GEORGIA DOT RESEARCH PROJECT 13-31

Final report

DETERMINING THE DISTRIBUTION AND HABITAT ASSOCIATIONS OF THE NORTHERN LONG-EARED BAT IN NORTH GEORGIA

OFFICE OF PERFORMANCE-BASED MANAGEMENT AND RESEARCH

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Steven B. Castleberry, Ph.D. Jeffrey Hepinstall-Cymerman, Ph.D.	

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16. Abstract

Significant mortality from White-nose Syndrome (WNS) has made northern long-eared bats a management priority while simultaneously creating uncertainty around where the species remains prevalent on the landscape. The culmination of these factors results in the need to develop distinct habitat associations for northern long-eared bats in north Georgia. We used capture records from 2007-2017 to identify changes in the distribution and habitat use of the northern long-eared bat as it experienced population decline from WNS. We used dynamic occupancy modeling relative to covariates to identify landscape features useful for predicting occupancy and extinction. We developed models at the home range (65 ha) and potential movement (491 ha) spatial scales surrounding sampling locations. Our models indicated that initial occupancy (pre-WNS) was best predicted by percent deciduous forest at the home range scale. In subsequent years (post-WNS), extinction was negatively related to year and elevation at the potential movement scale, indicating that fewer areas were occupied in successive years and that extinction was less likely at higher elevations. The species likely only persisted in areas of high elevation deciduous forest in the state by 2014. In contrast to our hypothesis that extinction rates would be highest at sites closer to WNS positive areas, we found that low-elevation deciduous forest in the southern extent of the distribution (farther from WNS-positive areas) had the highest probability of site extinction, revealing range retraction into areas where WNS was known to occur. Our results suggest that the most effective conservation will occur in areas of high-elevation deciduous forests in the northern extent of the range in the state.

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GDOT Research Project No. 13-31

Determination of Range and Potential Habitat for Cave-Dwelling Bat Species in North Georgia

Final Report

DETERMINING THE DISTRIBUTION AND HABITAT ASSOCIATIONS OF THE

NORTHERN LONG-EARED BAT IN NORTH GEORGIA

By
Steven B. Castleberry and Jeffrey Hepinstall-Cymerman
Warnell School of Forestry and Natural Resources
University of Georgia

Contract with
Office of Performance-based Management and Research
Georgia Department of Transportation

In cooperation with
U.S. Department of Transportation Federal Highway Administration

February 2020

SI* (MODERN METRIC) CONVERSION FACTORS

APPROXIMATE CONVERSIONS TO SI UNITS

SYMBOL	WHEN YOU KNOW	MULTIPLY BY	TO FIND	SYMBOL
LENGTH				
in	inches	25.4	millimeters	mm
ft	feet	0.305	meters	m
yd	yards	0.914	meters	m
mi	miles	1.61	kilometers	km
AREA				
in^2	square inches	645.2	square millimeters	mm^2
ft^2	square feet	0.093	square meters	m^2
yd^2	square yard	0.836	square meters	m^2
ac	acres	0.405	hectares	ha
mi^2	square miles	2.59	square kilometers	km^2
VOLUME				
fl oz	fluid ounces	29.57	milliliters	m
gal	gallons	3.785	liters	L
ft^3	cubic feet	0.028	cubic meters	L
yd^3	cubic yards	0.765	cubic	m^3
		meters NOTE: volumes greater than 1000 L shall be shown in m^3		m^3
MASS				
oz	ounces	28.35	grams	g
lb	pounds	0.454	kilograms	kg
T	short tons (2000 lb)	0.907	megagrams (or "metric ton")	Mg (or
TEMPERATURE (exact degrees)				
°F	Fahrenheit	5 (F-32)/9		°C
		Celsius or (F-32)/1.8		
ILLUMINATION				
fc	foot-candles	10.76	lux	lx
fl	foot-Lamberts	3.426	candela/m^2	cd/m^2
FORCE and PRESSURE or STRESS				
lbf	poundforce	4.45	newtons	N
lbf/in^2	poundforce per square inch	6.89	kilopascals	kPa

APPROXIMATE CONVERSIONS FROM SI UNITS

SYMBOL	WHEN YOU KNOW	MULTIPLY BY	TO FIND	SYMBOL
LENGTH				
mm	millimeters	0.039	inches	in
m	meters	3.28	feet	ft
m	meters	1.09	yards	yd
km	kilometers	0.621	miles	mi
AREA				
mm^2	square millimeters	0.0016	square inches	in^2
m^2	square meters	10.764	square feet	ft^2
m^2	square meters	1.195	square yards	yd^2
ha	hectares	2.47	acres	ac
km^2	square kilometers	0.386	square miles	mi^2
VOLUME				
mL	milliliters	0.034	fluid ounces	fl oz
L	liters	0.264	gallons	gal
m^3	cubic meters	35.314	cubic feet	ft^3
m^3	cubic meters	1.307	cubic yards	yd^3
MASS				
g	grams	0.035	ounces	oz
kg	kilograms	2.202	pounds	lb
Mg (or "t")	megagrams (or "metric ton")	1.103	short tons (2000 lb)	T
TEMPERATURE (exact degrees)				
°C	Celsius	1.8C+32	Fahrenheit	°F
ILLUMINATION				
lx	lux	0.0929	foot-candles	fc
cd/m^2	candela/m^2	0.2919	foot-Lamberts	fl
FORCE and PRESSURE or STRESS				
N	newtons	0.225	poundforce	lbf
kPa			h	lbf/in^2

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EXECUTIVE SUMMARY

Significant mortality from White-nose Syndrome (WNS) has made northern long-eared bats a management priority while simultaneously creating uncertainty around where the species remains prevalent in the landscape. The culmination of these factors results in the need to develop distinct habitat associations for northern long-eared bats in north Georgia. We used capture records from 2007-2017 to identify changes in the distribution and habitat use of the northern long-eared bat as it experienced population decline from WNS. We used dynamic occupancy modeling, which allows sites to be colonized or become unoccupied between years, relative to covariates to identify landscape features useful for predicting occupancy and extinction. We developed models at the home range (65 ha) and potential movement (491 ha) spatial scales surrounding sampling locations. Our models indicated that initial occupancy (pre-WNS) was best predicted by percent deciduous forest at the home range scale. In subsequent years (post-WNS), extinction was negatively related to year and elevation at the potential movement scale, indicating that fewer sites were occupied in successive years and that extinction was less likely at higher elevations. Our modeling results suggest that northern long-eared bats likely only persisted in areas of high elevation deciduous forest in the state by 2014. In contrast to our hypothesis that extinction rates would be highest at sites closer to WNS-positive areas, we found that low-elevation deciduous forests in the southern extent of the distribution (farther from WNS-positive areas) had the highest probability of site extinction, revealing apparent range retraction into areas where WNS was known to occur. In summary, our results identified areas where northern long-eared bats are most likely to persist following widespread WNS mortality and where managers should focus efforts. The most effective conservation will occur in areas of high-elevation deciduous forests in the northern extent of the range in the state. Given the higher extinction rates in the southern periphery

of the range, focusing conservation in areas with larger extents of deciduous forests at high elevations would provide the most benefit during population recovery. The results of our study have allowed state and federal agencies to refine the distribution model for the northern long-eared bat in north Georgia which would allow better-informed decisions regarding activities that may impact the species.

