



Indiana bats roost in ephemeral, fire-dependent pine snags in the southern Appalachian Mountains, USA



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ABSTRACT

The Indiana bat (*Myotis sodalis*), a species that is federally endangered in the U.S., is being impacted by white-nose syndrome and habitat loss across much of its range. A better understanding of summer roost ecology of the species will enable us to develop management strategies that promote summer survival for breeding adult females and their pups. We conducted a 5 year investigation of Indiana bat roost habitat selection and roosting behavior in a large (>250,000 ha) forested area of the southern Appalachian Mountains and compared our results to populations in different landscapes across the species' range. From May to August 2008–2012, we attached radio transmitters to 50 adult females, 3 juveniles, and 7 adult males captured at sites on the Cherokee and Nantahala national forests and Great Smoky Mountains National Park. We radiotracked bats to 95 roosts and measured characteristics of trees, 0.1 ha plots, and landscape attributes for 69 of these roosts and associated random trees. We used an AIC approach to compare 14 candidate conditional logistic regression models. The only plausible model, which carried 95% of total model weights, had 3 important terms. Indiana bats showed strong selection for yellow pine (*Pinus* subgenus *Diploxylon*) snags that were significantly taller than random trees and in areas with a greater number of snags within 0.1 ha. During this study, tree and stand structure were more important for roost selection than larger scale factors and Indiana bats responded to a pulsed and highly ephemeral resource, dead yellow pines, which were a significant component of the large forest tracts. Roosting behavior differed from what has been observed for Indiana bats in other parts of the eastern U.S.; maternity colonies tended to be smaller (<25 bats, but as large as 75 bats prior to pups being volant) and bats were more nomadic, using each roost tree for only 2–3 days on average and rarely for more than one year. The differences we observed in roosting behavior in the southern Appalachians suggest it would be wise to consider the broader landscape context when evaluating the roosting ecology of Indiana bats, as local forest types and disturbance events will affect stand structure and roost tree availability. Stand- and landscape-scale management practices that create or preserve large pine snags, such as prescribed fire, coupled with natural or manmade pulsed disturbances, should aid in the management and recovery of the Indiana bat in this region.

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1. Introduction

For most forest-dwelling bats, roost selection is linked primarily to the physical structure of the roost tree and stand in which it is found. In general, tree-roosting bats select tall, large diameter trees with an open canopy, surrounded by a high density of available roosts (Kalcounis-Rueppell et al., 2005); however, group size and local climate conditions may affect preferences for tree size and solar exposure (e.g., Patriquin et al., 2016). It is likely that optimal

roosts are both long-lasting (versus ephemeral) and abundant. Roost choice may be influenced by factors that minimize predation risk, allow energy conservation, and facilitate social interactions (Barclay and Kurta, 2007; Kunz and Lumsden, 2003). Cavity or crevice dwelling bats tend to roost in dead trees (snags) or trees with damage to limbs or to the tree bole (e.g., woodpecker cavities). Roosting in tall, large diameter trees with an open canopy allows females to roost in larger groups and to maintain a higher body temperature via passive warming and social thermoregulation (Pretzlaff et al., 2010; however, where forest structure is diverse, bats will select roosts that provide a range of microclimate conditions across the season or across years (Silvis et al., 2015; Patriquin et al., 2016). High snag density in the area surrounding a roost may

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facilitate frequent roost switching, which allows bats to evade predators, inhibit ectoparasite build up, or select for differing microclimates (Lewis, 1995).

While the physical structure of a roost (e.g., size and decay class) may be more important to a bat than the tree species (Cryan et al., 2001), forest managers aim to promote particular forest types and ages, not just the characteristics of individual trees. Bats' preferences for where to roost at the tree, stand, and landscape-level likely vary across a species' distribution due to differences in vegetative communities, topography, climate, amount of available forest, and management regimes (e.g., Lacki et al., 2010; Toth et al., 2015; Silvis et al., 2016). Therefore, it is essential to study roosting habits for individual species in different ecoregions; this is especially true for wide-ranging species because generalization across a species' range could lead to mismanagement in different ecoregions. For example, northern long-eared bats (*Myotis septentrionalis*) selectively roost in hardwood snags in New Brunswick, Canada (Broders and Forbes, 2004), but avoid hardwoods in favor of shortleaf pine (*Pinus echinata*) snags in Arkansas, USA (Perry and Thill, 2007). In a Midwestern population of Indiana bats (*M. sodalis*), 23 of 23 roost trees were in green ash (*Fraxinus pennsylvanica*) (Kurta et al., 1996), but in New York and Vermont Indiana bats use a variety of live and dead hardwoods and some conifers as roosts, with little evidence for specialization (Watrous et al., 2006).

It is particularly critical to advance our understanding of how management practices affect roosting habitat for rare or imperiled forest-dependent bat species. In this study, we focused on the federally endangered Indiana bat, which is a forest dwelling, insectivorous species distributed across 25 of the eastern United States. During summer, female Indiana bats form maternity colonies in cavities or crevices in large dead or damaged trees (Lacki et al., 2009) in a variety of forest types ranging from small riparian patches in parts of the Midwest (e.g., Whitaker and Brack, 2002) to large, contiguous tracts in the southern Appalachian Mountains (Britzke et al., 2003). Despite federal protection and the initiation of recovery measures, the overall Indiana bat population declined 57% from 1965 to 2000 (Clawson, 2002), probably due to human disturbance at hibernacula, changes in summer habitat (e.g., loss and fragmentation of forests and woodlands, and disrupted disturbance regimes), and other anthropogenic factors. Although populations in some parts of the range were beginning to increase in recent years (Thogmartin et al., 2012), white-nose syndrome (WNS) now poses an additional threat to Indiana bat populations and, thus, conserving healthy summer populations may be critical to the overall survival of the species (Thogmartin et al., 2013).

Indiana bats appear to have different preferences for tree species and exhibit different roosting behavior in different parts of their range. Most studies of summer roost habitat selection by female Indiana bats have been conducted in Midwestern states such as Michigan, Indiana, and Illinois (e.g., respectively, Kurta et al., 2002; Whitaker et al., 2004; Carter and Feldhamer, 2005). In the Midwest, colony sizes may range from 16 to >350 bats (Whitaker and Brack, 2002) and these large colonies move among sets of suitable hardwoods—usually dead ash (*Fraxinus* spp.), cottonwoods (*Populus* spp.), oaks (*Quercus* spp.), and hickories (*Carya* spp.) (e.g., Humphrey et al., 1977; Kurta et al., 1996; Whitaker and Brack, 2002; Carter and Feldhamer, 2005)—and show long term fidelity to roosts and roost areas (Humphrey et al., 1977; Whitaker et al., 2004). More recent work in the Northeast corroborates the importance of live and dead hardwoods as roosts (Jachowski et al., 2016; Watrous et al., 2006). Indiana bat maternity colonies were first discovered and radio-tracked in the southern Appalachians in 1999 (Harvey, 2002). Mountainous portions of this region are primarily forested and managed by state or federal agencies—thus providing a strong contrast with the fragmented

hardwood forest-agricultural matrix in most of the core of the Indiana bats' range in the Midwest. The sole study on Indiana bat roost selection in this region during summer suggests many differences from Midwestern populations. In the southern Appalachians, Indiana bats roost mainly in dead yellow pines (*Pinus* subgenus *Diploxylon*) on mid and upper slopes in mixed pine-hardwood stands (Britzke et al., 2003). Roosts are ephemeral—many roosts were unsuitable 1 year after they were found and Indiana bats vacated areas where they had roosted the previous year. Colony sizes in the southern Appalachians are also smaller than in the Midwest—only 1–81 bats (Britzke et al., 2003). Pine snags are also the dominant springtime tree roosts used by Indiana bats in a mixed pine-hardwood forest in northern Alabama (Roby and Gumbert, 2013).

It is important to understand the roosting ecology of Indiana bats in the southern Appalachian Mountains because this ecoregion is on the periphery of the species' range. Only one study has been conducted on roost site use in this area (Britzke et al., 2003) and it was limited in scope. Thus, we conducted a 5 year investigation of Indiana bat roosting ecology in a large (>250,000 ha) area of the southern Appalachians where the forests were primarily contiguous mixed pine-hardwood with a history of frequent fire. Our objective was to test the significance of tree, plot, and landscape characteristics on roost habitat selection and to describe the roosting behaviors of Indiana bats in this region. Due to differences in forest cover and composition, management strategies, and variation in the Indiana bat's roosting ecology across its range, we expected that Indiana bats would roost in different tree species when compared to bats in other areas and be less faithful to roost sites than bats in more fragmented forests where suitable roosts may be limiting.

