m^2 \cdot h$ pre-WNS and 8750.6 $m^2 \cdot h$ post-WNS; thus, expected capture probabilities used for analysis were 0.248 pre-WNS and 0.752 post-WNS. The Northern Long-eared Myotis declined from the most frequently captured bat before arrival of WNS to the 4th most-frequently captured species post-WNS at the focal sites. This decline in relative abundance, despite greater nightly sampling effort post-WNS, accounted for 87.2% of the total chi-square score. The next highest contribution was from Rafinesque's Big-eared Bat, at only 6.8%.

General linear models (GLM) analyses of the effect of year on capture rates across all 25 netting sites were significant for Rafinesque's Big-eared Bat ($F_{6,44} = 5.35$, $P < 0.0003$; Fig. 1a) and Northern Long-eared Myotis ($F_{6,44} = 6.42$, $P < 0.0001$;

Fig. 1b), with weak support for changes in capture rate of the Evening Bat ($F_{6,44} = 2.02$, $P = 0.08$; Fig. 1c). Capture rate for the Northern Long-eared Myotis was highest in 2010 but lowest in 2015 and 2016 ($P < 0.05$). Fisher's LSD also indicated significantly lower capture rates for Rafinesque's Big-eared Bat in post-WNS years ($P < 0.05$). Fisher's LSD suggested that capture rates of Evening Bats were significantly higher in 2014 and 2016, both post-WNS, compared with all other years of sampling ($P < 0.05$).

Big Brown Bat ($F_{6,44} = 0.51$, $P = 0.79$), Eastern Red Bat ($F_{6,44} = 0.72$, $P = 0.64$), Little Brown Myotis ($F_{6,44} = 0.78$, $P = 0.59$), and Tricolored Bat ($F_{6,44} = 0.69$, $P = 0.66$) showed no detectable change in capture rate over the 7-y period. However, Big Brown Bats exhibited large variations in capture rates in 2013 and 2015, when mean capture rates of these bats appeared to increase (Fig. 1d). We captured too few individuals of other species during pre-WNS sampling (2009–2011) for statistical analysis (Eastern Small-footed Myotis: $n = 3$; Gray Bat: $n = 0$; Indiana Bat; $n = 0$; and Silver-haired Bat, $n = 0$).

Totals for all bats captured by species from all 25 sites and all years confirmed the precipitous decline in Northern Long-eared Myotis following arrival of WNS (Fig. 2) and provided qualitative support for possible increases in relative abundance of Evening Bats, Big Brown Bats, and Eastern Red Bats; the latter 3 species were the most frequently captured bats post-WNS across the park.

Discussion

Mist-netting captures during the progression of WNS in MCNP suggested that the fungal disease was associated with declines of some species. Both the chi-square test of independence on relative abundance at the 6 focal sites and

Table 1. Capture rates (bats/net-night) and numbers of bats captured by species pre- (2009–2011) and post-arrival (2014–2016) of WNS to Mammoth Cave National Park, Kentucky. Percent contribution to the chi-square score ($P < 0.001$) is also presented. Data are based on 6 focal capture sites at which netting occurred both pre- and post-WNS.

Species*	Pre-WNS		Post-WNS		% contribution
	Capture rate	# captured	Capture rate	# captured	
CORA	0.24	29	0.21	26	6.8
EPFU	0.08	10	0.16	19	0.4
LABO	0.07	8	0.31	37	0.4
MYLE	0.03	3	0.14	17	0.3
MYLU	0.03	4	0.11	13	0.1
MYSE	1.08	130	0.20	24	87.2
NYHU	0.06	7	0.34	41	0.8
PESU	0.11	13	0.07	9	4.0
Total	1.70	204	1.54	186	100.0

*Species abbreviations are as follows: Rafinesque's Big-eared Bat (CORA), Big Brown Bat (EPFU), Eastern Red Bat (LABO), Eastern Small-footed Myotis (MYLE), Little Brown Myotis (MYLU), Northern Long-eared Myotis (MYSE), Evening Bat (NYHU), and Tricolored Bat (PESU).

