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Seven-year impact of white-nose syndrome on tri-colored bat (*Perimyotis subflavus*) populations in Georgia, USA

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ABSTRACT: White-nose syndrome (WNS) has emerged as the most serious threat to North American cave-dwelling bat species, with an estimated mortality of over 6 million since it was first documented in the USA in 2006. Tri-colored bat *Perimyotis subflavus* is one of the species most affected, with hibernaculum counts at caves in WNS-positive regions reduced by >90% from previous counts. While declines have been documented in hibernaculum surveys, long-term monitoring programs during active seasons provide a unique opportunity to examine population trends and impact of population declines post-WNS. We developed generalized linear mixed models using data from a state-wide, long-term (2011–2020) mobile bat acoustic monitoring program in Georgia, USA, to better understand *P. subflavus* population trends before and after disease detection and between WNS-negative and WNS-positive regions. We recorded 5046 *P. subflavus* passes across all acoustic routes during the 10 yr time period. We detected a significant decrease in activity 2 yr after disease detection in the WNS-positive region, whereas activity in the WNS-negative region remained stable over time. Understanding changes in bat populations as WNS spreads and measuring the magnitude of population declines to assess disease impacts is crucial for providing appropriate guidance for management. Our results provide evidence of the critical status of *P. subflavus* in the southernmost WNS-positive region, but also emphasize the importance of monitoring WNS spread to new regions, as those that remain WNS-free could provide refugia for the species and a potential source of recolonization to WNS-affected areas.

KEY WORDS: *Perimyotis subflavus* · Tri-colored bat · White-nose syndrome · Acoustic monitoring · Bat activity · GLMM · Mobile routes

1. INTRODUCTION

North American bat species face several conservation challenges throughout their range, including habitat loss and modification, pesticides, and mortality associated with wind-energy development (Mickleburgh et al. 2002, Voigt & Kingston 2016, Frick et al. 2020). Since first documented in New York in 2006 (Blehert et al. 2009), white-nose syndrome (WNS), an epizootic, infectious fungal disease caused by *Pseudogymnoascus destructans* (*Pd*), has emerged as the most serious threat to cave-dwelling North American bats, with mortality estimated at more than 6 million in eastern North America (US Fish and Wildlife Service 2019). *Myotis septentrionalis* (northern long-eared bat), *M. lucifugus* (little brown bat), and *Perimyotis subflavus* (tri-colored bat) are among the most susceptible species, with winter counts in WNS-positive regions declining by more than 90% for each species since WNS detection (Cheng et al. 2021).

Monitoring populations affected by WNS is a critical conservation action for bats in eastern North

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America. Many studies on the effects of WNS have focused on hibernating bat surveys or detecting *Pd* on captured bats or in environmental samples (e.g. Langwig et al. 2012, Powers et al. 2015, Verant et al. 2018). However, long-term acoustic monitoring programs can be used to characterize how WNS-associated mortality and colony declines observed within hibernacula translate into activity declines outside the hibernation period (e.g. Moosman et al. 2013, Pettit & O'Keefe 2017, Nocera et al. 2019, Hicks et al. 2020, Johnson et al. 2021). Acoustic monitoring is an efficient method for collecting data at large spatial scales and can be conducted in areas where bat capture is not possible (Duffy et al. 2000, Flaquer et al. 2007, Kunz et al. 2009). In addition, the creation of standardized protocols by national programs, such as the North American Bat Monitoring Program (Loeb et al. 2015), advance the collection of large-scale data on bat foraging activity (Simonis et al. 2020). These data are important for documenting changes in activity for species threatened by wind energy or WNS (Whitby et al. 2014, Loeb et al. 2015).

P. subflavus is a solitary bat species that roosts in trees or buildings in summer and hibernates in trees, caves, rock crevices, mines, bridges, and culverts (Fujita & Kunz 1984, Leivers et al. 2019). It was formerly considered one of the most common and widely distributed bats in eastern North America (see Fig. 1), but is currently listed as Vulnerable by the IUCN (Solari 2018) and is being considered for listing under the US Endangered Species Act (ESA) (US Fish and Wildlife Service 2017) due to WNS-related declines. Presence of WNS in *P. subflavus* hibernacula has been confirmed across an estimated 59% of the total distribution (Cheng et al. 2021), and population declines have been documented throughout most of the range (Hoyt et al. 2021).

