

Articles

Patterns of Acoustical Activity of Bats Prior to and Following White-Nose Syndrome Occurrence

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Abstract

White-nose Syndrome (WNS), a wildlife health concern that has decimated cave-hibernating bat populations in eastern North America since 2006, began affecting source-caves for summer bat populations at Fort Drum, a U.S. Army installation in New York in the winter of 2007–2008. As regional die-offs of bats became evident, and Fort Drum's known populations began showing declines, we examined whether WNS-induced change in abundance patterns and seasonal timing of bat activity could be quantified using acoustical surveys, 2003–2010, at structurally uncluttered riparian–water habitats (i.e., streams, ponds, and wet meadows). As predicted, we observed significant declines in overall summer activity between pre-WNS and post-WNS years for little brown bats *Myotis lucifugus*, northern bats *M. septentrionalis*, and Indiana bats *M. sodalis*. We did not observe any significant change in activity patterns between pre-WNS and post-WNS years for big brown bats *Eptesicus fuscus*, eastern red bats *Lasiurus borealis*, or the small number of tri-colored bats *Perimyotis subflavus*. Activity of silver-haired bats *Lasionycteris noctivagans* increased from pre-WNS to post-WNS years. Activity levels of hoary bats *Lasiurus cinereus* significantly declined between pre- and post-WNS years. As a nonhibernating, migratory species, hoary bat declines might be correlated with wind-energy development impacts occurring in the same time frame rather than WNS. Intraseason activity patterns also were affected by WNS, though the results were highly variable among species. Little brown bats showed an overall increase in activity from early to late summer pre-WNS, presumably due to detections of newly volant young added to the local population. However, the opposite occurred post-WNS, indicating that reproduction among surviving little brown bats may be declining. Our data suggest that acoustical monitoring during the summer season can provide insights into species' relative abundance on the landscape as affected by the occurrence of WNS.

Keywords: acoustical activity; bats; monitoring; *Myotis*; white-nose syndrome

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Introduction

The use of acoustical methods to investigate bat ecology has been commonplace worldwide over the past decade (Johnson et al. 2002; Milne et al. 2004; Menzel et al. 2005; Zukal and Rehak 2006; Furey et al. 2009). Despite imprecision with individual demarcation and some species identification (Barclay 1999), along with high intrahabitat variation (Sherwin et al. 2000), acoustic sampling has proven effective for understanding foraging habitat associations and fundamental ecological niches (Williams and Dickman 2004; Lloyd et al. 2005; Ford et al. 2006), as well as nightly (Broders et al. 2003) and seasonal (Johnson et al. 2011a, 2011c) activity patterns. This has been particularly true for the Northeast and mid-Atlantic portions of the United States, where bat communities have low species richness (<10) and acoustical identification is reasonably accurate (Ford et al. 2005; Britzke et al. 2011). Regionally, species typically partition foraging space based on open or cluttered habitat preferences, though with considerable overlap (Brooks and Ford 2005; Johnson et al. 2008). However, the preponderance of all bat activity in the area is associated with water, whether within a cluttered forested riparian area (Schirmacher et al. 2007) or over open-area ponds and lakes (Krusic et al. 1996; Zimmerman and Glanz 2000; Broders et al. 2006; Brooks 2009).

In the Northeast and mid-Atlantic, most bat population trends are derived from overwinter hibernacula (caves and mines) counts or postwinter exit counts (Hicks and Novak 2002). For areas where summer nonhibernating trends are the only available data, Weller (2008) demonstrated the efficacy of using acoustical sampling for occupancy estimation over large landscapes. Although useful, accepted sampling techniques for monitoring bat numbers or attempts to track trends over time using acoustical methodologies are still in their infancy. O'Shea et al. (2003) noted that comparisons or calibrations of acoustical survey methods against direct counts of bats from cave hibernacula or mist-netting efforts would be necessary to illustrate the utility of acoustical sampling for population monitoring with some reasonable certainty.