2. Materials and methods

2.1. Study area

We conducted this study in a 281,788 ha area in the southern Appalachian Mountains, surveying sites on federal lands managed by the Cherokee National Forest (CNF; Polk and Monroe counties, TN), Nantahala National Forest (NNF; Clay, Cherokee, Graham, and Swain counties, NC), and Great Smoky Mountains National Park (GSM; Swain County, NC; Blount and Sevier counties, TN). The two national forests used a variety of approaches to manage for a wide range of natural resources and values including rotational and selective timber harvests, prescribed fires, creation of early successional forest conditions, and preserving riparian areas. During the period of this study, active timber management activities such as harvesting and prescribed fires were conducted on <1% of the CNF and NNF lands annually (Dennis Krusac, USDA Forest Service, Southern Region, pers. commun.). In the national park, prescribed fire was the primary tool for forest management and tree clearing was limited mainly to removal of hazard trees. Most of the study area was forested, mainly mature forest, but also included young and old-growth forests (SAMAB, 1996). Forests in our study area were classified as mixed pine-hardwood forests in the Appalachian oak forest region (Dyer, 2006); oak forests dominated the southern Appalachians (68% of forest cover), but yellow pine stands were the second most common forest type (15% of forest cover; SAMAB, 1996). The primary natural community types in areas used by bats were pine-oak heath, hemlock forest (*Tsuga* spp.), white pine forest (*P. strobus*), low mountain pine-oak forest, and southern mountain xeric pine-oak woodland (Schafale, 2012). Various oak and cove forest types also occurred in our study area. Elevation ranged from 250 to 2025 m above sea level. Mean minimum and maximum daily temperatures from 1 May to 31 August

2008–2012 were 16.6 °C and 29.4 °C (State Climate Office of NC, www.nc-climate.ncsu.edu). Mean total precipitation in the same period was 38.3 cm per summer season.

2.2. Bat capture and radio-tracking

From May to August 2008–2012, we used mistnets to capture bats at 74 sites across CNF, NNF, and GSM. We erected double and single-high 4–12 m nets (Avinet, Dryden, NY, USA) over trails, gravel roads, and stream corridors; our most successful sites for Indiana bat capture had a 2–4th order perennial stream running alongside a densely forested road. We checked mistnets every 8–10 min and nets were open 3–4 h each night. We recorded species, sex, age, mass (g), and forearm length (mm) for each captured bat. We determined age (juvenile or adult) by the degree of ossification of the finger joints (Kunz and Anthony, 1982) and reproductive condition (pregnant, lactating, or non-reproductive for females and scrotal or non-reproductive for males; Racey, 1988). We banded bats with a unique 2.9 mm (most bats) or 4.2 mm (used only for *Eptesicus fuscus* and *Lasiurus cinereus*) aluminum forearm band (Porzana Ltd., East Sussex, UK) for individual identification. Starting in 2009, we recorded wing damage scores (Reichard and Kunz, 2009) as an index of WNS effects. We fitted Indiana bats with a 0.32–0.42 g radio transmitter (Holohil Systems Ltd., Ontario, Canada), giving higher priority to adult females or juveniles; up to 3 bats were transmitted on a given night. Radio transmitters were 3.2–6.9% of body weight. We followed the recommended WNS decontamination protocols (USFWS, 2011) and handling guidelines of the American Society of Mammalogists (Sikes et al., 2011), Clemson IACUC protocol 2009–16 and ISU IACUC protocol 226895. Field work was conducted under permits held by JM O'Keefe: USFWS federal recovery permit TE206872, North Carolina permit ES261, Tennessee permit 3148, and National Park Service Permits GRSM-2009-SCI-0075 and GRSM-2012-SCI-0085.

We used 3- and 5-element Yagi antennae and a receiver (Telonics, Mesa, AZ, USA) to locate day roosts for each bat, tracking each bat until the transmitter failed, fell off, or the bat was lost or left the area. As feasible, we watched roosts to count emerging bats, with counts beginning 30 min prior to sunset and continuing until 10 min after the last bat had left the tree. For selected roosts, we deployed a datalogging receiver (Lotek Wireless, SRX-DL2, Newmarket, Canada) to record body temperature of individual bats at roosts throughout the day (Hammond, 2013); this receiver scanned for all programmed frequencies within a small area around each tree and, thus, provided additional information on roost use.

For each roost tree used by a female or juvenile and for a corresponding random focal tree, we measured tree and plot-level characteristics in a 0.1 ha plot centered on the trees. To minimize disturbance to bats, plot surveys were conducted at least 2–3 months after the roosts were found, but always during the leaf-on period. We applied a novel landscape-scale method of finding random focal trees with the goal of facilitating stand-level comparisons between roosts and random trees (see discussion of this problem by Miller et al., 2003 and Kalcounis-Rueppell et al., 2005). To select the search area for a random focal tree to pair with a particular roost, we selected a random point from a search square centered on the capture site, with the side of the square corresponding to twice the distance between the capture site and that particular roost rounded up to the nearest km. For example, if a bat moved 2.2 km from the capture site to Roost 1, then we searched for a corresponding random point (Random 1) within a square buffer that extended 3 km in each cardinal direction from the capture site (1 side of the square was 6 km). Each 1 km block within the square was gridded into 100 1-ha cells. We used a random number generator to select a quadrant of cells (e.g., NE), then

to select a 1 km block (if there were multiple blocks in a quadrant), and then to select a cell within this block. We navigated to the center of the random cell and selected the nearest snag with visible roost potential (see below) as the random focal tree, regardless of stand type. Any cells that fell on private land were discarded and replaced.

2.3. Roost characteristics

For each focal (roost or random) tree, we recorded species, diameter at breast height (cm dbh), height (m), and distance (m) to the closest tree ≥ 10 cm dbh and the closest tree the same height or taller (Table 1). We also measured overall decay stage (1–4) based on a classification system developed by Ormsbee (1996), but modified slightly for our study area (Table A1), and distance (m) to the nearest dead tree that had roost potential. We defined roost potential as bark peeling away from the tree trunk with enough room for ≥ 5 Indiana bats to fit underneath. Although we found 2 crevice roosts in the last year of the study (2012), we did not consider crevices as potential roosts when selecting random focal trees. For all live and dead trees in a 0.1 ha plot around each focal tree that were ≥ 10 cm dbh, we recorded species and measured dbh (cm) to calculate live and dead tree basal areas. We tallied all saplings < 10 cm in diameter within a 0.025 ha plot centered on the focal tree. Standing at the base of the focal tree, we visually estimated percent canopy closure directly above the tree and percent midstory closure surrounding the tree, both to the nearest 25%. For each quarter plot, we estimated percent canopy closure to the nearest 25%, averaging the 4 values to yield a plot-level canopy closure value. We recorded focal tree coordinates with a GEO-XT (Trimble, Sunnyvale, CA, USA) or 60CSX (Garmin, Olathe, KS, USA) GPS to facilitate GIS analyses.

Noting that most roosts (44 of 69 roosts used in models) were yellow pine, we coded focal trees as yellow pine or not. To assess the importance of plot- and stand-level characters to roost habitat selection, we calculated importance values for tree species' groups based on the live trees present in each focal tree plot and identified the age of each stand. For each plot, we calculated importance values for yellow pines, white pines, hemlocks, oaks, and all other hardwoods. Importance values were the average of two numbers: the percent contribution of trees ≥ 10 cm dbh in that group to the total plot stem count and the percent contribution to total plot basal area. We classified each plot as old (≥ 75 years), mature (35–74 years), or young (≤ 34 years). We treated all stands in GSM as old, based on the date the park was established. We used harvest data from the USFS Continuous Inventory of Stand Conditions (CISC) to determine stand ages on the CNF and NNF.

In a GIS in ArcMap 10.2 (ESRI, Redlands, CA, USA), we overlaid focal tree points with existing and newly created raster layers for elevation, aspect, and distance-to-ridge. We extracted elevation values from 10 m digital elevation models (DEMs) for our study area (<http://ned.usgs.gov>, 1/3 arc-sec/10 m resolution) and used these same DEMs to generate aspect and distance-to-ridge raster layers (30 m resolution). Due to its circular nature, aspect was separated into East/West (+1 to –1) and North/South (+1 to –1) by calculating the cosine and sine of the original value, respectively. We used tools in Spatial Analyst (ESRI, Redlands, CA, USA) to filter DEMs and to generate a distance-to-ridge raster; this required a multi-step process detailed in Hammond et al. (2016).

We also measured the distance (m) from focal trees to features (streams, waterbodies, and linear openings) that we thought may be important to bats as foraging resources or potential travel corridors (DuChamp et al., 2007). Detailed lake, perennial stream, and river data were acquired from the National Hydrography Dataset (<http://nhd.usgs.gov>). We merged the flowline shapefiles for streams and rivers into one layer. Roads and trails layers were

Table 1
Measurements taken at Indiana bat (*Myotis sodalis*) roost and random sites in the southern Appalachian Mountains, NC and TN, USA, 2008–2012.

Category	Variable	Description
Roost tree characters	yellow pine	Focal tree species (1/0)
	height	Focal tree height (m)
	dbh	Focal tree dbh (cm)
	age1	Stand age mature (1/0)
	age2	Stand age old (1/0)
Clutter around roost	saplings	Count of saplings < 10 cm dbh
	mid_clos	Midstory closure under the focal tree (%)
	dist_nt	Distance to nearest tree from focal tree (m)
	ltba	Live tree basal area (m ² /0.1 ha)
	ltct	Live tree count (per 0.1 ha)
Solar exposure	dist_taller	Distance to nearest taller tree (m)
	roost_canclos	Canopy closure above the focal tree (%)
	plot_canclos	Canopy closure in the plot (%)
	north_south	North south facing (–1 to 1)
	east_west	East west facing (–1 to 1)
Switching opportunities	dist_ridge	Distance to ridge (m)
	dtba	Dead tree basal area (m ² /0.1 ha)
	dtct	Dead tree count (per 0.1 ha)
	dist_wt	Distance to closest potential roost (m)
	Forest composition	hdwd_iv
oak_iv		IV for oaks (proportion of plot)
hem_iv		IV for hemlocks (proportion of plot)
wtpi_iv		IV for white pines (proportion of plot)
yepi_iv		IV for yellow pines (proportion of plot)
Proximity to foraging areas	dist_linopen	Distance to linear opening (road or trail) (m)
	dist_stream	Distance to stream (m)
	dist_waterbody	Distance to large water body (m)
Elevation	elevation	Elevation (m)

developed from spatial data provided by the National Park Service and USDA, Forest Service; these were merged into one linear openings layer.