INTRODUCTION

Understanding habitat associations and the distribution of a species is imperative when managing for its long-term survival. Precipitous declines in several temperate bat species in North America, primarily due to White-nose Syndrome (WNS), have highlighted the need to better understand bat habitat and where species occur on the landscape (Blehert et al. 2009). Complicating the issue of bat conservation are temporal shifts in habitat use related to foraging during warmer periods, hibernation over winter months, and migration to and from these areas, creating the need to understand and protect a variety of habitats (Fleming and Eby 2003).

Previous studies relating landscape scale and forest stand features to northern long-eared bat (*Myotis septentrionalis*) occurrence have demonstrated a preference for large areas of contiguous forest (Yates and Muzika 2006), stands with partial harvests that favor vertical structure (Owen et al. 2003), closed forest canopy (Owen et al. 2003, Ford et al. 2005), and linear features within the forest to facilitate movement (Owen et al. 2003, Henderson and Broders 2008). Additionally, a number of studies exclusively examined roosting habitat, which often focused on smaller scales, such as within forest stands or plot-level metrics. These studies generally have shown that northern long-eared bat roosts are associated with areas of high canopy cover (Foster and Kurta 1999, Sasse and Perkins 1996, Menzel et al. 2002), high snag density (Lacki and Schwierjohann 2001, Owen et al. 2002, Perry et al. 2007), and deciduous forest stands, although use of coniferous trees has been documented (Foster and Kurta 1999, Lacki and Schwierjohann 2001, Broders and Forbes 2004).

Georgia occurs on the southern periphery of the northern long-eared bats' range, and peripheral populations, when compared to core populations, have been shown to exist in different habitat, display variation in behavior, and be genetically dissimilar (Kurta et al. 1993, Christopher

and Strobeck 2002, Grider et al. 2016). WNS first appeared in Georgia in the winter of 2012-2013 and has since spread across most of the northern portion of the state. Mortality from WNS has made northern long-eared bats a management priority while simultaneously creating uncertainty around where the bat remains prevalent on the landscape (U.S. Fish and Wildlife 2016). The culmination of these factors results in the need to develop distinct habitat associations for northern long-eared bats in north Georgia.

There are a number of ways to determine northern long-eared bat habitat use and distribution; however, doing so is complicated by the severe mortality this species has experienced within the last decade. Standard occupancy models that address habitat associations and detection probability are static in time and invalid when the population is not in equilibrium (Mackenzie et al. 2002), as is the case for northern long-eared bat populations in Georgia. Conversely, dynamic occupancy models allow for colonization and extinction between years, making them more appropriate for determining occupancy before and after disease-related mortality events such as WNS (Mackenzie et al. 2003). Using dynamic occupancy models allow us to identify landscape components most vital to the long term persistence of northern long-eared bat populations.

Using capture records from 2007–2017, our objective was to identify fluctuations in the distribution and habitat use of the northern long-eared bat as it experienced declines from WNS. Existing knowledge on habitat selection combined with morphological traits, such as low wing aspect ratio and high-frequency call morphology, which are associated with maneuverability and foraging in cluttered habitat, respectively, demonstrate this species preference for and adaptation to forested environments (Ratcliffe and Dawson 2003, Broders et al. 2004). Given this, we predict that northern long-eared bat occupancy prior to WNS would be positively associated with forest cover. As the populations began to decline, we predicted occupancy would be highest in larger

patches of forest with a preference for a mixed and deciduous forest. We also expected sites further from WNS positive areas to see lower extinction rates.

METHODS

Study Area

Our study was conducted in north Georgia and included parts of the Blue Ridge, Valley and Ridge, Appalachian Plateau, and northern portion of the Piedmont physiographic provinces. The topography of these regions ranges from dissected mountains in the Blue Ridge to rolling hills in the Piedmont (Hodgkins 1965). Two forest types dominate the regions, with the Blue Ridge and Appalachian Plateau comprised of mesophytic forest (oak and maple), and Piedmont and Valley and Ridge being southern mixed forest (oak and pine; Dyer 2006).

Field Data Collection

Mist-net surveys were conducted mid-May through early-August 2015-2017, with most surveys occurring in the Chattahoochee National Forest and wildlife management areas managed by the Georgia Department of Natural Resources. We used ArcMap to randomly generate potential sampling sites in patches of forest >20 ha that contained unimproved or low traffic roads, stream-road intersections, and small bodies of water that could accommodate mist-netting. We followed the Indiana bat survey protocol to maintain consistency with private contractors. Requirements in the guidelines included mist-netting beginning at sunset and continuing for five hours, mist-netting in temperatures above 10⁰ C, no precipitation or sustained high winds when mist-netting, no more than 2-3 consecutive nights at a single location, and predominate use of double high mist-nets (U.S. Fish and Wildlife Service 2019).

For all captured bats, we recorded weight, forearm length, sex, reproductive condition, age, and wing damage index and released all bats at the capture site (Reichard and Kunz 2009). Age (juvenile or adult) was based on the closure of epiphyseal plates in the hand bones (Kunz and Anthony 1982). The female reproductive condition was classified as pregnant, lactating, or post-lactating. Male reproductive condition was classified as reproductive or non-reproductive based on the swelling and descension of the testes. For all surveys, area (m^2) of mist-nets used, temperature, duration of the survey, and wind velocity were recorded.

Additional data, consisting of capture records from private sector contractors and agency biologists from 2007-2017, were acquired from the Georgia Department of Natural Resources and used to supplement our field data. Approximately 60% of the data used in modeling was collected by people indirectly associated with the project. In general, these data were collected in areas where environmental impact statements were required, or in areas thought to have suitable habitat for threatened or endangered bat species.

Spatial Analysis

We analyzed habitat associations at two spatial scales surrounding sampling locations, home range (65 ha), and potential movement (491 ha). The size of the home range scale was based on home range size of pregnant northern long-eared bats from the literature (Owen et al. 2003, Lacki et al. 2009). We assumed that the pregnant female range represented the smallest daily movements of the species. Potential movement scale was based on the furthest distance we tracked a radiotagged bat from the capture location to its roost during the concurrent roosting ecology study.

We derived landscape metrics to describe the composition and configuration of land cover for sampling locations at both spatial scales from the USGS 2011 National Land Cover Dataset

(NLCD). We reclassified NLCD cover classifications into 10 land cover classes and derived percent land cover within buffers around sampling locations representing each scale. Land cover data also were aggregated into forested (NLCD classes: 41, 42, 43) and non-forested (all other classes) areas. We used FRAGSTATS (McGarigal et al. 2012) to derive metrics of land cover area and shape including but not limited to number of land cover patches, largest patch, edge density, total core area, mean patch size, and parameter to area ratios of patches.