WNS was first documented in *P. subflavus* in northwestern Georgia in 2013 during hibernaculum counts, and the population subsequently experienced a significant decline (Georgia Department of Natural Resources 2020). *P. subflavus* predominately hibernates in caves in northwestern Georgia (Georgia Department of Natural Resources 2020), which is characterized by karst topography and high cave density. However, populations in the remainder of the state, which has low cave density, have not been assessed to document the full impact of WNS. Throughout the range, some *P. subflavus* individuals exhibit short- (Bisson et al. 2009, Samoray et al. 2019) or long-distance (Fraser et al. 2012) latitudinal migrations. Anecdotal information suggests that some individuals in Georgia undergo latitudinal migrations between summer areas and hibernation sites (Lutsch 2019, Samoray et al. 2019). However, the role of bat migration in spreading *Pd* between summer areas and hibernacula is not fully understood (Bernard et al. 2020). Our objective was to determine the magnitude of WNS-related population declines before and after the arrival of WNS and in areas with and without significant numbers of caves. Although *Pd* was detected in road culverts at 2 locations outside of the known WNS-affected area in the state during the study, no WNS-affected bats were observed (Georgia Department of Natural Resources 2020). Thus, we hypothesized a decline in *P. subflavus* activity in the northern region of the state after WNS was detected, but that activity would be stable across years in the southern region.

2. MATERIALS AND METHODS

2.1. Mobile acoustic route protocols

We used data from mobile acoustic surveys conducted by the Georgia Department of Natural Resources (GADNR) from 2011 to 2020. Surveys were conducted by GADNR biologists, federal agency biologists, and private citizens as part of a volunteer-based citizen science program. Volunteers were required to register with GADNR, have a vehicle capable of driving on secondary roads, and commit to conducting the surveys over multiple seasons. Volunteers were also required to watch an instructional training video prior to conducting surveys. Based on volunteer availability and weather conditions, some routes were not surveyed every year.

GADNR initially established mobile acoustic routes in 2011 following established protocols (Britzke & Herzog 2009, Loeb et al. 2015), adding routes throughout the study up to a total of 45 (Fig. 1). Route selection was based on long-term route accessibility, safety of surveyors and other motorists, and consideration for representing available habitat types. Roads selected for routes were primarily 2-laned secondary or tertiary roads with minimal stops. Route lengths ranged from 10 to 67 km. Surveys started 30 to 45 min after sunset, with surveyors driving 24 to 32 km h^{-1} to increase the likelihood that each bat detection was an individual bat without repeats (Roche et al. 2011).

2.2. Bat acoustic sampling

We recorded bat echolocation calls in zero-crossing format using Anabat SD1 and SD2 acoustic recording