2.4. Statistical analyses

Due to a low sample of bats for radio telemetry, we pooled roost data across years and used roosts rather than bats as the experimental unit, assuming observations were independent. We used Program R 3.3.2 (R Core Development Team, 2010) to conduct all statistical analyses outlined below. Prior to creating models, we conducted a correlation analysis to determine if pairs of variables were highly correlated (>0.6) and removed or combined any that we identified as such. We provide summary statistics for all roosts ($n = 95$) and report values as mean \pm 1 S.E., unless stated otherwise.

For 69 roosts used by adult female and juvenile Indiana bats for which we had matching random tree data, we used the lme4 package in R to construct case-control logistic regression models to assess roost habitat selection for tree-, plot-, stand-, and landscape-level factors. From the data collected in the field and with GIS, we developed a list of 28 predictor variables to enter into models (Table 1). We considered 14 candidate models (Table B1), plus the null model. Because our sample of roost trees was relatively small, we only examined candidate models containing 2–7 variables (minimum of 9 samples per variable). The 14 candidate models represented hypotheses about roost habitat selection that reflect our current knowledge of factors that might be important (e.g., roost switching, thermoregulation, proximity to foraging habitat; Table B1). We used Akaike's information theoretic procedures to rank models by their respective Akaike's information criterion for small sample sizes (AIC_C) and computed Akaike weights (w_i) to compare the plausibility of competing models. We considered the model with the lowest value for AIC_C to be the best model and models with $\Delta AIC_C < 4$ to be plausible (Burnham and Anderson, 2002). We defined the confidence set of models as those with Akaike weights within 10% of the highest weighted model;

none of the models met this criterion, so we only analyzed variables from the best model. Important variables in the best model, defined as those for which 85% confidence intervals excluded zero (Arnold, 2010), were considered useful for discriminating between roost and random sites, and we present adjusted odds ratios and unconditional standard errors for these variables.

3. Results

While conducting mistnetting surveys for Indiana bats, we captured 1517 bats during 142 nights from May to August 2008–2012. We captured 109 Indiana bats (78 adult females, 21 adult males, and 10 juveniles); three adult females were each captured twice at the same net site (3 sites; 1 month, 1 year, and 2 years apart). We also captured 402 *M. septentrionalis*, 389 *E. fuscus*, 292 *Lasiurus borealis*, 138 *M. lucifugus*, 111 *Perimyotis subflavus*, 20 *Lasionycteris noctivagans*, 15 *Corynorhinus rafinesquii*, 18 *M. leibii*, 15 *Nycticeius humeralis*, 5 *Lasiurus cinereus*, and 3 *Lasiurus seminolus*. We recorded WNS wing damage scores ranging from 0 to 2 for 1286 bats; many bats showed signs of wing scarring, but we scored only 4 bats with a 2.

3.1. Roosting behavior

We tracked 50 adult females (13 pregnant, 22 lactating, 13 post-lactating, and 2 non-reproductive). Two adult females were tracked in 2 separate years (Bat 1785 was tracked in June 2009 and 2010, and Bat 1948 was tracked in July 2009 and May 2011). We also tracked 3 juvenile bats (1 female, 2 male) and 7 adult males. Four adult females were never found and some bats were lost for ≥ 1 day during tracking. We found 1–4 trees/adult females and juveniles and 1–7 trees/adult males. Roosts were 157–3731 m from capture sites; roosts used by pregnant and lactating females were 1592 ± 166 m and 1253 ± 138 m from capture sites, respectively, while roosts used by post-lactating and non-reproductive females were 915 ± 161 m and 904 ± 339 m from capture sites, respectively.

Roosts for adult males and juveniles were 1271 ± 147 m and 1464 ± 407 m from the capture site, respectively.

It was difficult to track each bat daily, as bats switched roosts often and transmitter signals were easily lost in the rugged terrain of our study area. Switching rate data by bat are unreliable, but the total days each roost was used give some indication of roost fidelity; these totals include non-consecutive days. Individual roost trees were used from 1 to 10 days each over the entire tracking period. Pregnant females used individual roost trees for an average of 2.6 ± 0.4 days each, lactating females for 2.2 ± 0.3 days, post-lactating females for 2.2 ± 0.5 days, and non-reproductive females for 3.3 ± 2.3 days. Juveniles used individual roost trees for 2.6 ± 1.3 days each and adult males for fewer total days, only 1.2 ± 0.1 days. Only 1 roost, a yellow pine snag, was used in 2 years (2009 and 2010).

Adult females typically roosted in moderate group sizes (Table 2), though we detected large groups (>50 bats) in 4 unique parts of the study area >20 km apart. We observed an average of 18.4 ± 3.1 bats/night emerging from roost trees used by pregnant, lactating, and post-lactating bats; however, females in each reproductive condition were also found roosting alone on occasion (Table 2). Maximum colony sizes were largest during the lactation period (24.4 ± 5.5 , range 1–92 bats, Table 2), though we observed 1 juvenile male in a roost that we assumed was a maternity roost,

which contained 126 bats in July 2011. We assumed most adult males were roosting alone, but we detected 2 adult males roosting in groups; 1 male roosted with 5 other bats in a 39.7 cm dbh yellow poplar (*Liriodendron tulipifera*) snag and another roosted with ≥ 30 other bats in a 82.2 cm dbh hemlock snag. Before juveniles were likely to be volant, the largest colony size we detected was 75 bats; this colony emerged from a yellow pine snag used by a pregnant female on 16 June 2011.

3.2. Roost characteristics

We tracked bats to 95 snag roosts (Table 3), most of which were decayed pines (e.g., Fig. 1). We placed a greater emphasis on tracking reproductive adult females (73 roosts), but also located 4 roosts for non-reproductive adult females in 2012. We located 11 roosts for adult males and 7 roosts for juvenile bats. Most roosts (91.6%) were in yellow pines ($n = 61$) and white pines ($n = 26$). From residual bark, branches, and cones, we identified yellow pine roosts as shortleaf pine (41 roosts), Table Mountain pine *P. pungens*, 3 roosts), pitch pine (*P. rigida*, 2 roosts), Virginia pine (*P. virginiana*, 13 roosts), and *Pinus* sp. (2 roosts). We located 3 hardwood roosts (1 each in red maple, *Acer rubrum*; yellow poplar, *L. tulipifera*; and white oak, *Q. alba*) and 5 hemlock snag roosts. Three of the hemlocks were maternity roosts, with peak exit counts of 4, 31, and 37 bats; these

Table 2
Mean maximum colony sizes at roosts used by Indiana bats (*Myotis sodalis*) in the southern Appalachian Mountains, NC and TN, USA, 2008–2012. For each age, sex, and reproductive condition (for adult females only), we present the number of roosts watched, mean high emergence count, and minimum and maximum exit counts.

Age	Sex	Reproductive condition	Number of roosts	Mean high emergence count \pm SE	Minimum emergence count	Maximum emergence count
Adult	Female	Pregnant	16	$14.3 \pm 0.4.8$	1	75
		Lactating	28	24.4 ± 5.5	1	92
		Post-lactating	15	11.4 ± 4.0	1	52
		Non-reproductive	4	12.0 ± 8.1	1	36
Juvenile	Male	–	4	9.75 ± 7.2	1	31
	Male & Female	–	6	38.2 ± 19.1	1	126

Table 3
Mean and standard error of variables measured at Indiana bat (*Myotis sodalis*) roost trees in the southern Appalachian Mountains, NC and TN, USA, 2008–2012. Variables are defined in Table 1.