Occupancy Modeling

Standard occupancy models assume that the system being modeled is under equilibrium; however, this study occurred during the time period in which WNS was causing high mortality in some bat species in north Georgia. Therefore, bat populations likely were not at equilibrium during the study. To account for this disequilibrium, we modeled occupancy using dynamic occupancy modeling, which allows sites to be colonized or become unoccupied between years (Mackenzie et al. 2003). In the model, we combined all the years before 2011 and treated them as a closed single-season occupancy model. In subsequent years, the model predicted the likelihood that a site would be colonized or become extinct and modified the previous year's model. Colonization was left null in the model because no events of colonization were observed during sampling.

Covariates used to estimate the first season of occupancy and subsequent extinction events were percent land cover, landscape metrics generated in FRAGSTATS, physiographic region, elevation, distance to karst topography, and distance to WNS positive counties. Covariates used in estimating detection probability included Julian date, duration of sampling events, counts of bats captured, year and m^2 of mist-net used. Correlation between covariates was assessed using a Pearson's correlation, with variables with $| r | > 0.7$ being excluded from the same models. All models were constructed using program unmarked (Fiske and Chandler 2011).

Given that initial occupancy was the foundation on which the remaining model parameters were based, models that could not accurately predict initial occupancy were not considered during model selection. AIC values, parameter coefficients, and confidence intervals were used further assess models, with priority given to models with lower AIC values and coefficients whose confidence intervals did not include zero. Model fit was assessed using parametric bootstrapping, which entailed simulating data sets from the fitted model, refitting simulated data to the model, and assessing sampling distribution from results of the original data and refit data using a chi-squared test, with 0.5 indicating that fit to simulated data is consistent with the fit of the original data. We calculated cutoffs for occupancy models in R package ROCR (Sing et al. 2005) by minimizing the absolute value of the difference between sensitivity and specificity to balance the number of false positives and false negatives (Liu et al. 2005).

RESULTS

We conducted 1,093 nights of mist-netting at 533 unique locations, recording northern long-eared bat captures at 68 (12.8%) of the sites (Table 1). Mean number of sites sampled/year was 90.3 (SD = 53.3; range 2-159), and each site was visited a mean of 1.7/year (SD = 1.0; range 1-8). Throughout the study, 80 sites (15%) were visited in multiple years with no site being sampled in >5 years.

Table 1. Number of nights sampled, number sites surveyed, and occupied sites (sites with a northern long-eared bat detection) for each time period in the model. Pre-WNS includes the 5 years prior to presence of White-nose Syndrome in Georgia (2007-2011). Naïve occupancy rate was calculated as the number of sites occupied out of the total number of sites sampled in each year.

	Pre-WNS	2012	2013	2014	2015	2016	2017
Nights sampled	47	16	241	190	314	179	111
Sites surveyed	43	12	143	110	159	101	64
Occupied sites	21	3	27	9	8	5	1
Naïve occupancy	0.49	0.25	0.19	0.08	0.05	0.05	0.02

Three models best predicted northern long-eared bat occupancy (Table 2). The model with the lowest AIC value was disregarded due to 95% confidence intervals of both coefficients used to predict initial occupancy, forest (-5.996, 95% confidence interval [CI] -4.168 to 9.748) and elevation (-12.29, CI -42.513 to 17.933), containing zero. Of the remaining two models, only one covariate estimating extinction, largest patch index of deciduous forest, differed (Table 2). Due to a 95% confidence interval of the estimates of largest patch index of deciduous forest containing zero and increased AIC value when the covariate was included in the model, the model containing largest patch index of deciduous forest was disregarded.

Our best model indicated that initial site occupancy increased with percent forest at the home range scale, from 0.29 (CI 0.00 to 15.34) at 1% deciduous forest to 0.99 (CI 0.67 to 1.00) at 70% deciduous forest (Table 3). In subsequent years, mean elevation at the potential movement scale and year were the best predictors of extinction (Table 3). Probability of extinction ranged from 0.48 (CI 0.26 to 0.72) at 154 m to 0.10 (CI 0.03 to 0.29) at 1,038 m in year two and from 0.96 (CI 0.46 to 0.99) at 154 m to 0.20 (CI 0.56 to 0.92) at 1,038 m by year seven. Due to

confidence intervals surrounding the estimate becoming less accurate every subsequent year, predictions of areas occupied in later years are more uncertain (Figure 1). Colonization being an intercept only model had a baseline rate of 0.02 (CI 0.004 to 0.08) in every year. The probability of detection decreased over time from 0.53 (CI 0.40 to 0.67) in year one to 0.07 (CI 0.02 to 0.22) by year seven. Chi-squared tests assessing model fit indicated that there was only a small difference between the fit of original data and fit of simulated data ($\chi^2 = 0.47$, mean difference = 3.19, SD = 191; Figure 2). Based on ROC plots, the threshold at which a site was considered occupied was estimated to be 0.56. Site occupancy decreased every year following the arrival of WNS with pre-WNS site occupancy being estimated at 0.57 and decreasing to 0.05% by 2017 (Figure 3).

Table 2. The top supported dynamic occupancy models with corresponding Akaike's Information Criterion (AIC) and number of parameters (K) used to predict changing site occupancy of the northern long-eared bat in north Georgia from 2007-2017. Components of each model include detection (p), initial occupancy (ψ), seasonal colonization (γ) and seasonal local extinction (ε).

Model	AIC	K
ψ (Percent Forest[1]), γ (Null), ε (Mean Elevation[2] + LPI Deciduous Forest[2] + Year), p (Year)	420.806	9
ψ (Percent Deciduous Forest[1]), γ (Null), ε (Mean Elevation[2] + Year), p (Year)	428.559	8
ψ (Percent Deciduous Forest[1]), γ (Null), ε (Mean Elevation[2] + LPI Deciduous Forest[2] + Year), p (Year)	428.987	9

[1]Scale of effect is 65 ha

[2]Scale of effect is 491 ha

Table 3. Parameter description, estimates, and 95% confidence intervals for the top model used to predict changing site occupancy of the northern long-eared bat in north Georgia from 2007-2017.