GLM analysis of annual capture rates at all 25 sites demonstrated drops in relative abundance and capture success of the Northern Long-eared Myotis over time (Table 1; Figs 1b, 2). Rafinesque’s Big-eared Bat showed a similar decline (based on all 25 sites) but did not show a decrease in relative abundance at the focal sites (Figs. 1a, 2). Relative abundance of other species captured at the focal sites showed very little change with arrival of WNS, with each contributing slightly ($\leq 4\%$) to the overall chi-square score; however, based on complete netting data for all 25 sites, we found that several species were captured in numerically higher numbers after arrival of WNS including Big Brown Bat, Eastern Red Bat, Gray Bat, Eastern Small-footed Myotis, Little Brown Myotis, Indiana Bat, Evening Bat, and Tricolored Bat (Fig. 2). Some minor shifts can be attributed to stochastic effects or the greater overall netting effort over a wider range of sites post-WNS, but the increases in captures for Evening Bats, Big Brown Bats, and Eastern Red Bats were pronounced and suggestive of possible shifts in species abundance. Over the years of this study, netting occurred at various locations in the park, so these patterns should be interpreted with caution because local effects due to the netting

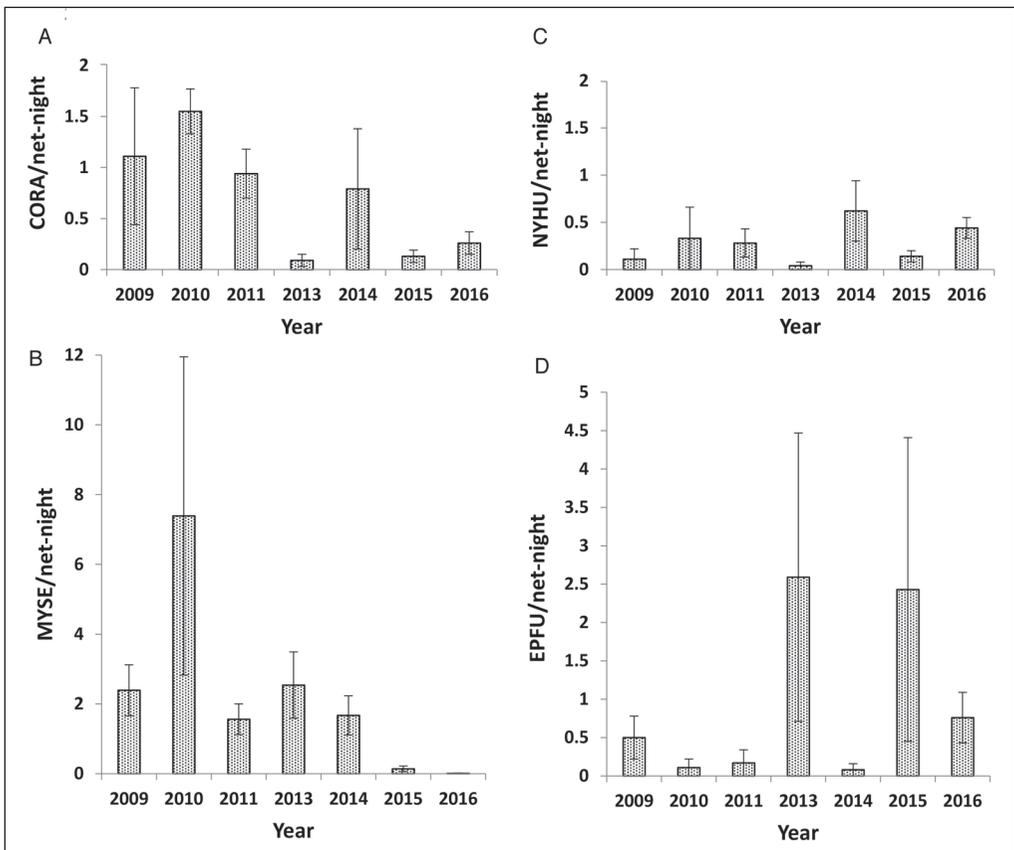


Figure 1. Comparisons of capture rate across all 25 netting sites for: (a) Rafinesque’s Big-eared Bat (CORA), (b) Northern Long-eared Myotis (MYSE), (c) Evening Bat (NYHU), and (d) Big Brown Bat (EPFU) at Mammoth Cave National Park, KY, over a 7-y period, 2009–2016.