	Adult females				Juveniles 7 roosts	Adult Males 11 roosts	Randoms 79 randoms
	Pregnant 18 roosts	Lactating 36 roosts	Post-lactating 19 roosts	Non-reproductive 4 roosts			
height (m)	19.7 ± 1.8	18.5 ± 1.3	18.7 ± 1.4	18.3 ± 3.3	25.9 ± 2.3	19.9 ± 2.6	12.0 ± 0.9
dbh (cm)	38.8 ± 3.4	36.3 ± 3.0	42.5 ± 6.6	28.3 ± 4.9	46.9 ± 4.6	47.2 ± 8.6	33.4 ± 1.8
Saplings/0.1 ha	53.2 ± 7.9	45.5 ± 5.1	37.3 ± 6.0	61.3 ± 19.4	33.6 ± 4.3	60.9 ± 16.7	48.4 ± 4.0
mid_clos (%)	47.5 ± 7.2	37.5 ± 5.3	44.7 ± 5.6	68.8 ± 15.7	35.7 ± 5.1	61.1 ± 6.7	46.5 ± 3.8
dist_nt (m)	3.0 ± 0.5	2.8 ± 0.3	3.2 ± 0.4	2.6 ± 0.3	2.4 ± 0.6	3.7 ± 0.7	2.9 ± 0.6
ltba (m ² /0.1 ha)	1.5 ± 0.1	1.9 ± 0.1	1.5 ± 0.2	2.5 ± 0.5	1.8 ± 0.3	1.7 ± 0.3	2.0 ± 0.1
ltct/0.1 ha	34.2 ± 3.2	39.0 ± 1.9	33.3 ± 3.5	44.5 ± 2.6	32.0 ± 5.7	34.1 ± 4.5	40.7 ± 1.7
dist_taller (m)	5.9 ± 0.7	5.2 ± 0.5	5.8 ± 0.9	4.1 ± 0.9	7.0 ± 1.0	6.5 ± 1.0	4.1 ± 0.4
roost_canclos (%)	32.5 ± 7.7	31.3 ± 6.1	14.5 ± 6.1	25.0 ± 25.0	10.7 ± 7.4	2.3 ± 2.3	61.7 ± 4.4
plot_canclos (%)	48.4 ± 6.0	63.1 ± 4.0	54.7 ± 4.7	65.6 ± 8.3	47.3 ± 3.3	56.9 ± 8.4	72.2 ± 2.8
north_south	-0.5 ± 0.1	-0.3 ± 0.1	-0.6 ± 0.1	0.3 ± 0.4	-0.1 ± 0.2	0.3 ± 0.2	-0.1 ± 0.1
east_west	-0.2 ± 0.1	-0.2 ± 0.1	-0.2 ± 0.1	0.3 ± 0.3	0.4 ± 0.3	-0.2 ± 0.3	-0.2 ± 0.1
dist_ridge	79.2 ± 10.1	56.9 ± 5.9	56.0 ± 6.3	78.6 ± 26.4	45.9 ± 16.4	62.7 ± 15.3	60.7 ± 4.5
dtba (m ² /0.1 ha)	0.9 ± 0.2	1.0 ± 0.1	1.4 ± 0.4	0.8 ± 0.3	0.9 ± 0.2	1.1 ± 0.2	0.4 ± 0.04
dtct/0.1 ha	13.0 ± 1.9	12.1 ± 1.4	13.3 ± 1.4	14.8 ± 3.4	9.4 ± 1.3	12.4 ± 2.9	6.0 ± 0.5
dist_wt	5.6 ± 0.7	7.3 ± 1.0	5.5 ± 1.0	16.0 ± 4.6	8.5 ± 1.7	5.8 ± 1.1	21.6 ± 2.0
hdwd_iv	0.3 ± 0.02	0.3 ± 0.03	0.3 ± 0.03	0.4 ± 0.07	0.3 ± 0.06	0.4 ± 0.09	0.4 ± 0.03
oak_iv	0.3 ± 0.04	0.2 ± 0.03	0.2 ± 0.04	0.1 ± 0.08	0.2 ± 0.07	0.2 ± 0.05	0.3 ± 0.02
hem_iv	0.1 ± 0.03	0.1 ± 0.02	0.1 ± 0.05	0.2 ± 0.1	0.1 ± 0.06	0.1 ± 0.05	0.1 ± 0.01
wtpi_iv	0.1 ± 0.05	0.2 ± 0.04	0.2 ± 0.04	0.2 ± 0.11	0.3 ± 0.07	0.1 ± 0.05	0.1 ± 0.02
yepi_iv	0.2 ± 0.03	0.2 ± 0.04	0.2 ± 0.04	0.0 ± 0.02	0.1 ± 0.06	0.2 ± 0.08	0.1 ± 0.02
dist_linopen (m)	479.4 ± 95.4	255.8 ± 35.5	286.3 ± 66.5	107.2 ± 32.0	289.5 ± 30.1	128.5 ± 32.7	319.9 ± 31.5
dist_stream (m)	144.2 ± 34.4	138.1 ± 19.8	188.5 ± 27.0	53.0 ± 14.1	114.6 ± 33.5	127.1 ± 36.2	173.9 ± 12.7
dist_waterbody (m)	2525.0 ± 351.3	2265.1 ± 241.5	2525.0 ± 558.7	1107.4 ± 229.7	2945.0 ± 469.3	4741.9 ± 1152.8	2466.4 ± 209.8
elevation (m)	648.4 ± 19.2	473.6 ± 21.8	596.4 ± 64.0	540.0 ± 37.0	645.0 ± 46.2	822.2 ± 109.3	562.6 ± 24.3

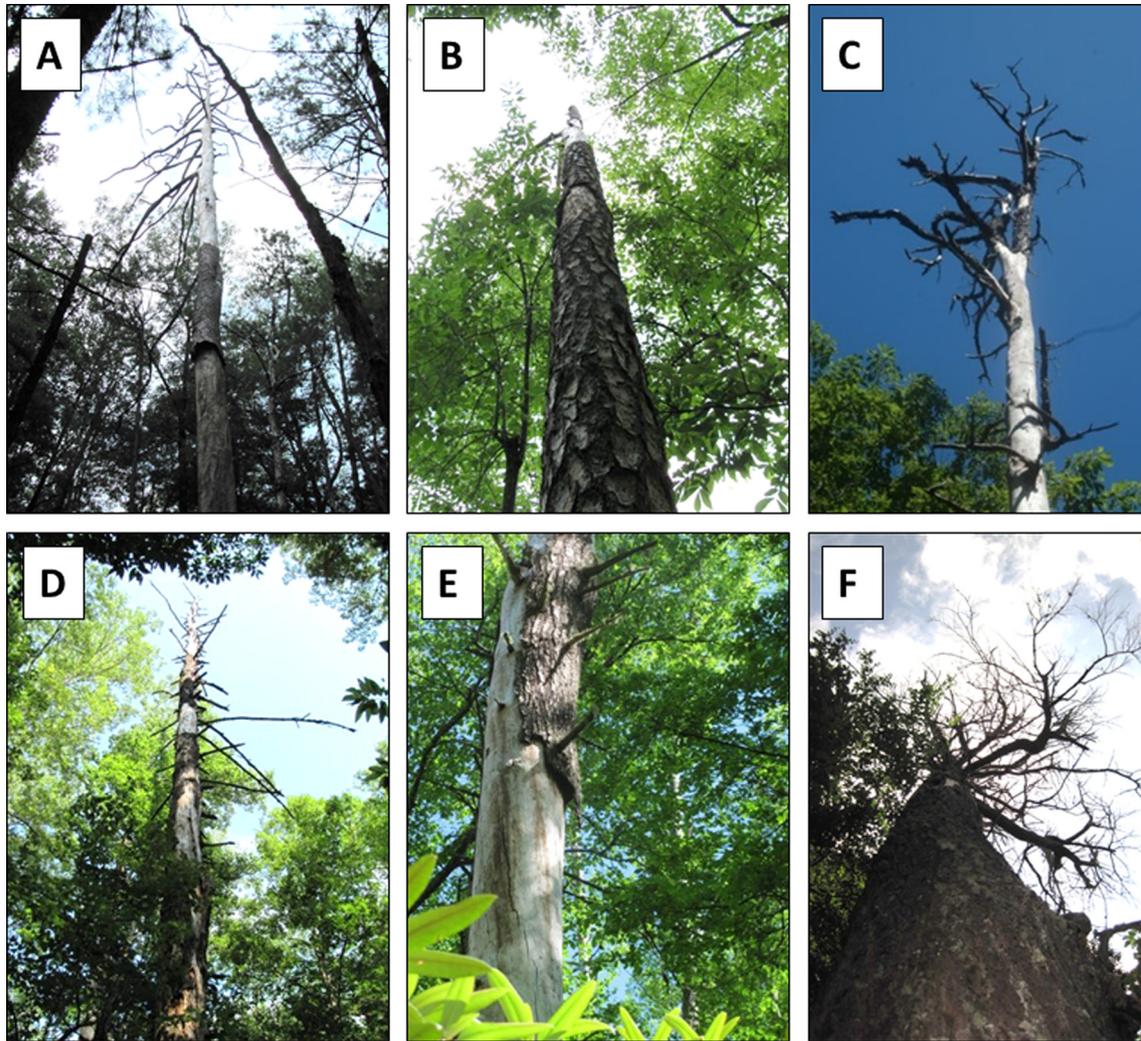


Fig. 1. Examples of Indiana bat (*Myotis sodalis*) roost trees found in the Cherokee National Forest (CNF), Nantahala National Forest (NNF), and Great Smoky Mountains National Park (GSM) in the southern Appalachian Mountains, NC and TN, USA, 2008–2012. (A) GSM 2010-5, 50 cm diameter at breast height shortleaf pine (*Pinus echinata*), 28 bats; (B) NNF 2011-1, 30 cm dbh yellow pine (*Pinus* subgenus *Diploxylon*), 75 bats; (C) CNF 2009-3, 35 cm dbh Table Mountain pine (*P. pungens*), 8 bats; (D) CNF 2010-4, 75 cm dbh white pine (*P. strobus*), 55 bats; (E) NNF 2012-1, 76 cm dbh white pine, 14 bats; (F) CNF 2012-3, 137 cm dbh hemlock (*Tsuga canadensis*), 37 bats.

roosts were very large—82.2–137.5 cm in diameter (Fig. 1F) and the 2 trees with higher exit counts were 37–37.2 m in height. Bats typically roosted under sloughing bark on the trunk of the tree (e.g., Fig. 1E), but there were 2 exceptions. A lactating female roosted with ≥ 38 bats in a crevice in the trunk of a dead yellow pine on CNF and a post-lactating female roosted with ≥ 6 bats in a crevice near the top of a dead yellow pine on the NNF. Roosts held $31.8 \pm 2.6\%$ of their bark (1–98%). Roosts were moderately decayed (2.4 ± 0.1), as were random snags (2.7 ± 0.1); a snag classified as ~ 2.5 had few to no branches, 30–80% bark remaining, and a broken top (e.g., Fig. 1B and Table A1).