| Description	Parameter	Estimate	95% CI
Asymptote of initial occupancy	$\beta_0^{(\psi)}$	0.002	0 - 0.147
Effect of deciduous forest within 65 ha on initial occupancy	$\beta_1^{(\psi)}$	0.538	0.510 - 0.565
Baseline recruitment	γ_0	0.017	0.003 - 0.079
Asymptote of extinction	$\beta_0^{(\varepsilon)}$	0.069	0.009 - 0.362
Effect of mean elevation within 491 ha on extinction	$\beta_1^{(\varepsilon)}$	0.27	0.128 - 0.481
Effect of year on extinction	$\beta_2^{(\varepsilon)}$	0.655	0.495 - 0.786
Asymptote of capture probability	β_0^p	0.643	0.457 - 0.795
Effect of year on capture probability	β_1^p	0.389	0.326 - 0.455
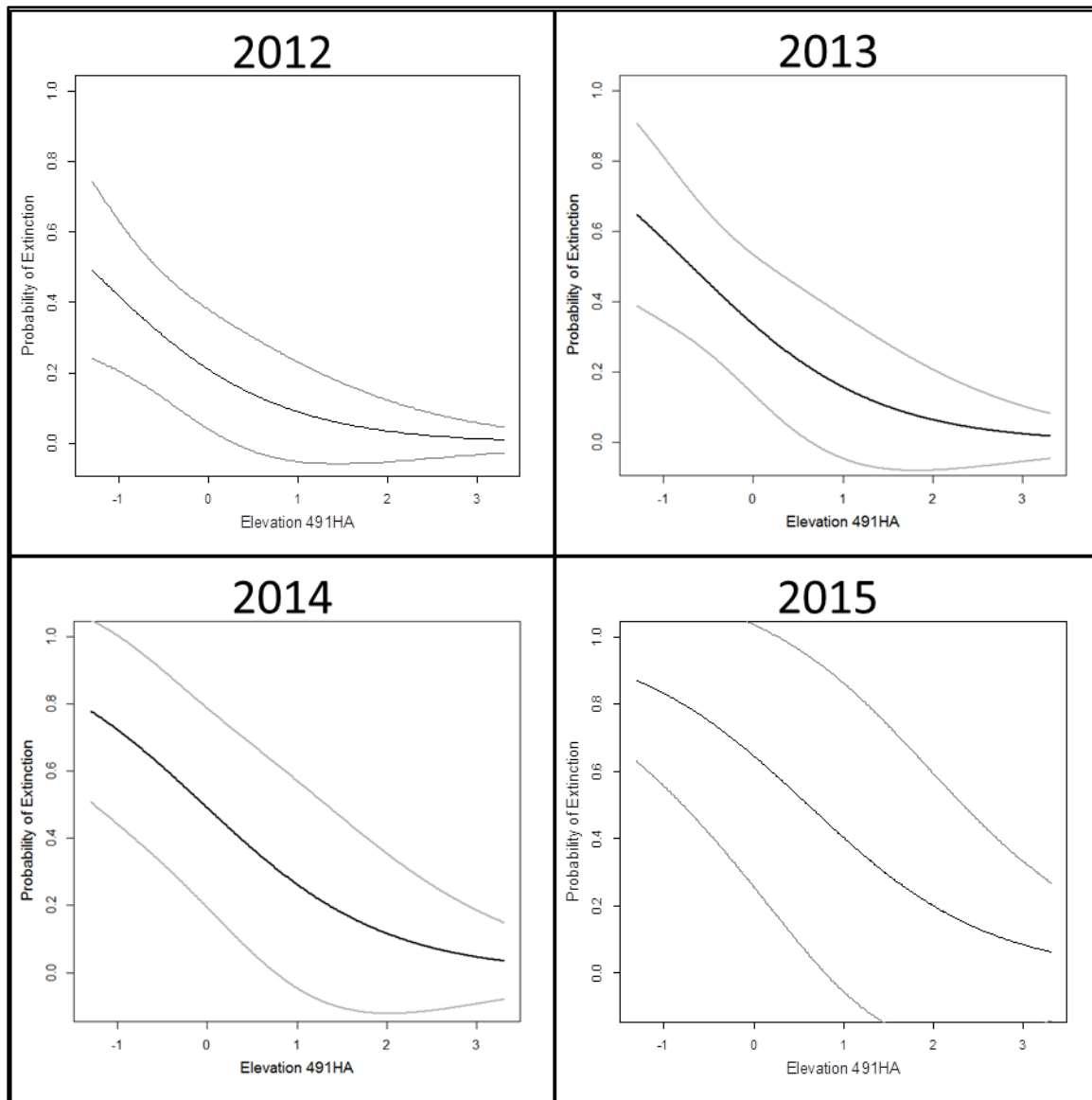
Figure 1. Change in the effect of mean elevation on northern long-eared bat occupancy at the potential movement scale (491 ha) by year. Elevation was scaled using the equation (elevation-mean [elevation]/sd[elevation]) for inclusion in models.
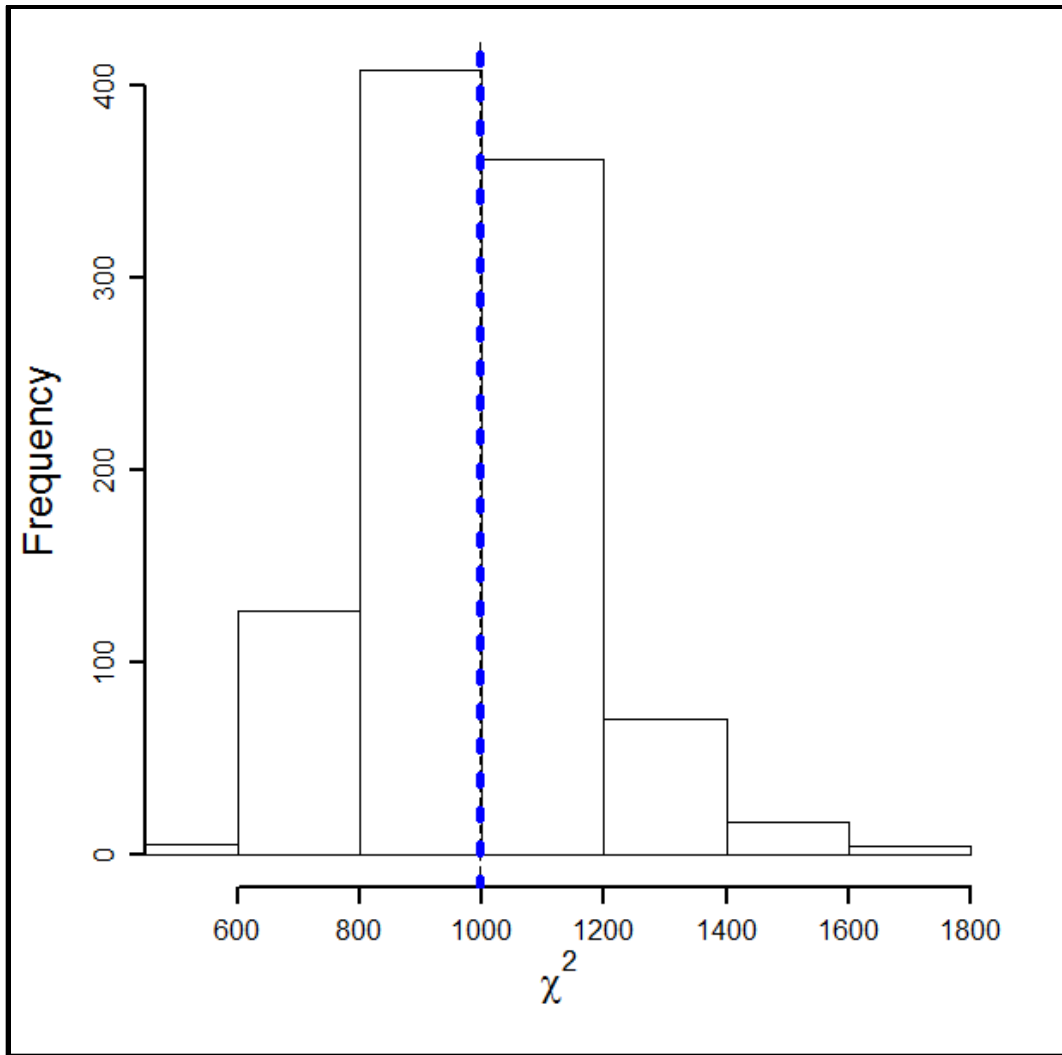
Figure 2. Model fit based on chi-squared test that compared residual sum-of-squares between the original data and data generated using the model. Bars depict the sample distribution of the residual sum-of-squares for data generated using the model, and the dashed blue line depicts the residual sum of squares for the original data.
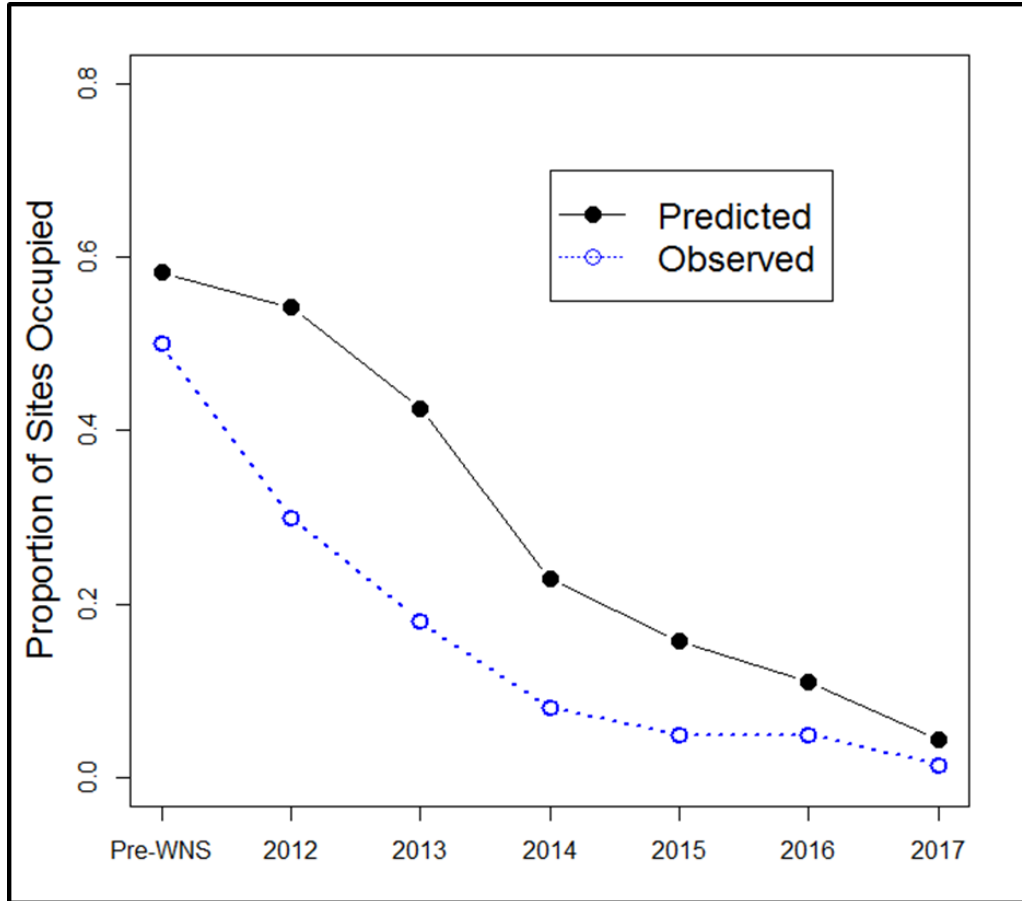
Figure 3. Proportion of sites occupied by the northern long-eared bat in north Georgia pre-White-nose Syndrome (Pre-WNS) and yearly post-WNS (2012-2107). The blue line (observed) represents the data collected in the field, and the black line (predicted) represents model outputs that have been adjusted based on the probability of detection.

