Changes in the Forest Bat Community After Arrival of White-Nose Syndrome in the Ouachita Mountains of Arkansas

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Abstract - Populations of some cave-hibernating bats have undergone declines in recent years due to an introduced fungus (*Pseudogymnoascus destructans*) that causes the disease white-nose syndrome (WNS), which is often fatal to bats during hibernation. Unprecedented declines in cave-hibernating species have the potential to change community composition via numerous mechanisms, including competitive release. We trapped bats for 6 years in the Ouachita Mountains of Arkansas prior to the arrival of WNS in the region and compared capture rates of 7 species to capture rates collected in 2020–2021 after WNS establishment. We found a 98% decline in *Myotis septentrionalis* (Northern Long-eared Bat) and a 77% decline in *Perimyotis subflavus* (Tricolored Bat) after WNS became prevalent. *Nycticeius humeralis* (Evening Bat) captures increased by 220% after WNS. Capture rates of *Eptesicus fuscus* (Big Brown Bat) increased by 100%, but this increase was not significant. We also found no significant differences in captures rates for *Lasiurus borealis* (Eastern Red Bat), *Lasiurus seminolus* (Seminole Bat), and *Lasiurus cinereus* (Hoary Bat) after the arrival of WNS. Our results indicate that the forest bat community of the Ouachita Mountains has been altered since the arrival of WNS in 2012, but it is unknown if these changes are permanent or if species will decline further or recover via adaptive or genetic changes in their populations in the future.

Introduction

Populations of some cave-hibernating bats have declined precipitously in the past 15 years due to white-nose syndrome (WNS), a disease caused by the fungus *Pseudogymnoascus destructans* (Blehert & Gargas) Minnis & D.L. Lindner (*Pd*). *Pd* is a psychrophilic (cold-loving) fungus that damages the skin of bats and causes them to arouse during hibernation, which in turn exhausts their fat reserves and causes mortality (Blehert et al. 2009, Frick et al. 2010, Langwig et al. 2012). Based on hibernacula counts, range-wide declines of over 90% have occurred in some species, including *Myotis septentrionalis* Trouessart (Northern Long-eared Bat), *Myotis lucifugus* (Le Conte) (Little Brown Bat), and *Perimyotis subflavus* (F. Cuvier) (Tricolored Bat) (Cheng et al. 2021). Summer surveys in forests have also found substantial declines in the activity of these bat species (e.g., Dzal et al. 2011, Francl et al. 2012). These declines prompted the US Fish and Wildlife Service (USFWS) to list the Northern Long-eared Bat as federally endangered, and the Tricolored Bat and Little Brown Bat are currently undergoing review (USFWS 2017, USFWS 2022).

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Substantial declines in some bat species due to WNS could affect the abundance of non- susceptible species through competitive release. Spatial and temporal niche partitioning likely occurs in sympatric bat species, especially at foraging areas (Arlettaz 1999, Arlettaz et al. 2000, Kunz 1973, Nicholls and Racey 2006), and changes in bat community structure and niche partitioning have been observed in areas where WNS has become widespread (Jachowski et al. 2014). Recent studies have found increases in bat species that are not affected by WNS, including *Lasiurus borealis* Müller (Eastern Red Bat), *Eptesicus fuscus* (Palisot de Beauvis) (Big Brown Bat), and *Nycticeius humeralis* (Rafinesque) (Evening Bat) in response to declines in WNS-affected species (Francl et al. 2012, Johnson et al. 2021, Petit and O'Keefe 2017, Thalken et al. 2018).

In the Ouachita Mountain region of Arkansas and Oklahoma, the status of WNS-vulnerable species and the overall effects of WNS on the bat community is unknown. *Pd* was first reported in Arkansas in 2012 (AGFC 2017) and has since spread throughout the Interior Highlands region. *Pd* was first detected in the Ouachita Mountains during winter 2014–2015. Because sites where WNS-affected bats hibernate in winter are mostly unknown in the Ouachita region, surveys of bat activity in forests are a more suitable method than hibernacula counts to determine status of these populations. Prior to the invasion of WNS into Arkansas (pre-WNS), we conducted extensive netting in an area of the Ouachita National Forest to characterize the forest bat community during the active season (Perry et al. 2010). Our goal here was to resample this area after WNS became widespread in Arkansas (post-WNS) to determine how this disease has affected the overall bat community and status of bat species in forests of the Ouachita Mountains.