A typical roost was tall, with high solar exposure in the stand and in its landscape position. For adult females, the average roost tree was 18.8 m tall and 36.5 cm in diameter. Adult males and juveniles used trees 19.9–25.9 m in height and 46.9–47.2 cm in diameter (Table 3); for adult males the large mean diameter was skewed by 2 large eastern hemlock snags (82.2 and 109.7 cm dbh) used by 2 different adult males. Bats roosted at 10.8 ± 0.6 m above ground (range 3–25 m). Adult females used trees with $< 33\%$ canopy closure above (roost_canclos, Table 3), but canopy closure ranged from 48.8 to 65.6% in the surrounding plot (plot_canclos, Table 3). Live tree basal area (ltba) and counts (ltct) were similar for all bat groups—averaging $1.8 \text{ m}^2/0.1 \text{ ha}$ and 36 trees/0.1 ha (Table 3). Dead tree basal area (dtba) and counts (dtct)

averaged $1.0 \text{ m}^2/0.1 \text{ ha}$ and 12.5 trees/0.1 ha; note that dead trees were concentrated around roosts and these values may not indicate the condition of the larger stand (e.g., 1 ha) surrounding the roost. Reproductive adult females roosted on south-facing slopes at elevations averaging 573 m (Table 3), but as high as 1270 m (2 high elevation hemlock roosts). Based on importance values for trees located in 0.1 ha plots surrounding each focal tree, bats roosted in stands dominated by non-oak hardwoods, with oaks and pines as secondary elements (Table 3).

3.3. Roost habitat selection

The best case-control logit model for roost habitat selection by adult females and juveniles was high solar pines (conditional $R^2 = 0.65$; Table 4). This model contained yellow pine, focal tree height, canopy closure above the focal tree, aspect (north_south and east_west), distance to ridge, and dead tree count/0.1 ha plot (Table B1). There was a 95% probability that this model was the best approximating model for the data tested (Table 4) and no other model met our criteria for importance ($\Delta \text{AIC}_c < 4$; $w_i \geq 10\%$ of top model's weight). Three of the variables in this model were important (i.e., 85% confidence intervals did not include zero): dead tree count, focal tree species, and focal tree height. When compared to random focal trees, odds ratios showed that bats were

Table 4
Models, number of parameters in the model (K), Akaike's Information Criterion adjusted for small sample sizes (AIC_c), difference between the AIC_c value and the model with the lowest AIC_c (dAIC_c), and AIC_c weight (w_i) for the candidate set of models used to predict roost habitat selection by Indiana bats (*Myotis sodalis*) in the southern Appalachian Mountains, NC and TN, USA, 2008–2012. Model hypotheses are given in Appendix B.

Model	K	AIC _c	dAIC _c	w _i
High solar pines	8	127.636	0.00	0.948831
Switching opportunities	5	134.315	6.68	0.033653
Large dead trees	6	135.621	7.98	0.017510
Plot-scale solar exposure	5	151.995	24.36	<0.00001
High solar large trees	8	154.896	27.26	<0.00001
Midwestern riparian zones	6	182.381	54.74	<0.00001
Mountain riparian zones	6	188.121	60.48	<0.00001
Yellow pines	6	190.941	63.30	<0.00001
Proximity to water	3	191.519	63.88	<0.00001
Null	1	193.329	65.69	<0.00001
South ridge pines	7	194.822	67.19	<0.00001
Proximity to openings	5	197.155	69.52	<0.00001
Low plot clutter	6	198.201	70.56	<0.00001
Landscape-scale solar exposure	5	199.575	71.94	<0.00001
Fire-adapted stands	7	200.022	72.39	<0.00001

Table 5
Coefficient estimates and odds ratios (OR), and OR confidence limits (CL) for parameters in the Pine + Solar + Switching model that best predicted roost habitat selection by Indiana bats (*Myotis sodalis*) in the southern Appalachian Mountains, NC and TN, USA, 2008–2012. ORs are presented only for parameters for which the standard error (SE) is less than the estimate. Variables are defined in Table 1.

Parameter	Estimate	SE	Odds Ratio	Lower 85% OR CL	Upper 85% OR CL
Intercept	−5.84	1.40			
Yellow pine	1.96	0.58	7.09	3.09	16.27
Dtct	0.22	0.05	1.25	1.16	1.35
Height	0.18	0.04	1.20	1.12	1.27
North_south	0.09	0.35			
East_west	0.04	0.37			
Roost_cancelo	0.00	0.01			
Dist_ridge	0.00	0.01			

more likely to use tall yellow pine snags surrounded by a greater density of dead trees (Table 5). A tree was 7 times more likely to be a roost if it was a yellow pine snag. For every 1 m increase in tree height, a tree was 1.2 times more likely to be used. For every 10 additional dead trees in the 0.1 ha plot, a tree was 12 times more likely to be used as a roost.

4. Discussion

Indiana bats were part of a diverse community of bats in the southern Appalachian Mountains. We demonstrated that Indiana bats usually roosted in small groups and were relatively nomadic in the southern Appalachians. Further, bats primarily used yellow pine snags, which is a departure from what has been observed for Indiana bat maternity colonies in the Midwest and Northeast. Bats were likely selecting for pines because pine snags were more available than hardwoods snags and because they provide optimal roosting structure (tall, solar-exposed) for Indiana bats in the southern Appalachian Mountains.

In our southern Appalachian study area, Indiana bats exhibited different roosting behaviors than what has been observed in the Midwest, with lower roost fidelity and smaller colony sizes. A fission-fusion social dynamic was likely an important facet of the roost switching we observed (Kerth and König, 1999). However, the low roost fidelity we observed, with individual bats using each tree for only 2–3 days in total may also relate to high roost availability or to the fact that bats were using ephemeral roost trees and needed to explore alternative roost options (Timpone et al., 2010). In our study area, pine snag roosts only lasted for 1, or rarely 2, maternity seasons (Britzke et al., 2003; this study) and sometimes lost all their bark in 1 season. In contrast, in highly fragmented forests in the Midwest, Indiana bat maternity colonies use only 1 or a few primary roosts for the bulk of the maternity

season (e.g., Callahan et al., 1997) and for multiple seasons. For example, in a strip of riparian forest in central Indiana, an Indiana bat colony mainly roosts in 1–4 primary roosts (most often dead cottonwoods or bat boxes) from May to October (O'Keefe et al., 2012, 2016), using the same natural tree roost for up to 6 years (Whitaker et al., 2004) and a single bat box for up to 10 years (O'Keefe and Whitaker, unpublished data). However, bats may prefer to switch roosts regularly, as this should diminish parasite loads and reduce the risk of predation (Lewis, 1995); greater availability of trees in the southern Appalachians may facilitate these switches.

Indiana bat colonies may have been smaller in the southern Appalachians (typically < 25 bats) versus the Midwest (often > 100 bats; e.g., Callahan et al., 1997; Whitaker and Brack, 2002) because colonies were spread across a greater number of suitable roosts. Although we did not measure roost availability, the greater expanse of unfragmented forest in our area implies that more suitable roosts were present. Although colony sizes were relatively large (75–126 bats) on occasion, our data suggest that usually <25 bats used a particular roost and for only a few days. The forest conditions and more ephemeral roosts in our study area might not promote the development of large maternity colonies as are seen in floodplain/bottomland forests (e.g., Kitchell, 2008) and forest fragments (e.g., Whitaker and Brack, 2002) in the Northeast and Midwest. Our typical roost tree did not meet the definition of a primary maternity roost used by ≥30 bats for an entire maternity season (as defined for the Midwest by Callahan et al., 1997), which suggests a need for regional or site-specific definitions of primary roosts.