The top model was used to build predicted northern long-eared bat distribution maps. Within the pre-WNS distribution map (Figure 4), the smallest patch in which we documented a northern long-eared bat was 298 ha; therefore we eliminated all patches smaller than 295 ha. Maps of pre-WNS occupancy depict large patches of habitat in the northern portion of the state with

habitat becoming more fragmented towards the south. Throughout the population decline, we predicted that lower elevation forest increasingly became unoccupied and occupied areas began to shift northward (Figure 5). By 2014, the species likely only persisted in areas of high elevation deciduous forest in the state (Figure 6).
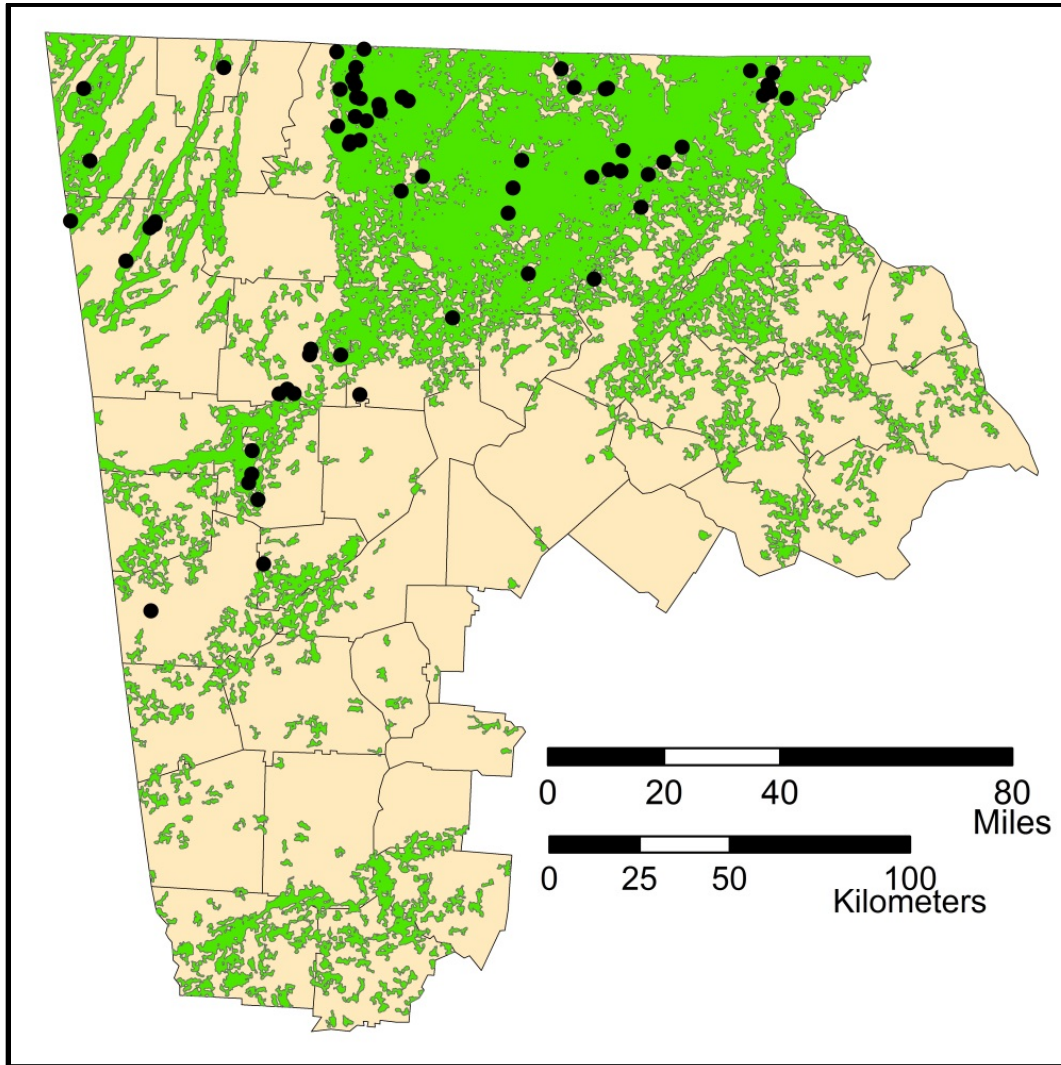