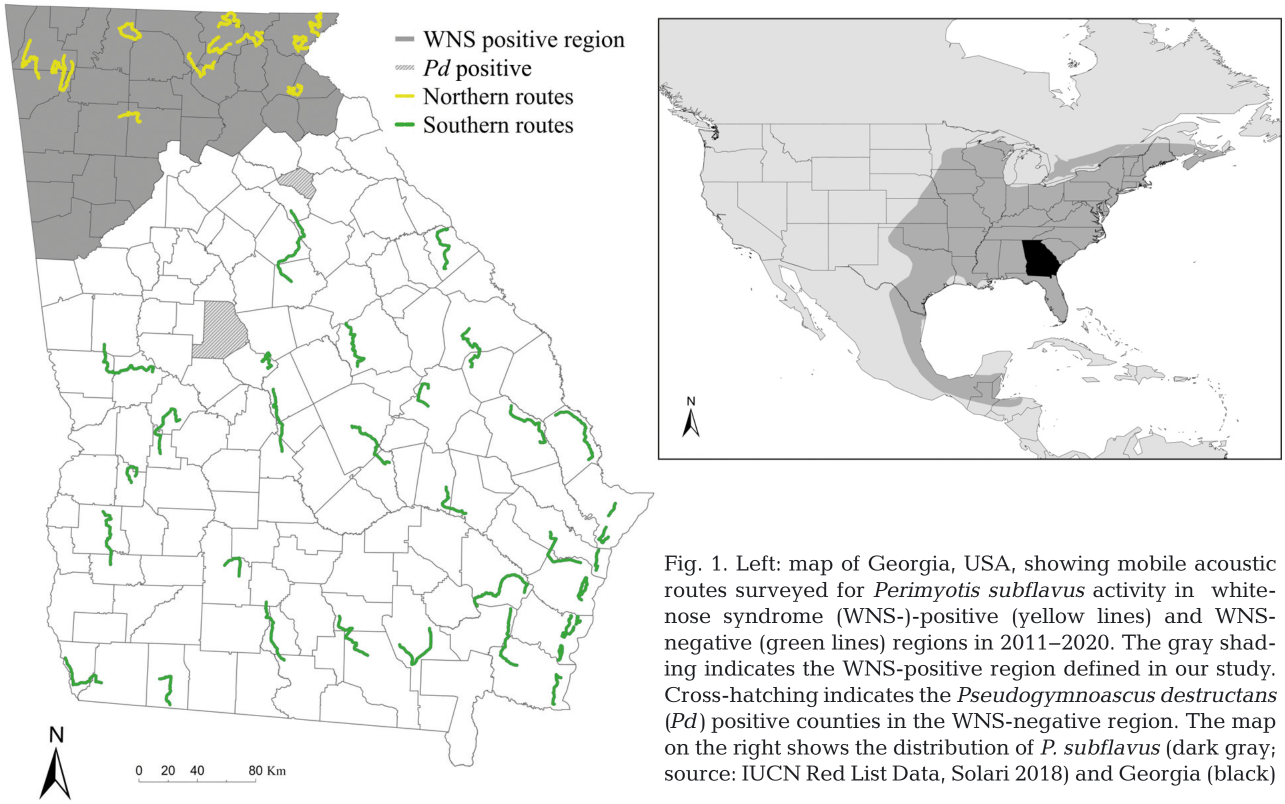

Fig. 1. Left: map of Georgia, USA, showing mobile acoustic routes surveyed for *Perimyotis subflavus* activity in white-nose syndrome (WNS-)-positive (yellow lines) and WNS-negative (green lines) regions in 2011–2020. The gray shading indicates the WNS-positive region defined in our study. Cross-hatching indicates the *Pseudogymnoascus destructans* (*Pd*) positive counties in the WNS-negative region. The map on the right shows the distribution of *P. subflavus* (dark gray; source: IUCN Red List Data, Solari 2018) and Georgia (black)

units (Titley Electronics) with omnidirectional microphones pointed straight up from the roof of a vehicle. Anabat units were calibrated each year to minimize variability in sensitivity among detectors (Larson & Hayes 2000). We set recording sensitivity to 7 (but adjusted when needed based on noise and environment throughout the route), audio division ratio to 16, and data division ratio to 8 to reduce data storage by reducing the resolution of each call (Britzke & Herzog 2009, Loeb et al. 2015). A Global Positioning System (GPS) accessory was connected to the acoustic recorder to geo-reference routes and call locations. Surveys were scheduled when the weather was forecasted to be optimal (i.e. no rain and light or minimal wind), and most were conducted twice from late May through early September. Start and end times, temperature, wind speed, and cloud cover were recorded before and after each survey. We recorded deviations to the route or survey protocol (inclement weather, prolonged periods of stopping, road closures, construction, etc.).

2.3. Bat call analysis

We used auto ID software and subsequent visual vetting to identify calls to species, as recommended by the North American Bat Monitoring Program (NABat; Reichert et al. 2018). We first filtered out noise files using Kaleidoscope Pro 5.4.1 software (Wildlife Acoustics). We selected default filter setting parameters for bat analysis specifying a signal of interest between 8 and 120 kHz, 2 to 500 ms, and at least 2 pulses per sequence. We used the Batch function in Kaleidoscope Pro to split each sequence to a maximum duration of 10 s for standardization, and the auto classifier of Kaleidoscope Pro with a balanced sensitivity level for classification to assist the visual vetting. Subsequently, we manually analyzed all non-noise files using call structure, frequency of minimum and maximum energy, duration, and interpulse interval (O'Farrell & Gannon 1999, Russo & Jones 2002).