In most studies of Indiana bat roosting ecology, maternity roosts have been documented in hardwoods. For example, in Missouri, maternity colonies mainly use pin oak (*Q. palustris*) and American elm (*Ulmus americana*) (Timpone et al., 2010), or oaks and shagbark hickory (*C. ovata*) (Callahan et al., 1997). American elm is also a favored roost type in New Jersey (Kitchell, 2008) and New York (Jachowski et al., 2016), and shagbark hickory is

avored in New Jersey (Kitchell, 2008), and Vermont and New York (Watrous et al., 2006). However, bats clearly selected for yellow pines in this study, which corroborates Britzke et al.'s (2003) work showing that yellow pines may serve as primary maternity roosts for Indiana bats in the southern Appalachians; we also found maternity roosts in 2 hemlocks and 26 white pine snags. Indiana bats occasionally roost in white pine snags in the Northeast (Watrous et al., 2006), and use dead loblolly (*P. taeda*) and shortleaf pines as maternity roosts in Alabama (Roby and Gumbert, 2013). Yellow pines are also important roosts for male Indiana bats in mixed pine-hardwood forests in eastern Kentucky (e.g., Gumbert et al., 2002; MacGregor et al., 1999) and northern Arkansas (Perry et al., 2016). At the time of this study, yellow and white pines comprised the bulk of the snags on the landscape in our area (O'Keefe and Loeb, unpublished data); these trees likely died during a southern pine beetle (*Dendroctonus frontalis*) outbreak in the early 2000s (Nowak et al., 2008). At low to moderate levels of decay, large (i.e., averaging ~60 cm in diameter in this study) yellow or white pine snags may provide the ideal structure for Indiana bat maternity roosts—tall and solar-exposed, with bark sloughing away from the tree trunk in large plates (Fig. 1). Yellow pines may also be ideal roosts due to their tendency to occur on ridgetops (Schafale, 2012) which, in mountainous terrain, yields greater solar exposure than roosts alongside streams.

Aside from selection for yellow pines, our top model suggested that tree height and snag density were important factors in roost habitat selection by Indiana bats in the southern Appalachians. Tree-roosting bats typically select for tall trees (Kalcounis-Rueppell et al., 2005), which provide greater solar exposure, likely facilitating growth and physiological processes for mothers and their pups (Callahan et al., 1997). Tall roosts may also be easier to access from above the canopy (Britzke et al., 2003; Cryan et al., 2001). Indiana bat roost trees are also relatively tall in Missouri (17.7 m; Timpone et al., 2010) and Illinois (17.5 m; Carter and Feldhamer, 2005), though mean roost height across studies in 12 states is only 8.6 m (Lacki et al., 2009). Selection for tall trees may partly explain the heavy use of pine snags in our study area, as these tended to be taller than hardwood snags we observed. High snag density surrounding roost trees may make it easier for bats to switch roosts in case of disturbance or for a change in microclimate, but we rarely observed bats using multiple roosts within the same stand. Rather, we suspect the preference for areas of high snag density is an artifact of using yellow pines, which tended to occur in clusters in our study area.

In our analysis, landscape-scale factors were not as important as tree- and plot-scale factors for explaining roost habitat selection by Indiana bats. Using a large-scale species distribution model to analyze Indiana bat maternity roost habitat selection in the same southern Appalachian landscape, Hammond et al. (2016) determined that these bats selectively roost near the ridgetop on south-facing slopes in mixed pine-hardwood forests from 260 to 575 m in elevation. The most important variables in Hammond's model, forest composition and elevation, were not important predictors of roost habitat selection in our analysis because roosts and random points were situated around the same capture site and, thus, were similar with respect to these landscape-scale characteristics. However, our finding that bats selected for yellow pines corroborates the significance of the landscape-scale factors that predict where yellow pines will occur, such as elevation and aspect.

Our data suggest that it would be wise to consider the broader landscape context, such as local disturbance dynamics, when evaluating various multi-scale factors that affect roost habitat preferences of Indiana bats. The primarily forested landscape where we worked differed significantly from other landscapes where Indiana bat roost preferences have been studied and this translated to differences in roosting behavior. While insects and fire are important

determinants of roost availability in the southern and central Appalachians (beetle-killed pines, this study, and fire-killed maples in West Virginia, Johnson et al., 2010), floods, tree diseases, and agricultural practices are predictors of Indiana bat roost tree availability in the other regions (e.g., Carter et al., 2002; Watrous et al., 2006; and Jachowski et al., 2016, respectively). In landscapes where the relative proportions of agriculture, forests, and development are more even, Indiana bats selectively roost in forested areas with a high density of suitable roosts (Miller et al., 2002), though forest patches containing roosts may be very isolated (Watrous et al., 2006) or more intermixed with agriculture than expected (Carter et al., 2002). Further, where there is less forest cover on the landscape, maternity colonies show long-term fidelity to rich riparian forests that provide large snags for roosting and productive foraging grounds (Carter, 2006). In contrast, in the larger forests of the southern Appalachian Mountains, bats were not restricted to roosting in riparian forests and, thus, could be more nomadic within the maternity season with respect to where they foraged or roosted. This could explain why bats showed low roost fidelity and why we often lost radio signals during this study. We found that distance to water was not an important factor in roost habitat selection, which further contrasts with the tendency for Indiana bats to roost near streams in the Midwest (e.g., Humphrey et al., 1977; Carter, 2006). However, on average bats roosted within 53–189 m from streams (Table 3), which were ubiquitous on our landscape, and we did locate 4 significant (>50 bats) maternity roosts in large (63–94 cm dbh) white pine snags in low lying areas; these trees were likely planted (Schafale, 2012).

5. Management implications

It would be impractical to manage for Indiana bat roosting habitat at the scale of the roost tree (i.e., protect individual trees) in large forested sites such as our study area, where Indiana bats regularly moved among roosting areas and used ephemeral snags. Instead, we suggest managers employ stand- and landscape-scale strategies that sustain snags and promote development of future roosts. During harvests, retaining patches of large snags (≥ 35 cm dbh, with ≥ 12 snags/0.1 ha) and buffering such patches with live trees to protect them from wind throw may benefit Indiana bats in this area. In the southern Appalachians, prescribed fire is commonly implemented at the landscape-scale (200–16,000 ha) to regenerate pine forests (Jenkins et al., 2011). Fire may be necessary for the persistence of yellow pine forests in this region (Lafon et al., 2007) and, because yellow pines are important roost types, fire could be a critical management tool for sustaining Indiana bat roosting habitat. The open canopy conditions created by frequent burning could be ideal for Indiana bats (Johnson et al., 2010; Silvis et al., 2016); indeed, male Indiana bats selectively roost in burned areas in Arkansas (Perry et al., 2016) and Kentucky (MacGregor et al., 1999). We suggest implementing management actions that will result in healthy pine-hardwood forests with a component of large snags in both the short- and long-term. To promote yellow pine regeneration and to limit competition by heath shrubs in the understory, we recommend conducting repeated low to moderate severity prescribed fires during warm, dry conditions in spring or fall (Jenkins et al., 2011). Brose and Waldrop (2010) propose that yellow pines and oaks are ecological analogs favored by the same types of disturbances and that, depending on the intensity of the fire, restoration of pine-oak forests will require prescribed fires to coincide with clearcuts or natural canopy disturbances like southern pine-beetle infestations and major storms. When implementing prescribed fire during times when Indiana bats are roosting in trees, it will be necessary to take precautions that give bats time to respond to approaching fire and

to weigh the costs (potential direct mortality of bats in snags) with the benefits (long-term restoration of suitable or optimal habitat) (Loeb and O'Keefe, 2014).

The pine snags are declining in our study area and it is not clear if future snags will be suitable as roosts. Indiana bats may respond to pulses in snag populations occurring as a result of natural processes such as windstorms, wildfires, insect infestations, floods, and disease. For example, in our study area, we might expect Indiana bats to respond to the pulse of hemlock snags available due to an infestation by the non-native hemlock woolly adelgid (*Adelges tsugae*) (Nuckolls et al., 2009). However, although a large hemlock snag provides ample roosting space for a group of bats, thermal conditions are likely suboptimal because hemlocks tend to occur at higher elevations, on north facing slopes, or in sheltered landforms (Schafale, 2012). Britzke et al. (2003) found a maternity roost in a 109 cm dbh hemlock on the NNF in 1999, and we occasionally observed both male and female Indiana bats using hemlocks during this study and in subsequent work in the same region in 2014–2015 (O'Keefe et al., unpublished data).

Managers in recreation areas may need to balance concerns for human welfare and risk of bat mortality when clearing hazard trees, such as pine snags, near roads and trails. In our study area, Indiana bat tended to roost 107–479 m on average from roads and trails, and distance to linear openings was not an important predictor of roost habitat selection. Only 4 of 82 roosts were <18 m (typical height of a roost in this study) from a linear opening. It is also important to note that Indiana bats in this study used snags for short periods of time and rarely for >1 year. However, to minimize the risk of killing or disturbing bats when removing hazard trees, we suggest surveillance at suitable trees (sufficient bark and height) prior to clearing.

As predicted by Thogmartin et al. (2013), the Indiana bat population in our study area appears to be in steep decline as a result of the effects of WNS. Capture rates for adult females decreased by 99% after this study was concluded and we no longer capture Indiana

bats at most of our historic netting sites in GSM (O'Keefe et al., unpublished data). If Indiana bats are functionally extirpated from this region, we suggest managers consider Thogmartin et al.'s (2013) more hopeful “acquired immunity” scenario when making decisions about forest management for Indiana bats in the southern Appalachians. Under this scenario, populations of Indiana bats are expected to reach their lowest numbers by 2022 and then slowly begin to recover, so it will be important for managers to consider the roosting habitat requirements of much smaller colonies of Indiana bats.

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Appendix A

See Table A1.