Methods

We conducted the study in a 6545-ha area on the Jessieville–Fourche–Winona Ranger District of the Ouachita National Forest situated in Saline County in the Ouachita Mountains of west-central Arkansas (approximately 34º48'N, 92º58'W). The Ouachita Mountain ecological subregion extends from central Arkansas into eastern Oklahoma. The area is humid, with hot, frequently dry summers and mild winters. Predominant forest types are *Pinus echinata* Mill. (Shortleaf Pine)–hardwood and *Quercus* (oak)–*Carya* (hickory). Few caves exist, but abandoned mines serve as hibernacula for bats throughout the region. However, no known caves or abandoned mines existed in the study area.

Pre-WNS invasion, we captured bats using 1−8 mist nets (2.6−12.0 m wide x 2.6 m tall) at 6 sites between 24 May and 17 September, 2000−2005 and 2007−2008 (Perry et al. 2010). We revisited these sites for post-WNS sampling in 2020 and 2021. Netting sites were centered on stream pools (typically ~600 m^2) that occurred beneath the forest canopy (n = 5), or on the Alum Fork of the Saline River (n = 1). For all sampling, we opened mist nets at dusk (~2115–2200 h CST, depending on month) and monitored them continuously for 2–5 h. We sampled each site 9–22 times pre-WNS and 5–8 times post-WNS.

For all captured bats, we determined sex, reproductive condition, and age class (juvenile or adult) based on the degree of ossification of metacarpal–phalanx joints (Racey 1974); we could not distinguish juveniles from adults for most species beyond the first week of August. We banded bats during the pre-WNS sampling but did not band bats in the post-WNS sampling; therefore, to make pre- and post-WNS data comparable, we included all captures regardless of recapture status. We followed the Guidelines of the American Society of Mammalogists for the use of wild mammals in research (Gannon et al. 2007) for pre-WNS surveys, and post-WNS sampling methods were approved by the US Forest Service Institutional Animal Use and Care Committee (2020-004).

To ensure pre- and post-WNS sampling was comparable, we sampled the same sites using similar net placement both pre- and post-WNS. Because perceived abundance of bat species may differ throughout the summer due to changes in reproductive condition and migratory status (Perry et al. 2010), we sampled each trap site multiple times during the same periods of summer in both pre- and post-WNS sampling. For example, if a site was sampled in early July in pre-WNS sampling, this site was sampled during this same period in post-WNS sampling. Overall, we included in our analysis 92 nights of trapping pre-WNS arrival and 38 nights of trapping post-WNS.

Multiple mist-nets were typically concentrated over a single stream pool for each trapping session. We found no significant positive correlation (Pearson correlation coefficients) between the total number of bats captured each night and sample effort, including number of nets placed ($r = 0.04$, $P = 0.622$), the total area of nets (m^2 of net area; $r = -0.03$, $P = 0.726$), number of nets x hours open ($r = 0.15$, $P = 0.073$), or total area of nets x hours open ($r = 0.10$, $P = 0.252$). Consequently, we used number of bats captured each night as our datum. We used mean captures/night for each species as an index of relative abundance, with all pre-WNS sample years combined and all post-WNS sample years combined. For each species, we compared the distributions of pre- and post-WNS capture rates using AIC (Burnham and Anderson 2002) to determine the best model distribution. We compared models with Poisson, zero-inflated Poisson, negative binomial, and zero-inflated negative binomial distributions, with and without "site" as a random variable using SAS 9.4 (SAS Institute Inc., Cary, NC). We used the distribution with the lowest AIC to compare *F*-values and significance of differences between pre- and post-capture rates.

Results

We captured 1477 bats over the 8 pre-WNS years and 697 bats over the 2 post-WNS sample years (Table 1). A negative binomial distribution was the best fit (lowest AIC) among the 4 distributions for all species except for Big Brown Bats, which exhibited a Poisson distribution; Northern Long-eared Bat, Evening Bat, and *Lasiurus cinereus* (Palisot de Beauvois) (Hoary Bat) models included "site" as a random effect. Eastern Red Bats were the most captured species, comprising 77% of pre-WNS captures and 82% of post-WNS captures. Northern Long-eared

Bats were the second-most captured species pre-WNS (9% of total captures) but constituted only 0.1% of post-WNS captures. Only a single Northern Long-eared Bat (juvenile female) was captured post-WNS, which was caught during the first night of trapping in 2020. Mean number of Northern Long-eared Bat captures/night declined significantly between pre-and post-WNS from 1.46 to 0.30 (a 98% decline in capture rates; Table 1). Tricolored bats comprised 3.5% of pre-WNS captures but only 0.7% of captures post WNS. Capture rates of Tricolored Bats declined from a mean of 0.57 captures/night pre-WNS to 0.13 captures/night post-WNS (a 77% decrease).