2.4. Data analysis

We examined trends in relative *Perimyotis subflavus* activity over 10 yr (2011–2020) between northern (WNS-positive) and southern (WNS-negative) regions of Georgia using generalized linear mixed-effects models (GLMM) in the R (R Core Team 2020) package 'glmmTMB' (Brooks et al. 2017). We quantified relative bat activity as the mean number of bat passes during the nights sampled each year divided by the length (km) of each route (passes km^{-1}). Because bats

Table 1. Summary of mobile acoustic routes conducted to examine *Perimyotis subflavus* activity in Georgia, USA, 2011–2020, including number of nights sampled, total route distance (km) surveyed, number of white-nose syndrome (WNS)-negative (–) and WNS-positive (+) routes, total number of passes recorded on WNS– and WNS+ routes, and mean activity (passes km^{-1} of route) in WNS– and WNS+ areas each year

Year	Nights	Total route distance	WNS– routes	WNS+ routes	WNS– total passes	WNS+ total passes	WNS– mean activity (SD)	WNS+ mean activity (SD)
2011	15	525.7	11	4	230	107	0.76 (0.62)	0.63 (0.27)
2012	23	812.0	10	7	253	189	0.59 (0.41)	0.57 (0.37)
2013	24	1040.0	9	7	274	205	0.44 (0.34)	0.56 (0.38)
2014	31	1125.5	15	5	395	228	0.70 (0.66)	0.62 (0.42)
2015	34	1249.5	15	5	518	149	0.81 (0.99)	0.41 (0.22)
2016	45	1671.0	21	8	488	130	0.59 (0.95)	0.22 (0.35)
2017	43	1517.2	19	10	560	59	0.94 (1.42)	0.10 (0.07)
2018	50	1796.75	20	10	351	54	0.45 (0.58)	0.09 (0.08)
2019	41	1435.5	16	8	402	44	0.51 (0.46)	0.11 (0.09)
2020	48	1731.3	17	9	363	47	0.41 (0.49)	0.09 (0.13)

are assumed to be encountered only once along a route, our measure of relative activity can be considered an index of relative abundance (Roche et al. 2011, Braun de Torrez et al. 2017). We performed a Shapiro-Wilks test for normality and found that the response variable (relative bat activity) was not normally distributed ($p < 0.001$). Therefore, we used a negative binomial distribution, which also accounts for overdispersion (Brooks et al. 2017). We included route as a random effect to account for inconsistencies due to surveyors. We created 1-county buffers adjacent to known WNS-positive counties (those in which bats were observed with lesions indicative of WNS) to define the WNS-positive and WNS-negative regions (Fig. 1). With relative activity as the response variable, we built 11 candidate models (including global and null) that included individual variables and plausible additive and interactive combinations of region (WNS-positive and WNS-negative), year, elevation, and climate variables (wind and cloud cover at the beginning of the survey, and mean temperature). We specified the WNS-negative region as the reference group. We determined mean elevation on each route using the summarize elevation tool in ArcGIS Pro 2.8.0 (Esri). We tested for correlation among continuous predictor variables using Pearson's correlation coefficient to ensure that highly correlated ($r \geq |0.7|$) variables were not included in the same model. We used Akaike's Information Criterion corrected for small sample sizes (AIC_c) to calculate Akaike model weights (ω_i) and determine the most parsimonious model(s) (Burnham & Anderson 2002). We considered models <2 AIC_c units from the top model to be potentially informative. We evaluated the best-supported models for goodness-of-fit and over- and under-dispersion in the form of a QQ plot, residual plot, and a 1-sample Kolmogorov-Smirnov test using the DHARMa package (Hartig 2020) in R.

3. RESULTS

We recorded a total of 5046 *Perimyotis subflavus* echolocation passes on routes from 2011 (2 yr prior to the detection of WNS in northwestern Georgia) through 2020 (Table 1). The top model explaining *P. subflavus* relative activity included the variables region (WNS-positive and WNS-negative), year, and their interaction (Table 2). No other model was within $\Delta AIC_c < 2$ of the top model.