Appendix B

See Table B1.

Table A1

Definitions of 4 decay stages assigned to snags encountered in plots around Indiana bat (*Myotis sodalis*) roosts and random trees, southern Appalachian Mountains, NC and TN, USA, 2008–2012. Decay categories modified from Ormsbee (1996).

	Overall decay status			
	1	2	3	4
Branches	80–100	Few–no branches	Limb stubs to none	None
Bark tightness	80–100	30–80% remaining	>50% height and ≤30% bark, or <50% of height and ≥80% bark	<80% bark
Height	Full–broken top	Broken top	Broken top to <50% height	<50% of height

Table B1

Candidate models representing various hypotheses and variables entered into each model to assess roost habitat selection by Indiana bats (*Myotis sodalis*) in the southern Appalachian Mountains, NC and TN, USA, 2008–2012. Variables are defined in Table 1.

Model	Hypotheses about where bats prefer to roost	Variables in models and expected direction of selection
Large dead trees	In large dead trees	height (+), dbh (+), age_mature (+), age_old (+), dtba (+)
Low plot clutter	In areas with low plot clutter for easier exit	saplings (–), mid_clos (–), dist_nt (–), ltba (–), ltct (–)
Switching opportunities	Near other available trees	dtca (+), dtct (+), dist_snag (–), yelp_iv (+)
Proximity to water	In close proximity to water	dist_stream (–), dist_wbody (–)
Proximity to openings	In close proximity to open areas	age_old (+), saplings (–), ltct (–), dist_linopen (+)
Plot-scale solar exposure	At points in the forest with high solar exposure	height (+), dist_taller (+), roost_canclos (–), plot_canclos (–)
Landscape-scale solar exposure	At points on the landscape with high solar exposure	north_south (–), east_west (+), dist_ridge (–), elevation (–)
Yellow pines	In areas where yellow pines occur	yellow pine (1), north_south (–), east_west (+), yelp_iv (+), elevation (–)
Mountain riparian zones	In riparian zone trees in mountain riparian zones	dist_ridge (–), hem_iv (+), wtpi_iv (+), dist_stream (–), dist_wbody (–)
Fire-adapted stands	In fire adapted forests on the landscape	north_south (–), east_west (+), dist_ridge (–), oak_iv (+), yelp_iv (+), elevation (–)
Midwestern riparian zones	In stands of large hardwoods near streams	dbh (+), age_old (+), hdwd_iv (+), oak_iv (+), dist_stream (–)
High solar pines	In tall pines, high solar, and switching opportunities	yellow pine (+), height (+), roost_canclos (–), north_south (–), east_west (+), dist_ridge (–), dtct (+)
South ridge pines	Near ridge, south facing, pine hardwood forest at low elevation	north_south (–), east_west (+), dist_ridge (–), wtpi_iv (+), yelp_iv (+), elevation (–)
High solar large trees	Large tree, low closure, south facing, with other dead trees	dbh (+), age_old (+), roost_canclos (–), north_south (–), east_west (+), dist_ridge (–), dtct (+)