Figure 4. Distribution of the northern long-eared bat in north Georgia in 2012 (prior to White-nose Syndrome). Areas in green represent potential habitat and back dots indicate locations with capture records.
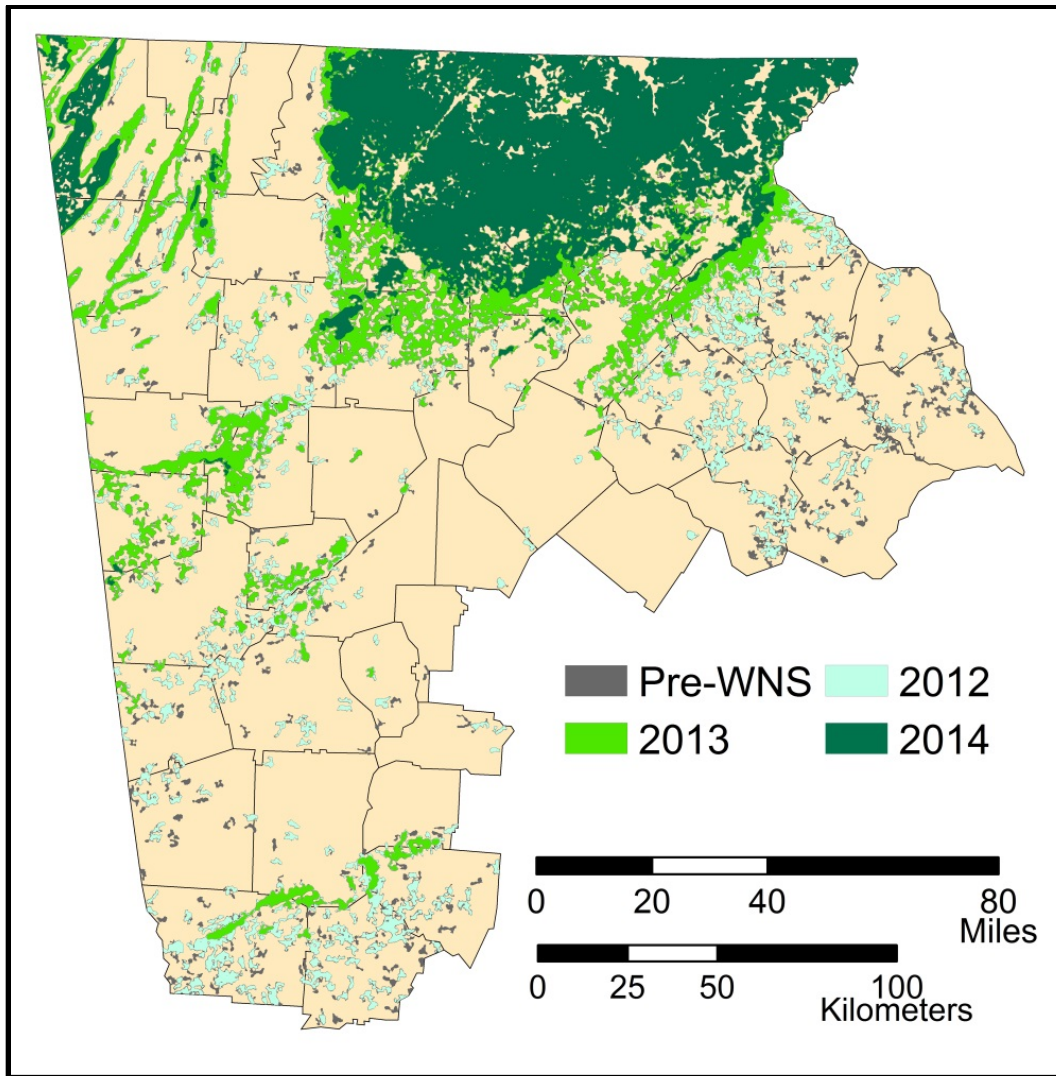
Figure 5. Year-by-year range contraction of the northern long-eared bat in north Georgia. Annual distributions include the current year and every succeeding year.
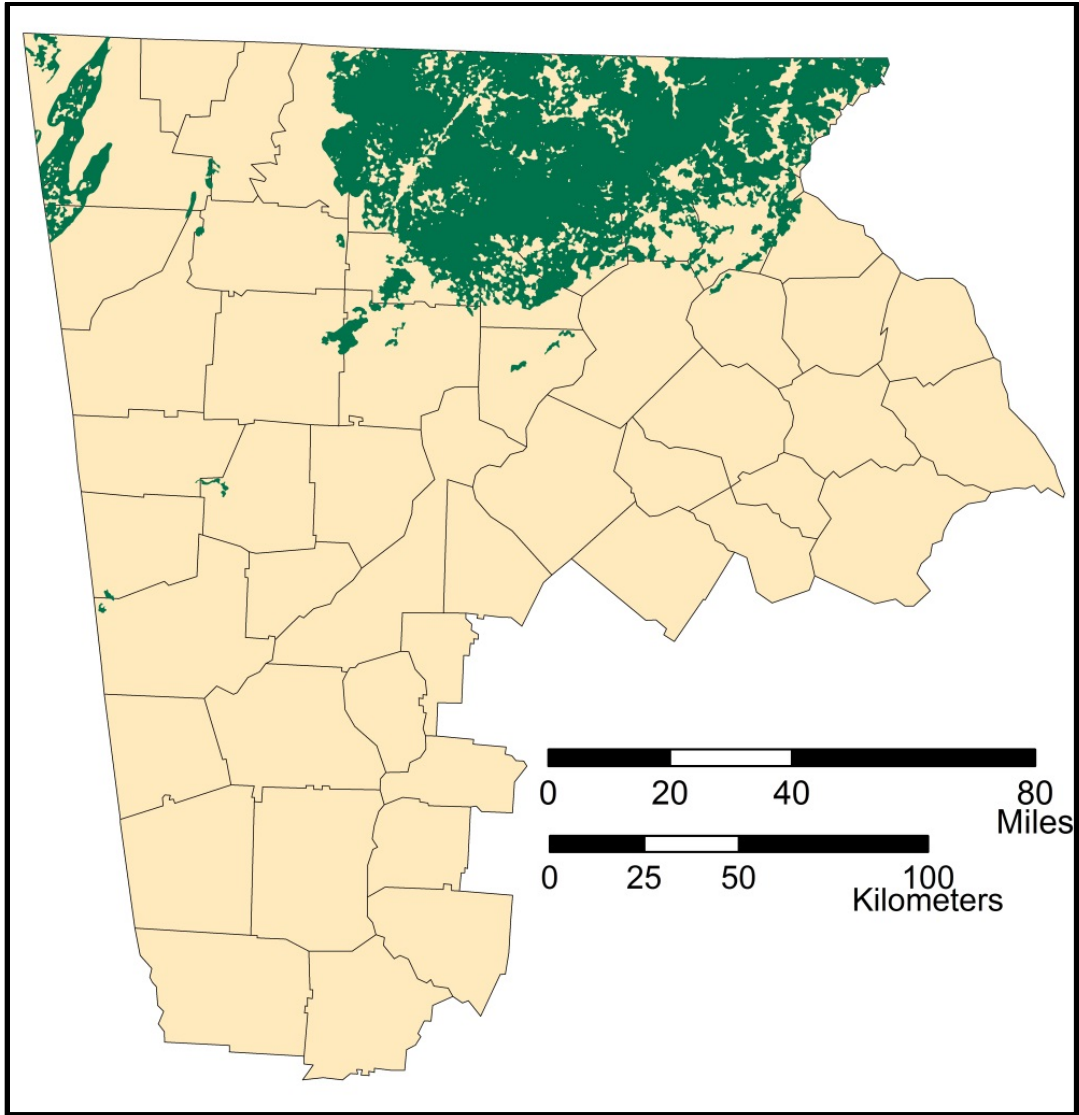
Figure 6. Predicted distribution of the northern long-eared bat in north Georgia in 2014 (following mortality from White-nose Syndrome). The shaded areas have the potential to be occupied based on elevation and area of deciduous forest.