Since 2006, the presence of White-nose Syndrome (WNS) and the increase in wind energy development in the eastern United States and Canada have necessitated monitoring population trends not only of endangered species such as the Indiana bat *Myotis sodalis* and other cave-hibernating species such as the little brown bat *M. lucifugus*, northern bat *M. septentrionalis*, eastern small-footed bat *M. leibii*, tri-colored bat *Perimyotis subflavus*, and big brown bat *Eptesicus fuscus*, but also migratory bats such as the eastern red bat *Lasiurus borealis*, hoary bat *L. cinereus*, and silver-haired bat *Lasionycteris noctivagans*. White-nose Syndrome has been implicated in the mortality of >1,000,000 bats since 2006 and is believed to be caused by the psychrophilic fungus, *Geomyces destructans* (Kannan et al. 2010). This pathogen first appeared in eastern New York and has since spread throughout the Northeast (including adjacent portions of

Canada) and mid-Atlantic and as far west as Oklahoma (USFWS 2010). Hibernating bats with WNS exhibit dermal lesions, whereby fungal hyphae displace hair follicles and sebaceous glands, eventually breaching the epidermis (Blehert et al. 2009). Hyphae-disrupted water balances from fungal invasion and growth leads to severe dehydration (Cryan et al. 2010). Consequently, affected bats experience altered torpor-arousal cycles causing premature fat depletions, which forces midwinter emergences and results in death from exposure (Gargas et al. 2009; Reichard and Kunz 2009). Posthibernation survivors are believed to have reduced reproductive output (Frick et al. 2010b). To date, the little brown bat, the most abundant bat in the area, has been the most impacted and the regional population (ca. 6,000,000) could become functionally extirpated within 20 y (Frick et al. 2010a).

Efforts to track trends in bat populations relative to the spread of WNS by using acoustical recorders are gaining acceptance as new restrictions on cave-entry and precautionary protocols for mist-netting are limiting methods to enumerate bats (Rodhouse et al. 2011). At present, acoustical data on WNS-induced changes in bat activity in the Northeast are limited to two pilot studies. Without pre-WNS baseline data, Dzal et al. (2010) showed a 3-y progressive decrease in little brown bat activity in the Hudson River Valley region of eastern New York, 2007–2009, following the onset of WNS in 2006. Brooks (2011) reported a 72% decrease in little brown bat activity in central Massachusetts when comparing a single post-WNS year (2010) with pre-WNS 2004–2006 surveys. Activity in other species believed unaffected or less susceptible to WNS, such as the migratory *Lasiurus* species or the big brown bat, either increased or were shown to be highly variable without evident links to WNS onset. Many unaffected areas outside these WNS-impacted regions either contain overwintering hibernation habitat or summer maternity habitat but typically not both in close proximity. These poorly established links between extant summer populations and hibernating populations introduces considerable uncertainty for natural resource managers trying to utilize acoustical methodologies to monitor trends in bats at local and regional scales.

An exception to the inability to correlate summer activity levels with known hibernation populations is the extensive passive acoustical survey work conducted 2003–2010 at Fort Drum, a U.S. Army installation located in northern New York State. The federally endangered Indiana bat was discovered in the summer of 2006 on Fort Drum, and subsequent monitoring revealed a summer maternity colony on the installation. To fulfill regulatory obligations under the U.S. Endangered Species Act as amended (ESA 1973) for the Indiana bat, numerous summer mist-net surveys and comprehensive acoustical surveys have been conducted throughout the installation (USFWS 2009; Johnson et al. 2011b). Herein, we describe changes in acoustically recorded bat activity at Fort Drum from 2003 through 2010. Our analyses were framed in the context of known WNS occurrence and

awareness of population trends in counts from surrounding hibernacula and summer counts within artificial roost structures. Accordingly, we hypothesized the following changes in bat activity at Fort Drum: 1) communally hibernating bats associated with caves would show a significant decline in summer activity; 2) nonhibernating migratory bats and less communally hibernating bats would show no response or less response, respectively; 3) little brown bat activity would decrease the most of any species; and 4) activity patterns from early to late summer, post-WNS, among affected species would reflect reduced natality as evidenced by reduced activity.