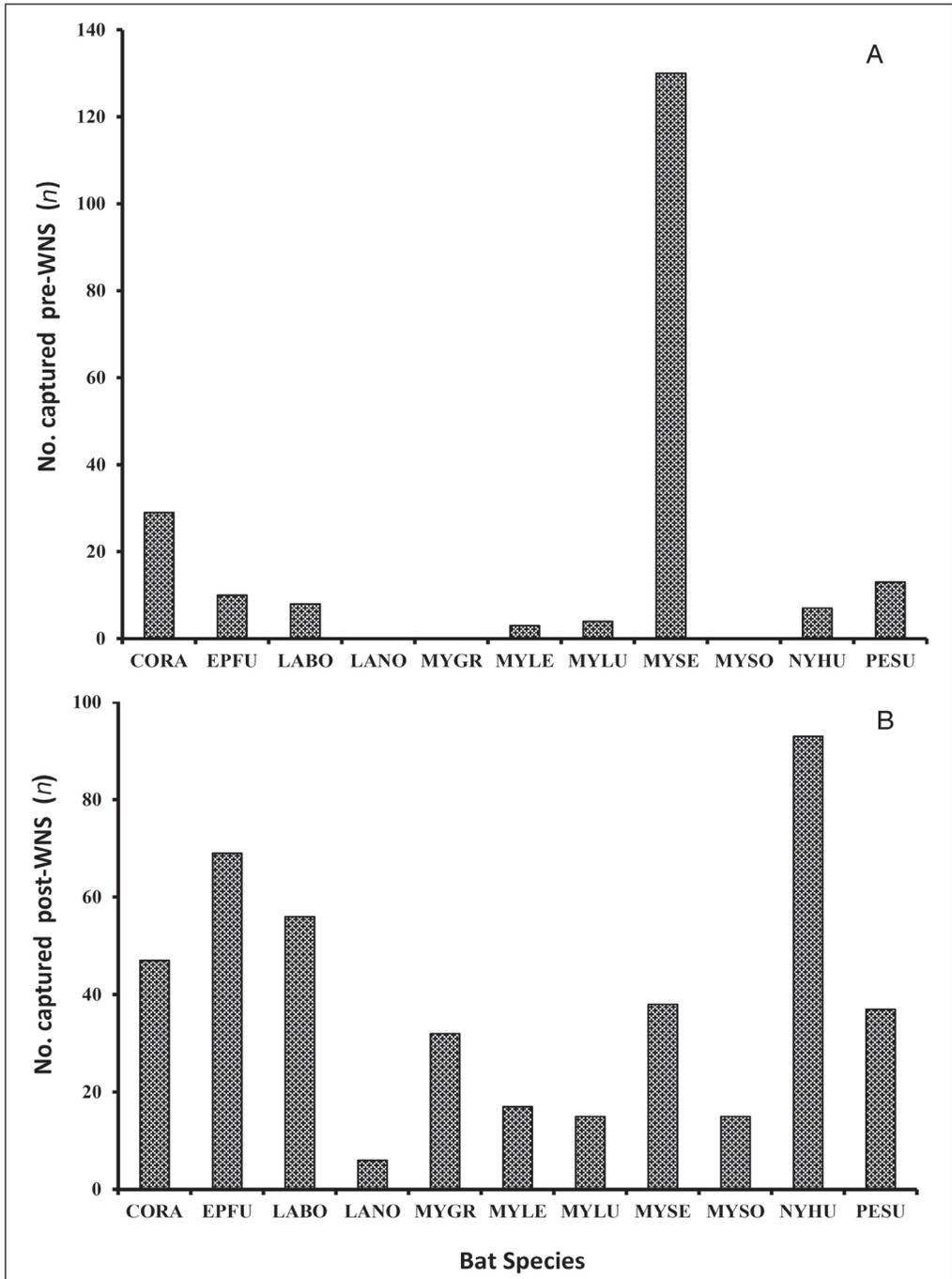


Figure 2. Totals for all species captured at 25 mist-netting sites (a) before the arrival of WNS, and (b) after the onset of WNS at Mammoth Cave National Park, KY. Species include: Rafinesque’s Big-eared Bat (CORA), Big Brown Bat (EPFU), Eastern Red Bat (LABO), Silver-haired Bat (LANO), Gray Bat (MYGR), Eastern Small-footed Myotis (MYLE), Little Brown Myotis (MYLU), Northern Long-eared Myotis (MYSE), Indiana Bat (MYSO), Evening Bat (NYHU), and Tricolored Bat (PESU).

sites that were chosen within a particular year cannot be ruled out. Nevertheless, the results of our mist-netting surveys are comparable to evidence from other states, indicating a decline in summer populations of the Northern Long-eared *Myotis* following exposure to WNS (Francl et al. 2012, Moosman et al. 2013, Reynolds et al. 2016), but differ from those studies, which did not report associated increases in abundance of other species.

Although considerable overlap in habitat use can occur, many species of bats partition niche space, which maximizes resource use within a habitat (Patterson et al. 2003). For example, bats in forests partition resources based on preferences for cluttered versus uncluttered foraging space (Law et al. 2015) and for roosting in trees of varying conditions of decay (Barclay and Kurta 2007, Kunz and Lumsden 2003). A release from competitive exclusion could possibly account for the shift in relative abundance of Evening Bats after the onset of WNS, and we suggest that Evening Bats have benefited from increased access to roosting structures, which were previously unavailable to them, due to occupation by a formerly abundant species, the Northern Long-eared *Myotis*. During the maternity season in South Carolina, Missouri, and Arkansas, female Evening Bats roosted in cavities of trees that were in various stages of decay (Boyles and Robbins 2016, Hein et al. 2009, Istvanko et al. 2016). Much of the research completed on roosting