References

- Arnold, T.W., 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *J. Wildlife Manage.* 74, 1175–1178.
- Barclay, R.M., Kurta, A., 2007. Ecology and behavior of bats roosting in tree cavities and under bark. In: Lacki, M.J., Hayes, J.P., Kurta, A. (Eds.), *Bats in Forests: Conservation and Management*. The Johns Hopkins University Press, Baltimore, Maryland, pp. 17–60.
- Britzke, E.R., Harvey, M.J., Loeb, S.C., 2003. Indiana bat, *Myotis sodalis*, maternity roosts in the southern United States. *Southeast. Nat.* 2, 235–242.
- Broders, H.G., Forbes, G.J., 2004. Interspecific and intersexual variation in roost-site selection of northern long-eared and little brown bats in the Greater Fundy National Park ecosystem. *J. Wildlife Manage.* 68, 602–610.
- Brose, P.H., Waldrop, T.A., 2010. A dendrochronological analysis of a disturbance–succession model for oak–pine forests of the Appalachian Mountains, USA. *Can. J. For. Res.* 40, 1373–1385.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York, NY.
- Callahan, E.V., Drobney, R.D., Clawson, R.L., 1997. Selection of summer roosting sites by Indiana bats (*Myotis sodalis*) in Missouri. *J. Mammal.* 78, 818–825.
- Carter, T., 2006. Indiana bats in the Midwest: the importance of hydric habitats. *J. Wildl. Manage.* 70, 1185–1190.
- Carter, T.C., Carroll, S.K., Hofmann, J.E., Gardner, J.E., Feldhamer, G.A., 2002. Landscape analysis of roosting habitat in Illinois. In: Kurta, A., Kennedy, J. (Eds.), *The Indiana Bat: Biology and Management of an Endangered Species*. Bat Conservation International, Lexington, Kentucky, pp. 160–164.
- Carter, T.C., Feldhamer, G.A., 2005. Roost tree use by maternity colonies of Indiana bats and northern long-eared bats in southern Illinois. *For. Ecol. Manage.* 219, 259–268.
- Clawson, R.L., 2002. Trends in population size and current status. In: Kurta, A., Kennedy, J. (Eds.), *The Indiana Bat: Biology and Management of an Endangered Species*. Bat Conservation International, Lexington, KY, pp. 2–8.
- Cryan, P.M., Bogan, M.A., Yanega, G.M., 2001. Roosting habits of four bat species in the Black Hills of South Dakota. *Acta Chiropterologica* 3, 43–52.
- DuChamp, J.E., Arnett, E.B., Larson, M.A., Swihart, R.K., 2007. Ecological considerations for landscape-level management of bats. In: Lacki, M.J., Hayes, J.P., Kurta, A. (Eds.), *Bats in Forests: Conservation and Management*. The Johns Hopkins University Press, Baltimore, Maryland, pp. 237–261.
- Dyer, J.M., 2006. Revisiting the deciduous forests of eastern North America. *Bioscience* 56, 341–352.
- Gumbert, M.W., O'Keefe, J.M., MacGregor, J.R., 2002. Roost fidelity in Kentucky. In: Kurta, A., Kennedy, J. (Eds.), *The Indiana Bat: Biology and Management of an Endangered Species*. Bat Conservation International, pp. 143–152.
- Hammond, K.R., 2013. *Summer Indiana Bat Ecology in the Southern Appalachians: An Investigation of Thermoregulation Strategies and Landscape Scale Roost Selection*. Indiana State University, p. 87.
- Hammond, K.R., O'Keefe, J.M., Aldrich, S.P., Loeb, S.C., 2016. A presence-only model of suitable roosting habitat for the endangered Indiana Bat in the southern Appalachians. *PLoS ONE* 11, e0154464.
- Harvey, M.J., 2002. Status and ecology in the southern United States. In: Kurta, A., Kennedy, J. (Eds.), *The Indiana Bat: Biology and Management of an Endangered Species*. Bat Conservation International, Lexington, KY, pp. 29–34.
- Humphrey, S.R., Richter, A.R., Cope, J.B., 1977. Summer habitat and ecology of the endangered Indiana bat, *Myotis sodalis*. *J. Mammal.* 58, 334–346.
- Jachowski, D.S., Rota, C.T., Dobony, C.A., Ford, W.M., Edwards, J.W., 2016. Seeing the forest through the trees: considering roost-site selection at multiple spatial scales. *PLoS ONE* 11, e0150011.
- Jenkins, M.A., Klein, R.N., McDaniel, V.L., 2011. Yellow pine regeneration as a function of fire severity and post-burn stand structure in the southern Appalachian Mountains. *For. Ecol. Manage.* 262, 681–691.
- Johnson, J.B., Ford, W.M., Rodrigue, J.L., Edwards, J.W., Johnson, C.M., 2010. Roost Selection by Male Indiana Myotis Following Forest Fires in Central Appalachian Hardwoods Forests. *J. Fish Wildlife Manage.* 1, 111–121.
- Kalcounis-Rueppell, M.C., Psyllakis, J.M., Brigham, R.M., 2005. Tree roost selection by bats: an empirical synthesis using meta-analysis. *Wildl. Soc. Bull.* 33, 1123–1132.
- Kerth, G., König, B., 1999. Fission, fusion, and nonrandom associations in female Bechstein's bats (*Myotis bechsteinii*). *Behaviour* 136, 1187–1202.
- Kitchell, M.E., 2008. *Roost Selection and Landscape Movements of Female Indiana Bats at the Great Swamp National Wildlife Refuge*. New Jersey M.S. Thesis. William Paterson University, Wayne, New Jersey, p. 187.
- Kunz, T.H., Anthony, E.L.P., 1982. Age estimation and post-natal growth in the bat *Myotis lucifugus*. *J. Mammal.* 63, 23–32.
- Kunz, T.H., Lumsden, L.F., 2003. Ecology of cavity and foliage roosting bats. In: Kunz, T.H., Fenton, B. (Eds.), *Bat Ecology*. University of Chicago Press, Chicago, Illinois, pp. 3–89.
- Kurta, A., Murray, S.W., Miller, D.H., 2002. Roost selection and movements across the summer landscape. In: Kurta, A., Kennedy, J. (Eds.), *The Indiana Bat: Biology and Management of an Endangered Species*. Bat Conservation International, Lexington, KY, pp. 118–129.
- Kurta, A., Williams, K.J., Mies, R., 1996. Ecological, behavioural, and thermal observations of a peripheral population of Indiana bats (*Myotis sodalis*). In: Barclay, R.M.R., Brigham, R.M. (Eds.), *Bats and Forests Symposium*. British Columbia Ministry of Forests, pp. 102–117.
- Lacki, M.J., Baker, M.D., Johnson, J.S., 2010. Geographic variation in roost-site selection of long-legged myotis in the Pacific Northwest. *J. Wildlife Manage.* 74, 1218–1228.
- Lacki, M.J., Cox, D.R., Dickinson, M.E., 2009. Meta-analysis of summer roosting characteristics of two species of *Myotis* bats. *Am. Midl. Nat.* 162, 318–326.
- Lafon, C.W., Waldron, J.D., Cairns, D.M., Tchakerian, M.D., Coulson, R.N., Klepzig, K. D., 2007. Modeling the effects of fire on the long-term dynamics and restoration of yellow pine and oak forests in the southern Appalachian Mountains. *Restor. Ecol.* 15, 400–411.
- Lewis, S.E., 1995. Roost fidelity of bats: a review. *J. Mammal.* 76, 481–496.
- Loeb, S.C., O'Keefe, J.M., 2014. Indiana bats, northern long-eared bats, and prescribed fire in the Appalachians: challenges and considerations. *Gen. Tech. Rep. SRS-199*. In: Waldrop, T.A. (Ed.), *Wildland Fire in the Appalachians: Discussions among Managers and Scientists*. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, North Carolina, p. 208.
- MacGregor, J.R., Kiser, J.D., Gumbert, M.W., Reed, T.O., 1999. Autumn roosting habitat of male Indiana bats (*Myotis sodalis*) in a managed forest setting in Kentucky. In: Stringer, J.W., Loftis, D.L. (Eds.), *12th Central Hardwood Forest Conference*. USDA, Forest Service, Southern Research Station, Lexington, KY, pp. 169–170.
- Miller, N.E., Drobney, R.D., Clawson, R.L., Callahan, E.V., 2002. Summer habitat in northern Missouri. In: Kurta, A., Kennedy, J. (Eds.), *The Indiana Bat: Biology and Management of an Endangered Species*. Bat Conservation International, Lexington, Kentucky, pp. 165–171.
- Miller, D.A., Arnett, E.B., Lacki, M.J., 2003. Habitat management for forest-roosting bats of North America: a critical review of habitat studies. *Wildl. Soc. Bull.* 31, 30–44.
- Nowak, J., Asaro, C., Klepzig, K.D., Billings, R., 2008. The southern pine beetle prevention initiative: working for healthier forests. *J. Forest.* 106, 261–267.
- Nuckolls, A.E., Wurzbarger, N., Ford, C.R., Hendrick, R.L., Vose, J.M., Kloeppel, B.D., 2009. Hemlock declines rapidly with hemlock woolly adelgid infestation: impacts on the carbon cycle of southern Appalachian forests. *Ecosystems* 12, 179–190.
- O'Keefe, J.M., Weber, J.A., Bergeson, S.M., Castor, L.K., Kaiser, Z.D.E., Walters, B.L., Whitaker, Jr., J.O., 2012. 2012 monitoring program for the Indiana myotis (*Myotis sodalis*) near the Six Points Interchange in Hendricks and Marion counties, Indiana as required under the Six Points Interchange Habitat Conservation Plan. Report to Indianapolis Airport Authority, Indianapolis, Indiana. 83pp.
- O'Keefe, J.M., Bergeson, S.M., Castor, Linda K., Divoll, T.J., Hoeh, Julia P.S., Walters, B. L., 2016. 2015 monitoring program for the Indiana bat (*Myotis sodalis*) near the Six Points Interchange in Hendricks and Marion counties, Indiana as required under the Six Points Interchange Habitat Conservation Plan. Report to Indianapolis Airport Authority, Indianapolis, Indiana. 87pp.
- Ormsbee, P.C., 1996. Characteristics, use, and distribution of day roosts selected by female *Myotis volans* (long-legged myotis) in forested habitat of the Central Oregon Cascades. In: Barclay, R.M., Brigham, R.M. (Eds.), *Bats and Forest Symposium*. Canada Research Branch, B.C. Ministry of Forestry, Victoria, B.C., pp. 124–131.
- Patriquin, K.J., Leonard, M.L., Broders, H.G., Ford, W.M., Britzke, E.R., Silvis, A., 2016. Weather as a proximate explanation for fission–fusion dynamics in female northern long-eared bats. *Anim. Behav.* 122, 47–57.
- Perry, R.W., Brandebura, S.C., Risch, T.S., 2016. Selection of tree roosts by male Indiana bats during the autumn swarm in the Ozark Highlands, USA. *Wildl. Soc. Bull.* 40, 78–87.
- Perry, R.W., Thill, R.E., 2007. Roost selection by male and female northern long-eared bats in a pine-dominated landscape. *For. Ecol. Manage.* 247, 220–226.
- Pretzlaff, I., Kerth, G., Dausmann, K.H., 2010. Communally breeding bats use physiological and behavioural adjustments to optimise daily energy expenditure. *Naturwissenschaften* 97, 353–363.
- Racey, P., 1988. Reproductive assessment in bats. In: Kunz, T.H. (Ed.), *Ecological and Behavioral Methods for the Study of Bats*. Smithsonian Institution Press, Washington, D.C., pp. 31–45.
- R Core Development Team, 2010. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reichard, J.D., Kunz, T.H., 2009. White-nose syndrome inflicts lasting injuries to the wings of little brown myotis (*Myotis lucifugus*). *Acta Chiropterologica* 11, 457–464.
- Roby, P., Gumbert, M.W., 2013. Spring roosts used by female Indiana bats in the Talladega National Forest, Shoal Creek Ranger District, Cleburne County, Alabama. Unpublished report to U.S. Fish and Wildlife Service, Richmond, Kentucky, 54pp.
- Southern Appalachian Man and the Biosphere (SAMAB), 1996. *The Southern Appalachian assessment terrestrial technical report*. Report 5 of 5. U.S. Department of Agriculture, Forest Service, Southern Region, Atlanta, Georgia. <http://www.samab.org/wp-content/uploads/2011/06/SAMAB_SAA_terrestrial_report.pdf> (accessed 1.12.16).
- Schafale, M.P., 2012. *Guide to the Natural Communities of North Carolina*, 4th Approximation. North Carolina Natural Heritage Program, Department of Environment and Natural Resources, Raleigh, NC.
- Sikes, R.S., Gannon, W.L. Animal Care and Use Committee of the American Society of Mammalogists, 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J. Mammal.* 92, 235–253.

- Silvis, A., Ford, W.M., Britzke, E.R., 2015. Day-roost tree selection by northern long-eared bats—What do non-roost tree comparisons and one year of data really tell us? *Glob. Ecol. Conserv.* 3, 756–763.
- Silvis, A., Perry, R.A., Ford, W.M., 2016. Relationships of three species of bats impacted by white-nose syndrome to forest condition and management General Technical Report SRS-214. USDA Forest Service, Asheville, NC, p. 57.
- Thogmartin, W.E., King, R.A., McKann, P.C., Szymanski, J.A., Pruitt, L., 2012. Population-level impact of white-nose syndrome on the endangered Indiana bat. *J. Mammal.* 93, 1086–1098.
- Thogmartin, W.E., Sanders-Reed, C.A., Szymanski, J.A., McKann, P.C., Pruitt, L., King, R.A., Runge, M.C., Russell, R.E., 2013. White-nose syndrome is likely to extirpate the endangered Indiana bat over large parts of its range. *Biol. Conserv.* 160, 162–172.
- Timpone, J.C., Boyles, J.G., Murray, K.L., Aubrey, D.P., Robbins, L.W., 2010. Overlap in roosting habits of Indiana bats (*Myotis sodalis*) and northern bats (*Myotis septentrionalis*). *Am. Midl. Nat.* 163, 115–123.
- Toth, C.A., Cummings, G., Dennis, T.E., Parsons, S., 2015. Adoption of alternative habitats by a threatened, “obligate” forest-dwelling bat in a fragmented landscape. *J. Mammal.* 96, 927–937.
- U.S. Fish and Wildlife Service (USFWS), 2011. Supporting decontamination documentation for researchers (WNS Decontamination Supplement 2 of 2). Version 01.25.2011.
- Watrous, K.S., Donovan, T.M., Mickey, R.M., Darling, S.R., Hicks, A.C., Von Oettingen, S.L., 2006. Predicting minimum habitat characteristics for the Indiana bat in the Champlain Valley. *J. Wildlife Manage.* 70, 1228–1237.
- Whitaker Jr., J.O., Brack Jr., V., 2002. Distribution and summer ecology in Indiana. In: Kurta, A., Kennedy, J. (Eds.), *The Indiana Bat: Biology and Management of an Endangered Species*. Bat Conservation International, pp. 55–65.
- Whitaker Jr., J.O., Sparks, D.W., Brack Jr., V., 2004. Bats of the Indianapolis International Airport area, 1991–2001. *Proc. Indiana Acad. Sci.* 113, 151–161.