Methods

We conducted our study at Fort Drum, a 43,000-ha U.S. Army installation in Jefferson and Lewis counties, New York, USA. Located in the northwestern portion of the state, Fort Drum lies at the intersection of three eco-regions: the Tug Hill Plateau, the St. Lawrence–Great Lakes Lowlands and the foothills of the Adirondack Mountains. Limestone “Karst” formations in the Niagara Escarpment lay 10–15 km west of Fort Drum and contain caves where bats hibernate. Topography is rolling with some incised water-courses along the Black and Indian river drainages. Elevations range from 125 to 278 m. Approximately 70% of Fort Drum is forested. Mature forests are northern hardwood associations of sugar maple *Acer saccharum*, American beech *Fagus grandifolia*, white ash *Fraxinus americana*, American elm *Ulmus americana*, along with a conifer component of white pine *Pinus strobus* and eastern hemlock *Tsuga canadensis*. In addition to developed areas within the installation’s 4500-ha cantonment and airfield, open areas maintained for training, such as drop-zones, firing ranges, maneuver areas, and forest regeneration areas, occur throughout. Small lakes, beaver *Castor canadensis* ponds, and open wet meadows cover approximately 20% of the landscape.

Varying amounts of data exist on bat numbers from hibernation sites that presumably provide most of the “nonmigratory” bats to the Fort Drum area. Indiana bats on the installation primarily overwinter in nearby Glen Park Cavern and, based on band recoveries, Fort Drum’s little brown bats are thought to overwinter in caves in the Champlain Valley east of the Adirondack Mountains in New York and Vermont (A. Hicks, New York Department of Environmental Conservation, personal communication). Additionally, displacement of a large maternity colony of little brown bats from a historic mansion on the installation into a constructed bat house in 2004 has allowed for precise summer counts for a concentrated subset of this species since 2006. Immediate postparturition colony numbers were estimated at 1,250 in the summer of 2006, declining to 155 by 2010 (C.A. Dobony, unpublished data).

From June through early September, 2003–2010, we used Anabat II frequency-division bat detectors linked to zero-crossing analysis interface modules with compact flash storage (Titley Scientific, Ballina, Australia) to

passively record bat echolocation passes (*Supplemental Material*, Table S1; <http://dx.doi.org/10.3996/042011-JFWM-027.S1>). We encased detectors in waterproof housing and placed each on the ground pointed at a 30–45° angle with an unobstructed path over structurally uncluttered riparian–water habitats (i.e., streams, small lakes, beaver ponds, and open wet meadows). Our site selections were not random, but were intended to maximize our documentation of the general spatial and temporal characteristics of the bat community. Typically, we acoustically surveyed sites for two consecutive nights and over the course of 5 y; 12 of the 15 sites sampled in 2004 and 9 of the 18 sampled in 2005 also were revisited in 2009 and 2010, respectively. We did not conduct acoustical surveys if temperatures were below 10° C or if there was a prolonged precipitation event. We programmed detectors to start recording 1 h before the end of civil twilight when the sun is fully below the horizon (Seidelman 2006) and to stop at sunrise, local time.

We filtered recorded echolocation passes prior to analysis to remove extraneous noise (Britzke and Murray 2000) and then identified passes to species using Analook 4.7j and Analyze 2.0 software. We defined a pass as a series of ≥ 4 search-phase echolocation pulses emitted by a bat. We assigned passes with < 4 search-phase echolocation pulses to an unidentified bat category. To identify bat passes, we employed dichotomous keys based on call parameters (Ford et al. 2005; Johnson et al. 2008) in 2003–2008 and a discriminant function analysis (Britzke et al. 2002, 2011) in 2009–2010. Developed from the same library of known bat passes from the eastern United States (Britzke et al. 2002), both quantitative methods examined the same echolocation call characteristics, such as minimum and mean call-note frequency and call shape and slope, for species identification. To ensure these two methods of echolocation pass identification were congruent, we compared results of both methods from a subset of 10 unique “site-nights” from the pre-WNS portion of the data. Specifically, we examined for differences in overall species composition and abundance using Simpson’s Index of Diversity (Magurran 1988) and also the number of Indiana bats, the species present most likely to be misidentified as “false positives” in the extant species pool at Fort Drum (*Supplemental Material*, Table S2; <http://dx.doi.org/10.3996/042011-JFWM-027.S2>). There was no significant difference between Simpson’s Index of Diversity (paired *t*-test, $t = 0.23$, $df = 9$, $P = 0.8266$) or in the number of Indiana bats counted (paired *t*-test, $t = -0.49$, $df = 9$, $P = 0.6343$).