preferences of the Northern Long-eared *Myotis* during summer suggests potential overlap in preferences for roosting sites with that of Evening Bats. Female Northern Long-eared *Myotis* commonly roost under exfoliating bark or in cavities and crevices of dead and live trees (Broders and Forbes 2004, Carter and Feldhamer 2005, Lacki et al. 2009, Silvis et al. 2015, Timpone et al. 2010). This scenario, though, is complicated by evidence for expansion of the geographic distribution of the Evening Bat along the northern limits of its range, which may be caused by climate change (Auteri et al. 2016). Moreover, Evening Bats readily use roosting sites in forests that have been burned (Boyles and Aubrey 2006), and it is likely that recent prescribed burns also have made conditions more suitable for this species at MCNP.

We detected no difference in yearly capture rates of Big Brown Bats (Fig. 1d), despite an apparent increase in the relative proportion of these bats in mist-netting captures following arrival of WNS. Big Brown Bats in other geographic locations have remained common in forested landscapes following exposure to WNS (Ford et al. 2011, Francl et al. 2012, Reynolds et al. 2016). Furthermore, Big Brown Bats are larger than many cave-hibernating bats in eastern North America and likely possess sufficient fat stores to enhance their overwinter survival, regardless of WNS exposure, relative to smaller-sized species of *Myotis* and *Perimyotis* (Frank et al. 2014, Lacki et al. 2015, Moore et al. 2017). Although we did not detect significant increases in Big Brown Bats, that species did experience an ecological release following WNS-related declines of the Little Brown *Myotis* near Fort Drum, NY (Ford et al. 2011). Those authors postulated that removal of another previously common species due to WNS, such as the Northern Long-eared *Myotis*, would prompt additional changes in habitat use and frequency of occurrence of species remaining in the region (Ford et al. 2011).

