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Going, going, gone: the impact of white-nose syndrome on the summer activity of the little brown bat (*Myotis lucifugus*)

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Since its discovery in the winter of 2005–2006, white-nose syndrome (WNS) has killed over one million little brown bats (*Myotis lucifugus*) in the American northeast. Although many studies have reported die-offs of bats at winter hibernacula, it is important to understand how bat mortality linked to WNS at winter hibernacula affects bat activity levels in their summer ranges. In the summer (May–August) of 2007, 2008 and 2009, we recorded echolocation calls to determine bat activity at sites along the Hudson River, NY (within approx. 100 km of where WNS was first reported). We documented a 78 per cent decline in the summer activity of *M. lucifugus*, coinciding with the arrival and spread of WNS. We suggest that mortality of *M. lucifugus* in winter hibernacula is reflected by reduced levels of activity in the summer and that WNS affects the entire bat population of an area, and not only individual hibernacula.

Keywords: white-nose syndrome; *Myotis lucifugus*; bats; summer activity; bat mortality

1. INTRODUCTION

White-nose syndrome (WNS) is a condition identified by a visible white fungus (*Geomyces destructans*) found on the tissue of the face, ears or wings of hibernating, cave-roosting bats [1,2]. The exact link between the fungus and mortality remains unclear, however, to date all bats with WNS have tested positive for *G. destructans* [2–4]. WNS appears to alter the arousal patterns of bats during hibernation, depleting the fat reserves crucial for overwinter survival [5]. Many bats affected by WNS emerge from winter hibernacula well before spring, presumably in search of food, which consequently leads to their death [1,3,5].

Since the first documented case of WNS in the winter of 2005–2006 [1], bat populations at winter hibernacula have plummeted by 75–99 per cent, and over one million little brown bats (*Myotis lucifugus*) have died in the American northeast [1,6]. Although *M. lucifugus* has borne the brunt of WNS, several other species have been affected (e.g. the northern long-eared bat—*Myotis septentrionalis*, and the endangered Indiana bat—*Myotis sodalis*), although some are not known to be affected at all (e.g. hoary bats, *Lasiurus cinereus*) [1,6]. Currently, WNS appears to be confined to bats that hibernate in caves, therefore, comparing the activity of bats affected (*M. lucifugus*) and unaffected (*L. cinereus*) by WNS provides insight into the impact of this disease on bat activity in the summer, away from hibernacula.

Prior to the spread of WNS, *M. lucifugus* was one of the most common and widespread bats in North America, but the rapid spread of WNS throughout northeastern, mid-Atlantic America, and recently eastern Canada, leaves *M. lucifugus* susceptible to imminent regional extinction [6]. Many studies (i.e. [1,6]) have reported substantial *M. lucifugus* mortality at certain hibernation sites, yet reports on how winter mortality has affected summer populations are not yet available. Here, we demonstrate how summer activity levels of a species affected and a species unaffected by WNS coincide with bat mortality linked to WNS at hibernation sites.

2. MATERIAL AND METHODS

From May–August of 2007, 2008 and 2009, we collected data on summer bat activity along a 37 km stretch of the Hudson River, New York (figure 1). We recorded echolocation calls at six sites, sub-sampling at six to eight locations within each site. We began recording upon confirming the presence of the first bat and continued to record for 10 min before moving to the next recording location. Overall, each site was sampled 40–81 times. We did not survey when temperatures were $<10^{\circ}$C, neither in strong winds, nor heavy rain.

We recorded echolocation calls with a four-microphone array (CMPA/CM16 condenser microphones arranged in a tetrahedron, 1 m away from one another, Avisoft-Bioacoustic, Berlin). The microphones were connected to a multi-channel Avisoft ultrasound gate 416–200 bat detector, connected to a laptop running Avisoft-SAS Lab Pro (v. 4.3) software. Signals were recorded simultaneously onto four separate channels at a sampling frequency of 250 kHz with 8-bit sample resolution.

In each 10 min recording file, we selected the channel with the highest number of echolocation calls and counted the number of bat passes (series of more than five calls with similar inter-call interval). We identified each pass to species based on characteristics of the echolocation calls.