Prior to statistical analysis, we assigned echolocation calls to pre-WNS year (2003–2007) or post-WNS year (2008–2010) treatments. We divided the summer into an early period (June 1–July 15) when female little brown bats at Fort Drum are either pregnant or lactating, and a late summer period (after July 15) during which young bats become volant and bat activity levels on the landscape should increase (Anthony et al. 1981). To test whether echolocation activity levels differed between pre-WNS (2003–2008) and post-WNS (2008–2010) and to examine the interactions between WNS period and

summer season, we fit generalized linear mixed models in a two-factor repeated-measure design for random main effects (i.e., WNS period years and summer season), using the PROC GLIMMIX procedure (SAS 9.3, SAS Inc., Cary, North Carolina) for each identified bat species. For those species with mean hourly passes ≥ 1 , we used a Poisson distribution with a logarithmic link function design, whereas for bat species with < 1 mean hourly passes, we used a binary (presence or absence) distribution with a logistic link function design. Our repeated measures were hourly divisions nested within an individual night from the hour prior to the end of civil twilight to sunrise, because activity hourly within a single night at a site can be temporally autocorrelated (Gehrt and Chelsvig 2004). We did not analyze within-night activity patterns because our data showed that activity across species at Fort Drum was not bi-phasic, as observed earlier in a bat community in central Massachusetts in a similar habitat setting (Brooks 2009). We use preplanned orthogonal contrasts to compare pre-WNS vs. post-WNS bat activity levels when significant WNS effects ($P < 0.05$) were observed. When significant WNS $\times$ summer period interactions were observed, we similarly used contrasts to compare bat activity pre-WNS early summer vs. pre-WNS late summer and post-WNS early summer and post-WNS late summer.

Results

From 2003 to 2010, we sampled 1,405 total “detector” hours over 175 site-night combinations and recorded 27,758 bat passes from nine bat species, including little brown bat ($n = 9,568$ passes), big brown bat ($n = 3,673$), eastern red bat ($n = 2,364$), hoary bat ($n = 2,382$), Indiana bat ($n = 1,132$), silver-haired bat ($n = 742$), northern bat ($n = 577$), tri-colored bat ($n = 459$), and eastern small-footed bat ($n = 37$). We were unable to positively identify the remaining passes to species; however, most appeared to belong to the genus *Myotis* and were presumably little brown bats. When partitioned between pre-WNS early summer (243 h), pre-WNS late summer (473 h), post-WNS early summer (90 h), and post-WNS late summer (599 h), activity patterns varied among species (Figure 1). We excluded small-footed bats from analyses due to small sample size.

Activity levels of little brown bats, northern bats, Indiana bats, silver-haired bats, and hoary bats significantly differed between pre- and post-WNS years, whereas no difference was observed for tri-colored bat, big brown bat, or eastern red bat activity levels (Table 1). Overall activity levels of little brown bats, northern bats, Indiana bats and hoary bats declined from pre- to post-WNS, whereas silver-haired bat activity levels increased (Table 2; Figure 1). Significant interactions between WNS period designation and early or late summer periods also were observed for little brown bats, northern bats, and Indiana bats (Table 1). Activity levels of little brown bats and northern bats increased from early to late summer in pre-WNS years, whereas activity levels for Indiana bats did not differ, although the same trend was apparent (Table 2; Figure 1). Post-WNS, activity levels of northern

bats and Indiana bats increased from early to late summer but overall activity was still lower than pre-WNS at the same period. Activity of little brown bats did not differ significantly between early and late summer post-WNS, although a declining trend is apparent (Table 2; Figure 1).