Our results indicated that Eastern Red Bats were captured in mist nets in relatively higher numbers compared to most species following arrival of WNS to the park. Eastern Red Bats commonly roost in the foliage of trees (Hutchinson and Lacki 2000, Limpert et al. 2007, Mormann and Robbins 2007, O’Keefe et al. 2009) rather than in crevices or beneath bark; thus, it is not plausible that Eastern Red Bats benefit from roosting spaces vacated by the Northern Long-eared Myotis. Dietary studies, however, have shown a great deal of overlap in prey of forest-dwelling insectivorous bats in eastern North America, including the Eastern Red Bat and Northern Long-eared Myotis, both of which feed extensively on moths (Brack and Whitaker 2001, Carter et al. 2003, Clare et al. 2009, Dodd et al. 2012, Feldhamer et al. 2009, Whitaker 2004). Before the arrival of WNS, the Northern Long-eared Myotis was an abundant species on the park landscape (Lacki et al. 2015), and with the disappearance of Northern Long-eared Myotis, the Eastern Red Bat may now be foraging on populations of moths previously unavailable due to interference and interspecies competition with the formerly abundant Northern Long-eared Myotis. Northern Long-eared Myotis is a gleaning bat (Faure et al. 1993) and takes only some of its prey in flight (Dodd et al. 2012), so it is difficult to fully assess the extent to which Eastern Red Bats might benefit from the decline of Northern Long-eared Myotis.

General linear model analysis indicated that, over the 7-y sampling period, capture rates of Rafinesque’s Big-eared Bat declined, especially in 2013, 2015, and 2016 (Fig. 1a). Reasons for this finding are unclear. Park officials continually monitor summer colonies of Rafinesque’s Big-eared Bat and have noted no difference in colony sizes since the arrival of WNS in 2013 (S. Thomas, USNPS, Mammoth Cave, KY, pers. comm.). Susceptibility of Rafinesque’s Big-eared Bat to WNS does not appear to be strong; physiological and behavioral traits during winter (e.g., shallow torpor and frequent roost switching) likely render it less vulnerable to WNS infection (Johnson et al. 2012).

In general, the susceptibility of a species to WNS is largely dependent on whether it is a cave-hibernator or migrates to other habitats to overwinter. For species of *Myotis*, hibernating in caves risks exposure to WNS. With drastic declines in populations of WNS-affected species, secondary impacts, such as lowered reproductive success, can be amplified, leading to reduced levels of recruitment and a decreased ability for populations to recover from WNS (Thogmartin et al. 2013). This potential for slow recovery will likely cause species like the Northern Long-eared Myotis to remain at reduced population numbers during the summer maternity season for years, if not indefinitely. Responses by other bats to this change in abundance of a previously common species are likely, and we believe the data presented here indicate these responses are already occurring on MCNP. We suggest that impacts of WNS and subsequent species responses are plausible explanations for the shifts in the bat assemblage that we examined. We believe that these data represent empirical evidence to support the prediction of novel restructuring of communities of forest bats following WNS infestation (Jachowski et al. 2014). It is unknown whether these patterns in species abundance are temporary or whether

they reflect permanent and lasting shifts in relative species abundance. Monitoring bat populations both regionally and at local scales is a necessary step in developing conservation efforts to target recovery of species affected by WNS.