Evening Bats showed a significant increase in captures/night from 0.74 captures/night pre-WNS to 2.37 captures/night post-WNS (a 220% increase in capture rate). We found no significant difference between pre- and post-WNS capture rates for *Lasiurus seminolus* (Rhoads) (Seminole Bat) or Hoary Bat. Although captures/night for Big Brown Bats increased 100% from pre- to post-WNS (0.12 captures/night pre-WNS versus 0.24 captures/night post-WNS), this increase was not significant. We captured no *Lasionycteris noctivagans* (Le Conte) (Silver-haired Bat) post-WNS, although we captured 13 bats pre-WNS.

Discussion

We found evidence of significant changes in the forest bat community after invasion of WNS, consistent with results from other studies (e.g., Francl et al. 2012, Johnson et al. 2021, Pettit and O'Keefe 2017, Thalken et al. 2018). The greatest

Table 1. Total number of bats captured (*n*), mean capture rates (number of captures/night), and percent change in mean capture rates from pre- to post-WNS for 7 bat species (and all species combined) captured in the Ouachita Mountains of Arkansas over 8 years (2000–2008) prior to the arrival of white-nose syndrome (pre-WNS) in the region in 2014, and during 2 years (2020–2021) after WNS became widespread (post-WNS). * indicates stastistically significant differences between periods. For reasons explained in the Discussion, we did not compare pre- and post WNS captures for Silver-haired Bats.

	Pre-WNS (*n* = 92 nights)			Post-WNS (*n* = 38 nights)			Percent		
Species	*n*	Mean	SE	*n*	Mean	SE	change	F^A	*P*
Eastern Red Bat	1137	12.35	1.71	569	14.97	2.25	+21	0.69	0.407
Northern Long-eared Bat[C]	134	1.46	0.19	1	0.03	0.03	-98	15.98	0.001*
Evening Bat[C]	68	0.74	0.10	90	2.37	0.45	+220	25.20	0.001*
Tricolored Bat	52	0.57	0.09	5	0.13	0.07	-77	8.64	0.004*
Seminole Bat	29	0.30	0.07	12	0.32	0.09	+7	0.00	0.997
Silver-haired Bat	13	0.21	0.08	0	0.00	0.00	-	-	-
Big Brown Bat[B]	11	0.12	0.04	9	0.24	0.08	+100	2.31	0.131
Hoary Bat[C]	37	0.40	0.10	10	0.26	0.08	-35	0.37	0.545
All species	1481	16.05	1.79	696	18.34	2.42	+14	0.49	0.488

[A]Test for fixed effects in negative binomial models.
[B]Poisson model was the best fit using AIC.
[C]Included site as a random effect.

change in the bat community was the near disappearance of Northern Long-eared Bats across the study area. Prior to invasion of *Pd* into the Ouachita Mountains, Northern Long-eared Bats were the second most captured species and they composed around 9% of all captures. However, we found a 98% decline in captures for this species, similar to range-wide decline estimates of >90% derived from hibernacula surveys (Cheng et al. 2021). Northern Long-eared Bats are greatly affected by WNS, with activity and capture rates in forests declining 77–94% in various regions of the eastern US after invasion of *Pd* (Ford et al. 2011, Francl et al. 2012, Moosman et al. 2013, Reynolds et al. 2016, Thalken et al. 2018).

Populations of Tricolored Bats have also experienced notable declines in the northeastern US after WNS invasion (e.g., Thalken et al. 2018). Cheng et al. (2021) found initial declines of 35% for Tricolored Bats during the *Pd* invasion phase (the first year of *Pd* detection and the year following; Langwig et al. 2015), but their decline increased to 93–100% after *Pd* became established in a region (years 5–7 following detection of *Pd*). We found capture rates of Tricolored Bats declined by 77%, which was the second-largest decline among bat species in our study for which we compared pre- and post-WNS capture rates. Francl et al. (2012) found a 77% decline in captures of Tricolored Bats in West Virginia and O'Keefe et al. (2019) found an 82% decline in the southern Appalachians after *Pd* became established, whereas capture rates of Tricolored Bats in other regions during *Pd* invasion have declined from 12% to 36% (Pettit and O'Keefe 2017, Thalken et al. 2018). Winter surveys of hibernating Tricolored Bats in abandoned mines in the Ouachita Mountains (years 2014–2022) indicated relatively persistent, yet small numbers returning to hibernate each year during and after invasion of *Pd* (Perry and Jordan 2020; R.W. Perry and P.N. Jordan, unpubl. data). However, the largest known colony of hibernating Tricolored Bats in the Ouachita Mountains was in Pip Mine, where the hibernating population (years: 1983–2014) averaged 667 bats (min–max = 513–1392) but declined to only 6 individuals in 2017 (a 99.1% decline) (B. Sasse, Arkansas Game and Fish Commission, Mayflower, AR, pers. comm.)