Discussion

Our results were consistent with our predictions and the findings of others (Dzal et al. 2010; Brooks 2011) that bat activity patterns would change between pre- and post-WNS years and within seasonal categories, specifically based on the species-specific susceptibility to WNS and/or hibernating vs. migratory overwintering habits. For little brown bats, in pre-WNS years, there was an increase in activity from early summer (when pregnant or lactating adult females forage on the landscape) to late summer (when volant young can leave the maternity site to forage, thereby adding to the activity levels). However, this trend did not continue post-WNS because, owing to overwintering mortality, initial numbers of adult bats returning during early summer were lower. As noted elsewhere in the region, many female little brown bats returning to the monitored maternity colony at Fort Drum have been in poor physiological condition, with a higher percentage of nonreproductive individuals than occurred prior to WNS (Frick et al. 2010a, 2010b). Additionally, if females surviving the winter were less successful reproductively, the cumulative effect would be far fewer young recruited into the population during the late summer period, a post-WNS pattern that similarly has been documented in the central Appalachians of West Virginia (K. Francl, Radford University, unpublished data). Energetic demands from dermal repair or tissue replacement due to WNS infection may also alter foraging activity. In concurrent research, we observed female little brown bats at Fort Drum engaging in repeated, very short feeding bouts in foraging areas very near maternity roosts (E.R. Britzke, unpublished data). This may further reduce activity on the wider landscape around maternity roosts, depending on their spatial distributions and proximity to sampling locations. Further, summer occupancy of surviving, nonreproductive females may be lessened in duration because the thermal benefits of a maternity roost confer no advantage to nonreproductive females. In light of intraspecific competition for foraging space where large aggregations of bats would typically occur, nonreproductive females may begin earlier migration toward areas near hibernation sites (Agosta et al. 2005). Alternatively, these females might be more dispersed on the larger landscape and, hence, less concentrated in the historic maternity colony area on Fort Drum. Although the sizes of little brown bat maternity colonies can exceed thresholds to become somewhat detrimental (Coleman and Barclay 2011), in cooler areas, such as Fort Drum, reduced adult numbers could contribute to less favorable intrarost microclimates that retard pup growth and prolong the time to weaning (Postawa and Gas 2009).