DISCUSSION

Our model predicted little change in northern long-eared bat site occupancy between pre-WNS and 2012, which is not surprising given that in the winter between these years, WNS had only recently been observed in two counties bordering northwest Georgia. In the subsequent two

years (2013-2014), WNS spread across multiple counties in north Georgia. During this time, our model predicted the most significant declines in site occupancy. In the remaining years (2015-2017), site occupancy continued to decline across north Georgia, with the rate of decline becoming less severe each succeeding year.

A particularly telling story of the decline was the difference between two sampling events recorded exactly seven years apart with equivalent levels of effort. On July 27, 2010, at a mine entrance at Fort Mountain State Park a single night of netting resulted in the capture of 114 bats, of which the primary species captured were northern long-eared bats (n = 55) and tri-colored bats (*Perimyotis subflavus*; n = 37). At the same location on July 27, 2017, we captured 10 bats consisting of 9 big brown bats (*Eptesicus fuscus*) and 1 eastern red bat (*Lasiurus borealis*).

Our dynamic occupancy model predicted a relatively large, contiguous occupied area for northern long-eared bats in north Georgia that became smaller disjunct patches moving south. Although suitable habitat was found in more southern portions of the study area, northern long-eared bats were never captured in many of these locations. One contributor to the absence of captures in more southern areas may have been a lack of sampling effort prior to WNS; however, we do not believe a lack of survey effort to be the sole reason for absence. Isolated habitat patches, like those in the southern portions of the northern long-eared bat distribution in Georgia, are known to inhibit colonization, even by volant species (Dunning et al. 1995). Further, northern long-eared bats are known to constrain movement to within forested areas (Henderson and Broders 2008) and have shown an aversion to small habitat patches (White et al. 2017), making colonization of fragmented habitat less likely. Thus, northern long-eared bats were likely absent or rare in the smaller habitat patches in the southern extent of the distribution prior to WNS.

With our knowledge that northern long-eared bats experienced high mortality from WNS, we expected detection probability to decrease post-WNS as detection probability is linked to abundance (Royle and Nichols 2003). Francl et al. (2012) reported northern long-eared bat capture rates in the two years after the arrival of WNS at 22.9% of pre-WNS capture rates. Reynolds et al. (2016) reported a 95% decrease in capture rate two years after the arrival of WNS. Although the decrease in captures and number of sites occupied we observed through trapping documented the yearly decline in abundance post-WNS, the mean number of captures was non-informative in explaining detection probability. Nonetheless, year effectively served as a surrogate for abundance to explain detection probability in our models.

Our model predicted range retraction in years following WNS, with southern habitat patches being the first to experience site extinctions (Figure 5). Species tend to be better adapted to the core of their range (Lawton 1993). Therefore, northern long-eared bats inhabiting the southern extent of their range likely were in marginal habitat prior to WNS (Pulliam 1998). Parameters in our models provide evidence that northern long-eared bats on the southern extent of their range existed in marginal habitat. Because the majority of mortality in our study area was from WNS and the disease is contracted through exposure to the fungus at hibernacula (Blehert et al. 2009, Lorch et al. 2011), we hypothesized that proximity to WNS positive areas would increase mortality and therefore extinction rates. However, our results indicate that low-elevation deciduous forest in the southern extent of the distribution had the highest probability of site extinction, rather than sites closest to WNS positive areas. Higher extinction rates on the edge of the distribution revealed range retraction into areas where WNS was known to occur (Figure 5). The combination of site extinction not being related to proximity to WNS and the model prediction of range retraction into WNS positive areas indicate that northern long-eared bats in the southern reaches

of our study likely were in marginal habitat that may have represented sink populations (Pulliam 1998).

White-nose syndrome took longer to reach southern populations of northern long-eared bats, but once it arrived, our model predicted those closest to the margins of the range were less likely to persist. Low persistence on the range periphery could be due to populations on the margins of the range being sinks and/or habitat on the southern edge of the range being of marginal quality, as previously suggested. On a continental scale, peripheral populations of bats affected by WNS may be the most likely to survive due to their relative isolation; however, in our specific case of a population occurring at the periphery of the range, our model predicts declines from the outer most edges of the population inwards toward the core. Our findings of declines leading to retraction of a species range into core areas correspond to the ideas of Lawton (1993), and observations of range retraction reported elsewhere (Mayfield 1973, Fuller et al. 1995). Further, patterns of WNS decline over the continental area follow patterns expected in a disease related decline, with mortality radiating from a focal area and spreading based on proximity and connectivity to known occurrences (Hudson et al. 2002, Osnas et al. 2009). Together these results highlight the importance of scale when monitoring population declines.