Although captures of Big Brown Bats doubled post-WNS, this difference was not statistically significant. Various studies have found increases in Big Brown Bats associated with declines in Little Brown Bats and Northern Long-eared Bats due to WNS (Deeley et al. 2021, Hauer et al. 2019, Johnson et al. 2021), and studies suggest that increases in activity of Big Brown Bats following the decline in *Myotis* species may be a result of competitive release (Johnson et al. 2021, Morningstar et al. 2019). However, others have found only marginal increases or no significant difference in Big Brown Bat detections after WNS (e.g., Francl et al. 2012, Huebschman 2019, Moosman et al. 2013, O'Keefe et al. 2019, Pettit and O'Keefe 2017). Francl et al. (2012) suggested that increases in captures of Big Brown Bats post-WNS were not necessarily due to an increase in abundance but may have been a result of reductions in Little-Brown Bats at foraging areas, which allowed Big Brown Bats access to forage in areas where they were previously suppressed.

We found capture rates of Evening Bats increased by 220% in our post-WNS sampling, similar to increases in Evening Bats captures following *Pd* invasion observed in Kentucky and Indiana (Pettit and O'Keefe 2017, Thalken et al. 2018). Capture rates of Evening Bats in our study increased by 1.63 captures/night after WNS, whereas capture rates of Northern Long-eared Bats decreased by a similar 1.43 captures/night. Consequently, Evening Bats and to a lesser extent Big Brown Bats, could be experiencing competitive release (Francl et al. 2012, Jachowski et al. 2014, Thalken et al. 2018) with the reduction in foraging activity of Northern Long-eared Bats in areas where we trapped. Bombaci et al. (2021) suggested that increases in species that are not susceptible to WNS likely arise only in areas where a greater opportunity for competitive release occurs, and because Northern Long-eared Bats were previously the second-most captured species in our study area, their decline could have provided an opportunity for competitive release of Evening Bats.

Silver-haired Bats are not believed to be negatively affected by WNS (Francl et al. 2011) but are often killed at wind turbines (Arnett et al. 2016). Although we captured 13 Silver-haired Bats pre-WNS and none post-WNS, we did not compare captures of Silver-haired Bats pre- and post-WNS. Silver-haired Bats are only winter residents in Arkansas and are just sporadically captured there in May and September during migration (Perry et al. 2010). Furthermore, apparent abundance of this species may vary widely among years (Whitaker and Hamilton 1998). In Arkansas, they typically first appear in mid- to late-September, though the arrival date can vary from year to year (Perry et al. 2010). Consequently, we believe our post-WNS sampling in late May and early September was inadequate to make inferences on relative abundance of Silver-haired Bats and we did not conduct comparative analyses for this species.

Wind turbines pose a risk to migratory bats, including Silver-haired Bats, Eastern Red Bats, and Hoary Bats, with the majority of mortalities occurring in Hoary Bats (Arnett et al. 2016). Frick et al. (2017) suggested mortality from wind turbines may reduce population size and increase the risk of extinction of Hoary Bats. Others have also suggested that Eastern Red Bat populations are in decline (Winhold et al. 2008), which could be exacerbated by wind development due to high numbers of this species killed at turbines. Although some studies have suggested increased captures or activity by Eastern Red Bats after arrival of WNS (e.g., Thalken et al. 2018) or slight decreases (Jachowski et al. 2014), most have found no difference in capture rates or acoustic activity of Eastern Red Bats after arrival of WNS (Ford et al. 2011, Francl et al. 2012, Huebschman 2019, O'Keefe et al. 2019). Wind-turbine farms do not currently occur in the Ouachita Mountains, but they could have a negative effect on Eastern Red Bats migrating from other regions. Nevertheless, although our pre- and post-WNS sampling was separated by an 11-year period, we found no significant differences in captures rates between pre- and post-WNS for Eastern Red Bats, Seminole Bats, or Hoary Bats.

We found that the bat community in forests of the Ouachita Mountains has been altered since the arrival of WNS in 2012, with significant declines in Northern

Long-eared Bats and Tricolored Bats and substantial increases in detections of Evening Bats. It is unknown if these changes are permanent or if species will recover via adaptive or genetic changes in their population. Alternatively, populations of Northern Long-eared Bats and Tricolored Bats could continue to decline until extirpation occurs.

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