Relative activity of *P. subflavus* declined over time following WNS detection in Georgia ($p = 0.001$, Fig. 2, Table 3). Our analyses also indicated differences in activity between regions ($p < 0.001$, Table 3), beginning in 2015 and stabilizing in the WNS-positive region at values below half of pre-WNS detection activity levels between 2016 and 2020 (Fig. 2). In contrast, relative activity remained constant throughout the study in the WNS-negative region.

Table 2. Top 5 models, number of parameters (*K*), corrected Akaike's Information Criterion (AIC_c), difference between a model and the model with the lowest AIC_c value (ΔAIC_c), and model weight (ω_i) used to predict *Perimyotis subflavus* relative activity in Georgia, USA, 2011–2020

Model	*K*	AIC_c	ΔAIC_c	ω_i
Region + Year + Region × Year + (1|Route)	6	1589.76	0.00	1
Global	15	1621.35	31.59	0
Region + Year + (1|Route)	5	1622.29	32.53	0
Year + (1|Route)	4	1631.42	41.66	0
Elevation + (1|Route)	4	1663.79	74.03	0

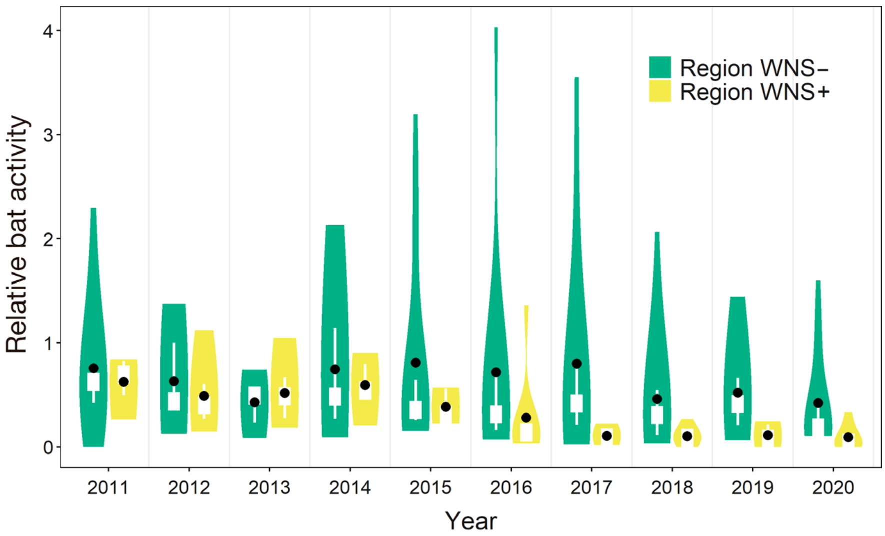

Fig. 2. Relative activity (bat passes per km of route) of *Perimyotis subflavus* determined using mobile acoustic routes for each year and region (WNS-positive [+] and WNS-negative [−]) in Georgia, USA, 2011–2020. WNS was first documented in northwestern Georgia in 2013. Density plots show the data distribution; white vertical lines: interquartile ranges; white squares: median; black circles: mean. Note: width of plots adjusted for visualization purposes

Table 3. Parameters with estimates, SE, 95% confidence intervals (CI), *z*-values, and p-values for top model output of *Perimyotis subflavus* relative activity in Georgia, USA, 2011–2020

Parameter	Estimate	SE	CI lower	CI upper	*z*	p
Intercept	151.69	46.49	75.22	228.18	3.26	0.001
Year	−0.07	0.02	−0.11	−0.04	−3.24	0.001
Region WNS-positive	583.22	102.95	413.89	752.55	5.67	<0.001
Region WNS-positive × Year	−0.29	0.05	−0.37	−0.21	−5.68	<0.001