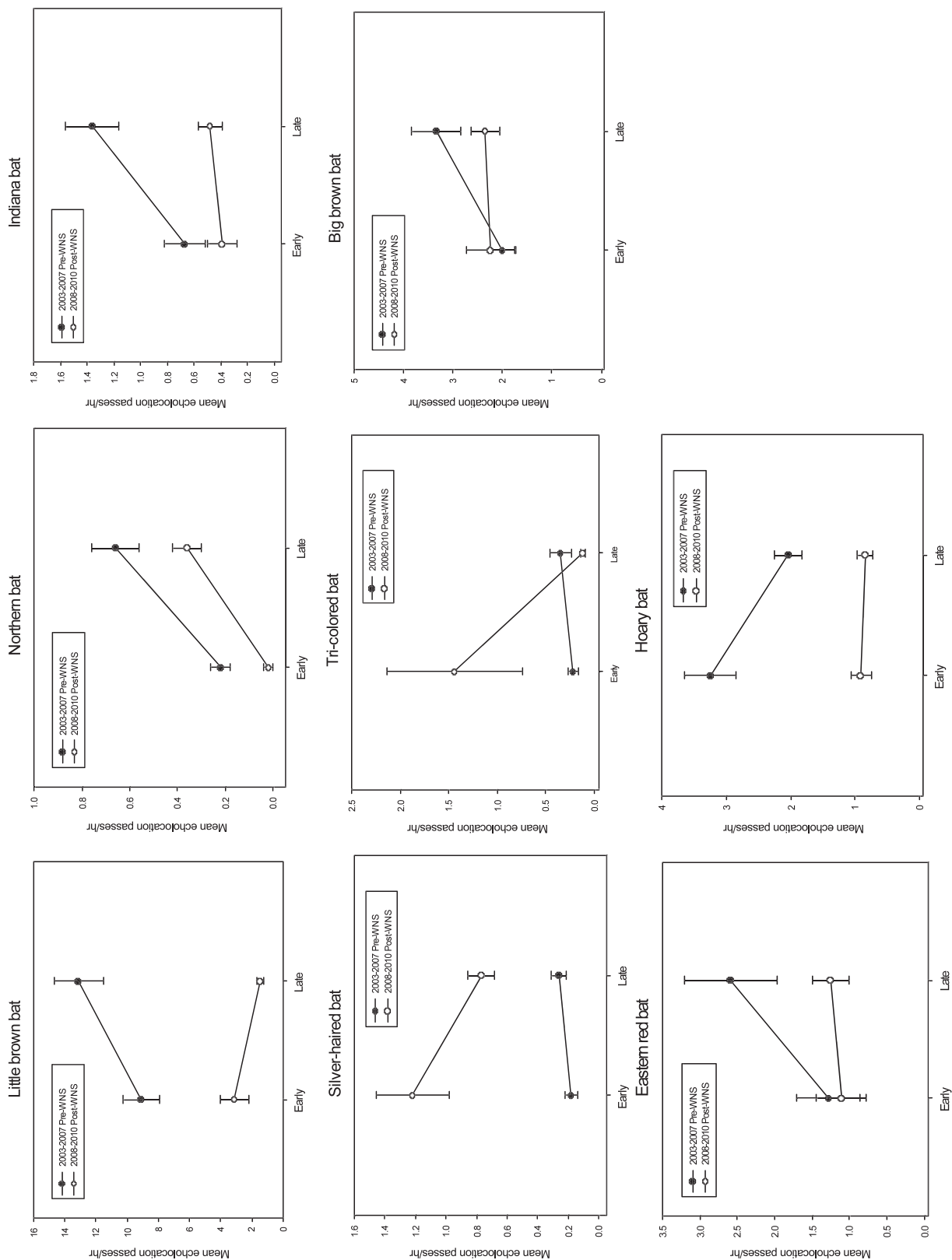


Figure 1. Mean number of echolocation passes per hour $\pm$ standard error of little brown bats *Myotis lucifugus*, northern bats *M. septentrionalis*, Indiana bats *M. sodalis*, silver-haired bats *Lasiurus noctivagus*, tri-colored bats *Perimyotis subflavus*, big brown bats *Eptesicus fuscus*, eastern red bats *Lasiurus borealis*, and hoary bats *L. cinereus* at Fort Drum, New York in pre-White-nose Syndrome (WNS) years, 2003–2007 and post-WNS years, 2008–2010 for early summer ($\leq$ July 15) and late summer ($>$ July 15).

Table 1. Generalized linear mixed model Type III tests of pre- and post-White-nose Syndrome (WNS) years, 2003–2007 and 2008–2010, respectively, and seasonal period (early and late summer) with interactions for measures of bat echolocation passes at Fort Drum, New York.

Species	Effect	df	F-value	P
Little brown bat ^a <i>Myotis lucifugus</i>	WNS	1,9	26.75	0.006
	Seasonal	1,9	0.67	0.436
	WNS × seasonal	1,9	5.13	0.050
Northern bat ^b <i>Myotis septentrionalis</i>	WNS	1,9	12.63	0.006
	Seasonal	1,9	18.08	0.002
	WNS × seasonal	1,9	6.40	0.032
Indiana bat ^b <i>Myotis sodalis</i>	WNS	1,9	8.47	0.017
	Seasonal	1,9	0.14	0.714
	WNS × seasonal	1,9	5.55	0.043
Silver-haired bat ^b <i>Lasionycteris noctivigans</i>	WNS	1,9	53.49	<0.001
	Seasonal	1,9	1.95	0.196
	WNS × seasonal	1,9	4.33	0.067
Tri-colored bat ^b <i>Perimyotis subflavus</i>	WNS	1,9	0.16	0.695
	Seasonal	1,9	7.98	0.020
	WNS × seasonal	1,9	2.58	0.143
Big brown bat ^a <i>Eptesicus fuscus</i>	WNS	1,9	0.00	0.957
	Seasonal	1,9	1.58	0.241
	WNS × seasonal	1,9	1.40	0.267
Eastern red bat ^a <i>Lasiurus borealis</i>	WNS	1,9	0.63	0.446
	Seasonal	1,9	0.92	0.363
	WNS × seasonal	1,9	0.54	0.480
Hoary bat ^a <i>Lasiurus cinereus</i>	WNS	1,9	23.17	0.001
	Seasonal	1,9	2.28	0.165
	WNS × seasonal	1,9	1.05	0.333

^a Poisson distribution.^b Binary distribution.