CONCLUSIONS AND RECOMMENDATIONS

Since the appearance of WNS in Georgia, northern long-eared bat abundance and occupancy have declined drastically throughout its range in the state. The northern long-eared bat was once one of the most common bat species documented in many eastern states but has experienced significant range-wide declines (Pauli et al. 2015, Reynolds et al. 2016). In Georgia, bat survey effort increased up to 6-fold in some years following WNS, yet successively fewer bats were captured and fewer sites were occupied annually between 2012 and 2017. Although the

species may be found in low numbers in optimal habitat, the species is likely functionally extirpated from the southern periphery of the range in the state.

Our results indicate that initial occupancy (pre-WNS) was best predicted by large patches of deciduous forest. This result is not surprising as northern long-eared bats are forest interior species and their association with the intact forest is well known (Yates and Muzika 2006). However, in years following WNS induced population declines, our models indicated a negative relationship between extinction and mean elevation, indicating that the species is most likely to persist in areas of high elevation deciduous forests. High elevation deciduous forests are restricted to northern areas in Georgia. While high elevation deciduous forests may be a more likely location for northern long-eared bats to persist, there is potential for any loss of habitat to be critical for long term viability of northern long-eared bats in Georgia. Severe population declines, low fecundity, site fidelity, and cryptic behavior make any disturbance a potentially large effect on the remaining population (Patriquin et al. 2010, Perry 2011, Ingersoll et al. 2013, Thompson 2013).

Our modeling results identified areas where northern long-eared bats are most likely to persist following widespread WNS mortality and where managers should focus efforts. The most effective conservation likely will occur in areas where northern long-eared bats were known to occur on the landscape based on predicted available habitat and previous capture records (Figure 7). Our results suggest that areas on the southern periphery of the range in Georgia likely were in marginal habitat and may have represented sink populations pre-WNS. Further, although some suitable habitat was present in the areas, lack of captures and the known preference of northern long-eared bats for larger habitat patches suggest that the species may not have been common or widespread in the southern extent. Therefore, focusing conservation in areas with larger extents of deciduous forests at high elevations likely will provide the most benefit during the recovery phase.

It is important to recognize that the rapid decline in northern long-eared bat populations was not a result of habitat loss. Although historic abundance and range in Georgia is unknown, northern long-eared bats were one of the most commonly captured bats in northern Georgia in the years preceding WNS. Thus, sufficient habitat existed to support this apparently large population. Although population recovery likely will occur slowly, protection of remaining habitat is paramount to the species recovery.

During the study, we cooperated extensively with the Georgia Department of Natural Resources (GADNR) Wildlife Conservation Section and the U.S. Fish and Wildlife Service (USFWS) Georgia Ecological Services Field Office. Data collected from our study have been incorporated into GADNR's Rare Species and Natural Community Database. These data are used to facilitate conservation efforts by the agency. For example, GADNR is developing an app for mobile devices to facilitate bat monitoring throughout the state. USFWS biologists have used the data to refine the distribution model for the northern long-eared bat in north Georgia. A more accurate model of the current northern long-eared bat distribution in the state allows USFWS biologist to make better-informed decisions regarding activities that may impact the species.
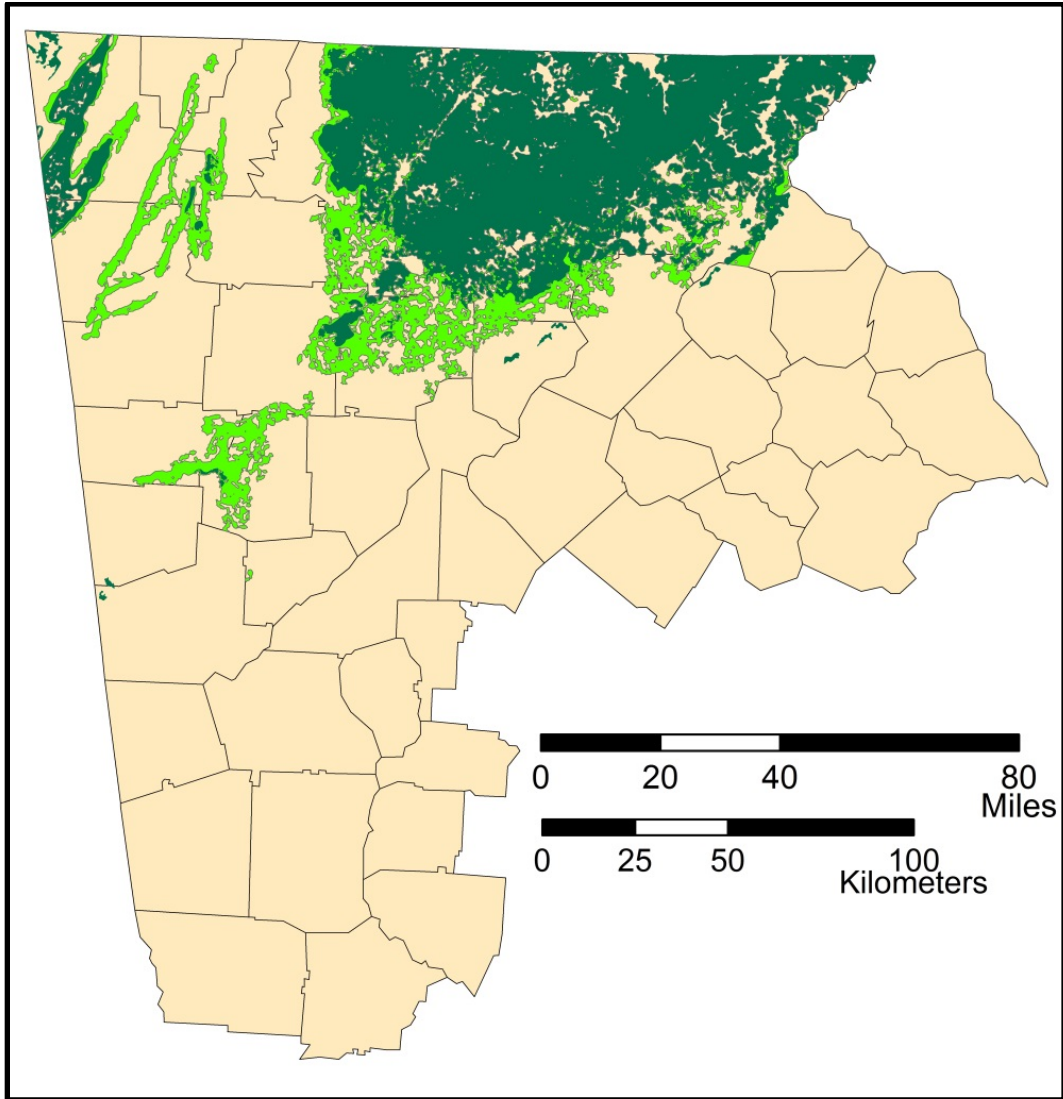
Figure 7. Area recommended for protection to facilitate recovery of northern long-eared bat populations in Georgia.

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