4. DISCUSSION

The changes in *Perimyotis subflavus* acoustic activity we observed were consistent with our predictions and similar to patterns in northern WNS-positive regions of eastern North America. Previous studies found a decrease in acoustic activity following WNS detection (Ingersoll et al. 2013, Nocera et al. 2019, Deeley et al. 2021). A similar trend in population decline was reported for the federally threatened *Myotis septentrionalis* following WNS detection in the same WNS-positive region in Georgia where our study occurred (Grider 2020). Both species were abundant and widely distributed in northern Georgia prior to WNS. As observed in multiple bat species affected by WNS across eastern North America, (Ingersoll et al. 2013, Powers et al. 2015, Reynolds et al. 2016, Nocera et al. 2019, Cheng et al. 2021), our temporal and spatial analysis of relative activity suggests no signs of recovery in the WNS-positive region since the disease was detected. Furthermore, our data indicate that *P. subflavus* populations are no longer declining, but stabilized at low densities within 3 yr of the arrival of WNS. Stabilization at low population densities following rapid initial decline is likely explained by density-dependent transmission due to the solitary hibernating behavior of *P. subflavus* (Langwig et al. 2012).

Although relative activity decreased in the WNS-positive region following WNS detection, as we hypothesized, activity remained relatively stable during the study in the WNS-negative region. *Pd* was detected in 2 counties in the WNS-negative region in 2020, but with no signs of the disease affecting individual bats or population abundance (Georgia Department of Natural Resources 2020). Whether *Pd* will continue to spread southward or whether bats outside the current WNS-positive area will acquire clinical disease is unknown. If populations in the southern extent of the range are not affected, that area could provide refugia and potentially function as a source to ultimately recolonize northern WNS-affected populations of *P. subflavus* and other WNS-susceptible bat species with distributions extending outside high cave density areas. Conversely, latitudinal movements from southern summer areas to northern hibernacula in WNS-positive areas (Samoray et al. 2019) could result in northern hibernacula functioning as a population sink in the long term.

We observed a time lag between initial WNS detection and significant changes in *P. subflavus* relative activity becoming evident. Although the disease was first documented in northwest Georgia in 2013 and spread across the northern part of the state during 2013 to 2014 (US Fish and Wildlife Service 2019), our results suggest that relative activity started declining 2 yr after WNS detection and reached a stable observed low by 2016. Similar time lags were observed in other bat species following initial detection (Reynolds et al. 2015, Nocera et al. 2020). Indeed, studies indicate that the transition from *Pd* introduction to populations showing signs of decline occurs within 1 to 5 yr, with variation among species and locations (Bernard & McCracken 2017, Frick et al. 2017, Barr et al. 2021). Based on disease progression, monitoring time lags in WNS manifestation is important for understanding how it will affect new populations and for implementing proactive management actions prior to the mass mortality characteristic of peak WNS (Bernard et al. 2019).

To date, few studies have used mobile acoustic monitoring to examine bat activity trends following disease outbreak and other mass mortality causes (Simonis et al. 2020). Stationary acoustic surveys may be more efficient than mobile acoustic surveys in sampling bat community richness and in detecting rare and/or road-avoiding species, such as bats of the genus *Myotis* (Tonos et al. 2014, Braun de Torrez et al. 2017). However, mobile acoustic surveys offer an effective way to increase the geographic scope of surveys, providing useful information on bat trends and distribution by sampling diverse habitats over large areas (Roche et al. 2011, Whitby et al. 2014, Fisher-Phelps et al. 2017). In our study, the mobile acoustic methodology used was effective in documenting changes in activity of a WNS-threatened species at a large scale across landscape conditions (Whitby et al. 2014, Loeb et al. 2015). Although volunteer-based surveys may introduce additional variability, the standardized approach, required training, and accounting for route variability in models ensured that the data were valid for making relative comparisons across temporal and spatial scales.

Our long-term study provides strong evidence of a decline in *P. subflavus* activity during summer in the WNS-positive region of Georgia since WNS detection and emphasizes the difference in activity within and outside WNS-positive regions. As not all areas within the species range are affected equally, monitoring and surveillance of unaffected areas is critical, as they could provide a refugium for the species and a potential source of recolonization to WNS-affected areas. Our results will be particularly useful considering that *P. subflavus* is currently under review for listing under the US ESA. In addition, our results exemplify the benefits of using a mobile acoustic monitoring program with volunteer participation to assess large-scale bat mortality trends for a species affected by WNS.

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