The pattern for northern bats and Indiana bats mirrored that of little brown bats, with overall lower observed activity in the post-WNS period. However, trends in activity still rose from early summer to late summer for both species, possibly indicating a relatively higher rate of reproductive success and recruitment than little brown bats, albeit still less than what was observed pre-WNS. However, declines we observed in northern bat and Indiana bat activity probably were conservative relative to extent of decline of these species regionally and locally, based on the decline in bat activity recorded by Brooks (2011) in cluttered habitats. Pre-WNS, the northern bat often was the third most common species (after big brown and little brown bat) in mist-netting surveys on the installation. Although occurring in numbers of an order of magnitude less than the little brown bat, Fort Drum had been recognized as an important Indiana bat maternity area and the species was relatively common in localized areas prior to the onset of WNS (C.A. Dobony, unpublished data). Our sampling scheme was concentrated over uncluttered ponds, streams, and wet meadows and, therefore, was most biased against recording northern bats because they forage primarily over wooded riparian and in upland wooded sites (Brooks 2009). Moreover, their high-frequency, low-amplitude echolocation characteristics

make them particularly prone to be missed by passive acoustical sampling even when actually present (Ford et al. 2005). To a lesser extent, the same is true for the Indiana bat because they also will forage over wooded riparian habitats (Ford et al. 2005) in addition to the open habitats we sampled.

Our observations supported our predictions for big brown and eastern red bat response. Big brown bats have only moderately been affected by WNS, presumably due to their relatively solitary hibernating habits, which do not facilitate bat-to-bat transmission and their larger body size provides greater protection against overwinter mortality from premature fat depletion (K. Francl, Radford University, personal communication). However, rather “flat” trends from early to late summer post-WNS in activity for big brown bats may indicate that a pattern of fully successful reproduction and potential addition of recruits concomitant with higher relative WNS survival is not actually occurring. Red bats are migratory and nonhibernating; therefore, they are believed to not be exposed to WNS. Although some researchers have questioned whether there has been a decline in the numbers of eastern red bats in the North American landscape (Winhold et al. 2008), we saw no change in activity in this species over the years we acoustically surveyed. Big brown bats and eastern red bats now

Table 2. A priori contrasts for pre- and post-White-nose Syndrome (WNS) years, 2003–2007 and 2008–2010, respectively, and seasonal period (early summer = E and late summer = L) stratified by pre- and post-WNS years when significant effects for WNS or WNS $\times$ season interactions (see Table 1) were noted for measures of bat echolocation passes at Fort Drum, New York.

Species	Contrast	df	F-value	P
Little brown bat ^a <i>Myotis lucifugus</i>	pre-WNS > post-WNS	1,9	26.75	0.0060
	pre-WNS E < pre-WNS L	1,9	4.60	0.0605
	post-WNS E = post-WNS L	1,9	2.72	0.1332
Northern bat ^b <i>Myotis septentrionalis</i>	pre-WNS > post-WNS	1,9	12.63	0.0062
	pre-WNS E < pre-WNS L	1,9	18.08	0.0021
	post-WNS E < post-WNS L	1,9	6.40	0.0322
Indiana bat ^b <i>Myotis sodalis</i>	pre-WNS > post-WNS	1,9	8.47	0.0173
	pre-WNS E = pre-WNS L	1,9	0.14	0.7135
	post-WNS E < post-WNS L	1,9	5.55	0.0322
Silver-haired bat ^b <i>Lasionycteris noctivagans</i>	pre-WNS < post-WNS	1,9	53.44	0.0001
Hoary bat ^a <i>Lasiurus cinereus</i>	pre-WNS > post-WNS	1,9	23.17	0.0010

^a Poisson distribution.

^b Binary distribution.

comprise the majority of captures from mist-net surveys on the installation (C.A. Dobony, unpublished data). Trends showing less activity of eastern red bats later in the summer on Fort Drum post-WNS do, however, merit further monitoring.

Significantly different pre- and post-WNS abundance patterns in silver-haired bat and hoary bat activity were contrary to our predictions. In contrast with eastern red bat, we recorded significant increases in silver-haired bat activity and decreases in hoary bat activity post-WNS. For silver-haired bats, the increase could simply be a sampling artifact, because we recorded relatively few of these bats over the duration of the study. Based on an examination of museum records, Cryan (2003) found that silver-haired bats in New York and southern New England can be relatively abundant in August. However, our actual proportion of acoustical surveys occurring in the month of August was less in post-WNS than pre-WNS years. Silver-haired bat ecology and population dynamics are poorly known in most aspects, but this species can vary substantially in their apparent abundance from year to year (Whitaker and Hamilton 1998). Conversely, we do not believe reduction in hoary bat activity is related to WNS, nor, based on the large sample size, were our findings a sampling artifact. Hoary bat mortality at the nearby Maple Ridge wind-energy production facility is among the highest per kilowatt produced in the country (Arnett et al. 2008). Although we are unaware of any documented causative link between Maple Ridge hoary bat mortalities and declines in activity at Fort Drum, further monitoring seems prudent.