We used a generalized linear mixed model (GLMMPQL method in R [7]) to test for differences in activity among years for *M. lucifugus* and *L. cinereus* separately. Other species were detected, but not in sufficient numbers to warrant statistical analyses (table 1). We chose a mixed model to account for repeated sampling at the same sites throughout the season and over the years. Data distributions for both species (*M. lucifugus* and *L. cinereus*) were overdispersed, so we ran a negative binomial generalized linear model (ignoring repeated sampling) to estimate the overdispersion parameter (theta) using three different methods (R commands theta.md, theta.mm, and theta.ml), ultimately selecting the estimate that resulted in the smallest residual standard deviation in the final GLMM. We included year, Julian day (day of the year), minutes after sunset, temperature and wind speed as main effects in all analyses. In the final GLMM, we included a random intercept for each site. Any variables that did not contribute significantly to the model were removed in a stepwise manner, removing the least significant variable and re-evaluating the model. We used Tukey's post hoc multiple comparison tests to assess pairwise differences in activity levels among years.

3. RESULTS

From 3750 min of recordings, we identified 13 494 passes to species (67 470 individual calls). *Myotis lucifugus* and *L. cinereus* produced more than 93 per cent of the bat passes we recorded (table 1).

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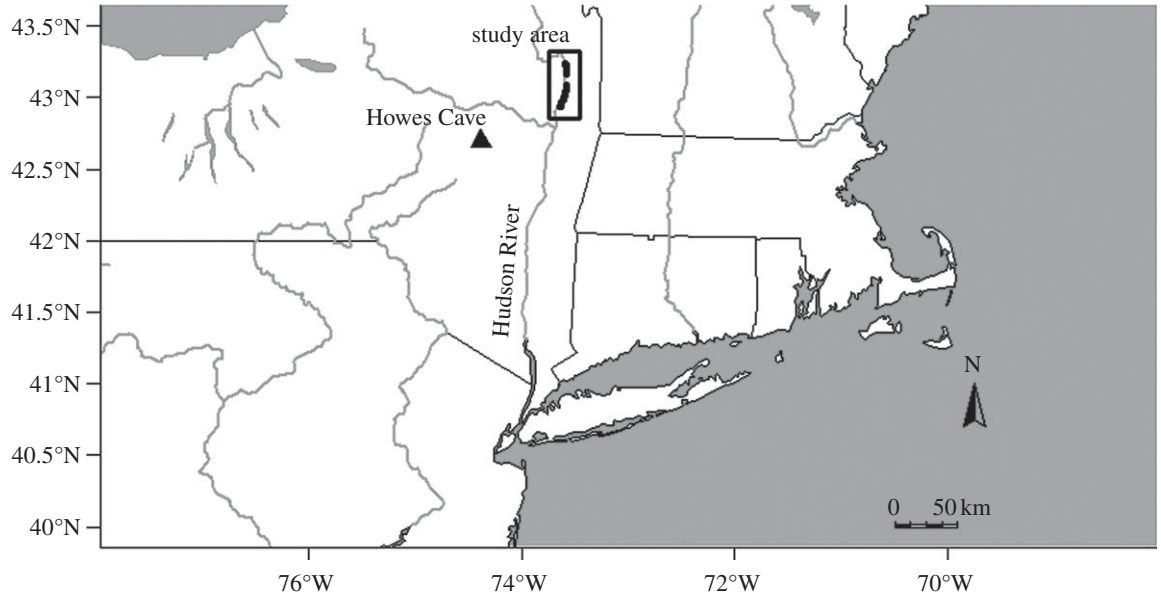

Figure 1. Map of the northeastern United States indicating the location of the study area in relation to Howes Cave (filled triangle), where WNS was first reported in the winter of 2005–2006. Filled circles indicate sampling sites along the Hudson River.