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Literature Cited

- Auteri, G., A. Kurta, T. Cooley, and J. Melotti. 2016. A new northern record of the Evening Bat in Michigan. *Michigan Birds and Natural History* 23:147–149.
- Barclay, R.M.R., and A. Kurta. 2007. Ecology and behavior of bats roosting in tree cavities and under bark. Pp. 17–59, *In* M.J. Lacki, J.P. Hayes, and A. Kurta (Eds.). *Bats in Forests: Conservation and Management*. Johns Hopkins University Press, Baltimore, MD. 329 pp.
- Boyles, J.G., and D.P. Aubrey. 2006. Managing forests with prescribed fire: Implications for a cavity-dwelling bat species. *Forest Ecology and Management* 222:108–115.
- Boyles, J.G., and L.W. Robbins. 2016. Characteristics of summer- and winter-roost trees used by Evening Bats (*Nycticeius humeralis*) in southwestern Missouri. *American Midland Naturalist* 155:210–220.
- Brack, V., and J.O. Whitaker Jr. 2001. Foods of the Northern Myotis, *Myotis septentrionalis*, from Missouri and Indiana, with notes on foraging. *Acta Chiropterologica* 3:203–210.
- Broders, H.G., and G. Forbes. 2004. Interspecific and intersexual variation in roost-site selection of Northern Long-eared and Little Brown Bats in the Greater Fundy National Park ecosystem. *Journal of Wildlife Management* 68:602–610.
- Carter, T.C., and G. Feldhamer. 2005. Roost-tree use by maternity colonies of Indiana Bats and Northern Long-eared Bats in southern Illinois. *Forest Ecology and Management* 219:259–268.
- Carter, T.C., M.A. Menzel, S.F. Owen, J.W. Edwards, J.M. Menzel, and W.M. Ford. 2003. Food habits of 7 species of bats in the Allegheny Plateau and Ridge and Valley of West Virginia. *Northeastern Naturalist* 10:83–88.
- Clare, E.L., E.E. Fraser, H.E. Braid, M.B. Fenton, and P.D.N. Hebert. 2009. Species on the menu of a generalist predator, the Eastern Red Bat (*Lasiurus borealis*): Using a molecular approach to detect arthropod prey. *Molecular Biology* 18:2532–2542.
- Daniel, W.W., and C.L. Cross. 2013. *Biostatistics: A Foundation for Analysis in the Health Sciences*. John Wiley and Sons, Hoboken, NJ. 960 pp.
- Dodd, L.E., E.G. Chapman, J.D. Harwood, M.J. Lacki, and L.K. Rieske. 2012. Identification of prey of *Myotis septentrionalis* using DNA-based techniques. *Journal of Mammalogy* 93:1119–1128.

- Faure, P.A., J.H. Fullard, and J. W. Dawson. 1993. The gleaning attacks of the Northern Long-eared Bat, *Myotis septentrionalis*, are relatively inaudible to moths. *Journal of Experimental Biology* 178:173–189.
- Feldhamer, G.A., T.C. Carter, and J.O. Whitaker Jr. 2009. Prey consumed by eight species of insectivorous bats from southern Illinois. *American Midland Naturalist* 162:43–51.
- Ford, W.M., E.R. Britzke, C.A. Dobony, J.L. Rodrigue, and J.B. Johnson. 2011. Patterns of acoustical activity of bats prior to and following white-nose syndrome occurrence. *Journal of Fish and Wildlife Management*. 2:125–134.
- Francel, K.E., W.M. Ford, D.W. Sparks, and V. Brack Jr. 2012. Capture and reproductive trends in summer bat communities in West Virginia: Assessing the impact of white-nose syndrome. *Journal of Fish and Wildlife Management* 3:33–42.
- Frank, C.L., A. Michalski, A.A. McDonough, M. Rahimian, R.J. Rudd, and C. Herzog. 2014. The resistance of a North American bat species (*Eptesicus fuscus*) to white-nose syndrome (WNS). *PLoS ONE* 9:e113958.
- Fukui, D., T. Hirao, M. Murakami, and H. Hirakawa. 2011. Effects of treefall gaps created by windthrow on bat assemblages in a temperate forest. *Forest Ecology and Management* 261:1546–1552.
- Habel, J.C., A. Segerer, W. Ulrich, O. Torchyk, W. Weisser, and T. Schmitt. 2015. Butterfly community shifts over two centuries. *Conservation Biology* 30:754–762.
- Hein, C.D., K.V. Miller, and S.B. Castleberry. 2009. Evening Bat summer roost-site selection on a managed pine landscape. *Journal of Wildlife Management* 73:511–517.
- Hoyt, J.R., K.E. Langwig, K. Sun, G. Lu, K.L. Parise, T. Jiang, et al. 2016. Host persistence or extinction from emerging infectious disease: Insights from white-nose syndrome in endemic and invading regions. *Proceedings of the Royal Society B* 283:20152861.
- Hutchinson, J.T., and M.J. Lacki. 2000. Selection of day roosts by Red Bats in mixed mesophytic forests. *Journal of Wildlife Management* 64:87–94.
- Ingersoll, T.E., B.J. Sewall, and S.K. Amelon. 2016. Effects of white-nose syndrome on regional population patterns of three hibernating bat species. *Conservation Biology* 30:1048–1059.
- Istvanko, D.R., T.S. Risch, and V. Rolland. 2016. Sex-specific foraging habits and roost characteristics of *Nycticeius humeralis* in north-central Arkansas. *Journal of Mammalogy* 97:1336–1344.
- Jachowski, D.S., C.A. Dobony, L.S. Coleman, W.M. Ford, E.R. Britzke, and J.L. Rodrigue. 2014. Disease and community structure: White-nose syndrome alters spatial and temporal niche partitioning in sympatric bat species. *Diversity and Distributions* 20:1002–1015.
- Johnson, J.S., M.J. Lacki, S.C. Thomas, and J.F. Grider. 2012. Frequent arousals from winter torpor in Rafinesque's Big-eared Bat (*Corynorhinus rafinesquii*). *PLoS ONE* 7(11):e49754.
- Johnston, C.E., and M.J. Maceina. 2008. Fish-assemblage shifts and species declines in Alabama, USA streams. *Ecology of Freshwater Fish* 18:33–40.
- Karl, I., T. Schmitt, and K. Fischer. 2009. Genetic differentiation between alpine and lowland populations of a butterfly is related to PGI enzyme genotype. *Ecography* 32:488–496.
- Kunz, T.H., and L.F. Lumsden. 2003. Ecology of cavity and foliage roosting bats. Pp. 3–19, *In* T.H. Kunz and M.B. Fenton (Eds.). *Bat Ecology*. University of Chicago Press, Chicago, IL. 798 pp.
- Lacki, M.J., D.R. Cox, and M.B. Dickinson. 2009. Meta-analysis of summer roosting characteristics of two species of *Myotis* bats. *American Midland Naturalist* 161:321–329.