Although it is probably too early into the WNS “event” enveloping the Northeast and mid-Atlantic to quantify, significant reductions in little brown bat populations and possible competitive release could potentially alter interspecific relationships among assemblages, distribution, and habitat use of bats. Whether or not removal of species from the WNS-affected landscapes will trigger population or habitat use changes in remaining species is unknown; however, indirect evidence from other regions

and bat communities suggest it is possible. For example, in the arid West, Adams and Thibault (2006) noted that temporal segregation of bat species at watering areas was often a function of numbers of individuals within a species relative to the numbers of other species. In Europe, presence of the serotine bat *Eptesicus serotinus* can often preclude foraging activity by other open-area-adapted species (Haupt and Schmidt 2007), and habitat changes that have favored increases in common pipistrelles *Pipistrellus pipistrellus* have contributed to the decline of lesser horseshoe bats *Rhinolophus hipposideros* (Arlettaz et al. 2008).

Conclusion

Overall, we believe that our analyses from Fort Drum have demonstrated that WNS-induced changes in bat numbers for some species can be tracked acoustically. Our study would have been improved by more repeated visits to survey sites within and among years (Brooks 2009). Also, efforts to include forested or “cluttered” riparian and upland habitats should be a priority in order to better track changes in activity of species such as the northern bat and, to a lesser degree, the Indiana bat (Ford et al. 2005). Nonetheless, efforts to establish and maintain long-term acoustical monitoring programs to document declines in bats affected by WNS should be a priority, especially in areas where WNS has yet to occur. Acoustical methodologies certainly will not be able to depict declines or possible future recoveries in exacting quantitative terms. However, these techniques may be increasingly viable methods to document changes in habitat associations of less affected bat species or to begin to understand whether these species are released from interspecific competition for foraging space by declining numbers of the little brown bat.

Supplemental Material

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Table S1. Acoustically recorded (Anabat II) bat activity data used for comparing pre- and post-WNS years and intraseasons at Fort Drum, New York, United States, 2003–2010. Data categories are: SITE (survey location), YEAR, MONTH, DAY, HOUR (in hourly block categories before or after end of civil twilight; values calculated from the day that acoustical monitor began), EPFU (hourly count of big brown bats, *Eptesicus fuscus*), LABO (hourly count of eastern red bats, *Lasiurus borealis*), LACI (hourly count of hoary bats, *Lasiurus cinereus*), LANO (hourly count of silver-haired bats, *Lasionycteris noctivagans*), MYLE (hourly count of small-footed bats, *Myotis leibii*), MYLU (hourly count of little brown bats, *M. lucifugus*), MYSE (hourly count of northern bat, *M. septentrionalis*), MYSO (hourly count of Indiana bats, *M. sodalis*), PEMY (hourly count of tri-colored bats, *Perimyotis subflavus*), NOID (hourly count of unidentified bats), WNS (pre-White-nose Syndrome year [0] or post-White-nose Syndrome year [1], LAC (early summer ≤ 15 July = 1 and late summer > 15 July = 2).

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Table S2. Subset of acoustically recorded (Anabat II) bat activity data from 10 unique site and night combinations used to compare Simpson's Index of Diversity for all bat activity data and Indiana bat *Myotis sodalis* activity data using dichotomous key and discriminant function analysis identification techniques at Fort Drum, New York, United States, 2003–2010. Data categories are: SITENIGHT (unique site and night combination), DIVERSITY-MANUAL (Simpson's Index of Diversity calculated using bat echolocation passes identified using dichotomous key), DIVERSITY-DFA (Simpson's Index of Diversity calculated using bat echolocation passes identified using discriminant function analysis), MYSO-MANUAL (Indiana bat echolocation passes identified using dichotomous key), and MYSO-DFA (Indiana bat echolocation passes identified using discriminant function analysis).

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