Table 1. Relative number of echolocation passes recorded per species from May to August of 2007, 2008 and 2009. Sample sizes indicate the number of 10 min recordings analysed for each year.

	year (% of bat passes per species)		
species	2007 ($n = 79$)	2008 ($n = 151$)	2009 ($n = 144$)
Myotis lucifugus	71.9	60.1	28.6
Lasiurus cinereus	17.9	31.1	61.2
Perimyotis subflavus	2.3	3.7	1.5
Eptesicus fuscus	3.5	1.1	2.8
Lasiurus borealis	1.9	0.2	5.2
Myotis leibii	0.4	0.3	0.2
Nycticeius humeralis	2.1	3.4	0.2
unknown	0	0	0.2
total number of bat passes recorded	3478	7102	2914

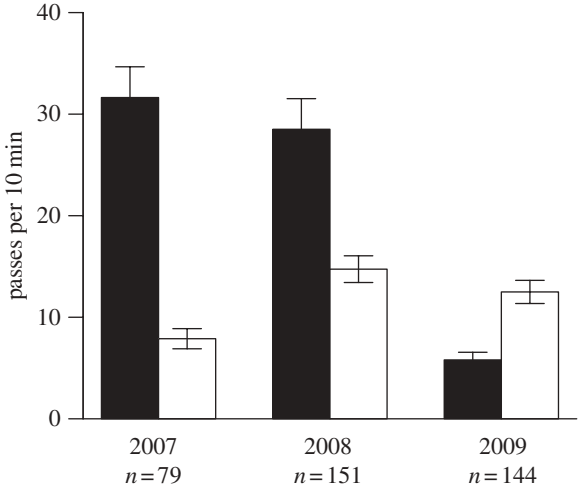

Figure 2. Summer bat activity during the spread of WNS. Little brown bats (*M. lucifugus*; filled bars) have been severely affected by WNS while hoary bats (*L. cinereus*; open bars) have not been affected. *Myotis lucifugus* activity decreased by 78% from 2008 to 2009, while *L. cinereus* experienced no precipitous declines. Sample sizes (number of 10 min files analysed) are indicated for each year.

Activity of *M. lucifugus* declined dramatically over our study. There was no change between 2007 and 2008 ($z = 1.347$, $p = 0.367$), but a substantial decline of 78 per cent in 2009, relative to 2008 ($z = -14.32$, $p < 0.0001$; figure 2). *Lasiurus cinereus* activity increased in 2008 ($z = 5.564$, $p < 0.001$), and then decreased slightly in 2009 ($z = -2.941$, $p = 0.009$), however, activity in 2009 remained greater than the activity in 2007 ($z = 3.095$, $p = 0.006$). Although activity of *L. cinereus* fluctuated among years, there was no evidence of a precipitous decline (figure 2).

4. DISCUSSION

Our study area ranges from 65 to 102 km northeast of Howes Cave, where WNS was first reported in the winter of 2005–2006 (figure 1; [1]). The substantial reduction we observed in the summer activity of *M. lucifugus* in 2009 appears to coincide with the outbreak and rapid spread of WNS, which had been reported from only four hibernacula in the winter of 2006–2007, but then from 38 in 2007–2008, and over 65 in 2008–2009 [8]. The absence of a decline in the activity of *M. lucifugus* during the summer of 2008 relative to 2007 suggests that bats wintering in the 38 sites affected by the end of 2007–2008 did not account for a large proportion of the summer population in our study area, despite the fact that our sites were within the typical migration range of *M. lucifugus* from the northeastern US (240–275 km;

[9]). Prior to the discovery of WNS, more than 80 per cent of *M. lucifugus* populations were projected to be stable or increasing [6], but with bat populations plummeting by 75–99 per cent since the discovery of WNS [1,6], the bat once considered as the most common bat species in North America may become regionally extinct within 16 years [6].

Our results demonstrate the impact of WNS on summer activity levels of *M. lucifugus*, and suggest that reduced levels of summer bat activity reflect mortality of *M. lucifugus* in winter hibernacula. We hypothesize that sites where broader ecological consequences of WNS (i.e. vastly reduced predation on nocturnal insects) will occur extend beyond the immediate vicinity of wintering hibernacula where WNS has killed bats, and cannot necessarily be predicted by assessing the mortality of bats at a given wintering site. Plummeting summer activity of *M. lucifugus*, but not *L. cinereus* further supports the claim that, to date, WNS affects only cave-dwelling bats, and suggests that there are few to none unaffected hibernacula left within the WNS epicentre. The drastic decline we observed in *M. lucifugus* activity suggests that WNS is most probably affecting many, if not most *M. lucifugus* populations in northeastern America. We propose that WNS affects the entire bat population of an area, and not only individual hibernacula.

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