- Lacki, M.J., L.E. Dodd, N.S. Skowronski, M.B. Dickinson, and L.K. Rieske. 2014. Fire management and habitat quality for endangered bats in Kentucky's Mammoth Cave National Park during the swarming and staging periods: Predator-prey interactions and habitat use of bats threatened by white-nose syndrome. US Forest Service, Joint Fire Science Program, Final Report No. 10-1-06-1.
- Lacki, M.J., L.E. Dodd, R.S. Toomey, S.C. Thomas, Z.L. Couch, and B.S. Nichols. 2015. Temporal changes in body mass and body condition of cave-hibernating bats during staging and swarming. *Journal of Fish and Wildlife Management* 6: 360–370.
- Law, B., K.J. Park, and M.J. Lacki. 2015. Insectivorous bats and silviculture: Balancing timber production and bat conservation. Pp. 105–150, *In* C.C. Voigt and T. Kingston (Eds.). *Bats in the Anthropocene: Conservation of Bats in a Changing World*. Springer International Publishing, New York, NY. DOI:10.1007/978-3-319-25220-9.
- Limpert, D.L., D.L. Birch, M.S. Scott, M. Andre, and E. Gillam. 2007. Tree selection and landscape analysis of Eastern Red Bat day roosts. *Journal of Wildlife Management* 71:478–486.
- Livesay, A. 1953. Geology of the Mammoth Cave National Park area. Kentucky Geological Survey, College of Arts and Sciences, University of Kentucky, Lexington, KY. Special Publication 7:1–40.
- Meyer, C.F.J., and E.K.V. Kalko. 2008. Assemblage-level responses of phyllostomid bats to tropical-forest fragmentation: Land-bridge islands as a model system. *Journal of Biogeography* 35:1711–1726.
- Moore, M.S., K.A. Field, M.J. Behr, G.G. Turner, M.E. Furze, D.W.F. Stern, P.R. Allegra, S.A. Bouboulis, C.D. Musante, M.E. Vodzak, M.E. Biron, M.B. Meierhofer, W.F. Frick, J.T. Foster, D. Howell, J.A. Kath, A. Kurta, G. Nordquist, J.S. Johnson, T.M. Lilley, B.W. Barrett, and D.M. Reeder. 2017. Energy-conserving thermoregulatory patterns and lower disease severity in a bat resistant to the impacts of white-nose syndrome. *Journal of Comparative Physiology B* 188:163–176. DOI:10.1007/s00360-017-1109-2.
- Moosman, P.R., Jr., J.P. Veilleux, G.W. Pelton, and H.H. Thomas. 2013. Changes in capture rates in a community of bats in New Hampshire during the progression of white-nose syndrome. *Northeastern Naturalist* 20:552–558.
- Mormann, B.M., and L.W. Robbins. 2007. Winter roosting ecology of Eastern Red Bats in southwest Missouri. *Journal of Wildlife Management* 71:213–217.
- O'Keefe, J.M., S.C. Loeb, J.D. Lanham, and H.S. Hill Jr. 2009. Macrohabitat factors affect day roost selection by Eastern Red Bats and Eastern Pipistrelles in the southern Appalachian Mountains, USA. *Forest Ecology and Management* 257:1757–1763.
- Patterson, B.D., M.R. Willig, and R.D. Stevens. 2003. Trophic strategies, niche partitioning, and patterns of ecological organization. Pp. 536–579, *In* T.H. Kunz and M.B. Fenton (Eds.). *Bat Ecology*. University of Chicago Press, Chicago, IL. 779 pp.
- Reynolds, R.J., K.E. Powers, W. Orndorff, W.M. Ford, and C.S. Hobson. 2016. Changes in rates of capture and demographics of *Myotis septentrionalis* (Northern Long-eared Bat) in western Virginia before and after onset of white-nose syndrome. *Northeastern Naturalist* 23:195–204.
- Scott, M.C., and G.S. Helfman. 2001. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. *Fisheries* 26:6–15.
- Silvis, A., E.R. Thomas, W.M. Ford, E.R. Britzke, and M.J. Friedrich. 2015. Internal cavity characteristics of Northern Long-eared Bat (*Myotis septentrionalis*) maternity day-roosts. Research Paper NRS-27. USDA Forest Service, Northern Research Station, Newtown Square, PA.

- The Pennsylvania State University. 2017. Stat 500: Applied statistics. 9.1 - Chi-square test of independence. Available online at <https://online.courses.science.psu.edu/stat500/node/56>. Accessed 10 August 2017.
- Thogmartin, W.E., C.A. Sanders-Reed, J.A. Szymanski, P.C. McKann, L. Pruitt, R.A. King, M.C. Runge, and R.E. Russell. 2013. White-nose syndrome is likely to extirpate the endangered Indiana Bat over large parts of its range. *Biological Conservation* 160:162–172.
- Timpone, J.C., J.G. Boyles, K.L. Murray, D.P. Aubrey, and L.W. Robbins. 2010. Overlap in roosting habits of Indiana Bats (*Myotis sodalis*) and Northern Bats (*Myotis septentrionalis*). *American Midland Naturalist* 163:115–123.
- US Fish and Wildlife Service (USFWS). 2016. White-nose syndrome decontamination protocol Version 4.12.2016. 6. Available online at https://www.whitenosesyndrome.org/sites/default/files/resource/national_wns_decon_protocol_04.12.2016.pdf. Accessed 25 October 2016.
- US National Park Service (USNPS). 2016. Learn about the park: Nature. Available online at <https://www.nps.gov/macal/learn/nature/index.htm>. Accessed 20 October 2016.
- Weather Underground. 2016. Mammoth Cave, KY. Available online at <https://www.wunderground.com/cgi-bin/findweather/getForecast?query=Mammoth+Cave%2C+KY>. Accessed 29 October 2016.
- Whitaker, J.O., Jr. 2004. Prey selection in a temperate zone insectivorous bat community. *Journal of Mammalogy* 85:460–469.
- Winhold, L., and A. Kurta. 2008. Netting surveys for bats in the Northeast: Differences associated with habitat, duration of netting, and use of consecutive nights. *Northeastern Naturalist* 15:263–274.