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Tree roosts used by an endangered bat require almost a century to develop

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ABSTRACT

As a forest-dependent species, the endangered Indiana bat (*Myotis sodalis*) is reliant on large-diameter tree roosts (hereafter, "roosts"), which are usually snags. Such large trees develop as a product of time and species-specific growth rates. To better understand the ecology of bat roost habitat, we explore the putative trade-offs between tree age, size, and growth rates on the development of roosts. Specifically, we quantify the age, size, and longevity of roosts of Indiana bats using dendrochronology at three study sites across the species' range in the eastern USA. On average, roosts were alive for 97.8 years (range = 31–283), 7.4 years elapsed after tree death before bats used them as roosts, and snag longevity was 10.8 years. Bats selected roosts based on size and not age. Fast-growing, early-successional species attained desirable roost size more quickly than slow-growing, mid- and late-successional species. Early-successional species, e.g. *Populus deltoides* and *Pinus strobus*, were suitable as roosts at ~72 years versus 130 years for late-successional species. Tree growth rate, a trait related to successional status, was negatively correlated with roost age at use, and longevity prior to falling. Consequently, fast-growing trees fell more quickly. Therefore, species' successional status and growth rate are key factors that determine the timeframe necessary for roost development, and their longevity as snags. A lack of selection by bats for tree age indicates that desirable roost habitat can be developed within decades, by promoting early-successional trees, but speed of development must be weighed against snag longevity.

1. Introduction

Although forests only cover about 31% of global land area, they are habitat to greater species richness of amphibians, birds, mammals, and reptiles than non-forested biomes (Hilton-Taylor et al., 2009, FAO, 2022). Centuries of habitat loss have reduced forested area by about 40% (MEA 2005) and only about 34% of remaining forests can be considered primary, naturally regenerating, and lacking significant impact by humans (FAO, 2022). Thus, conservation of forest-dependent fauna requires the ability to manage altered forest ecosystems, in addition to protecting primary forests. For example, a recent assessment found most forest types in the U.S. (65%) would be considered critically endangered, endangered, or vulnerable based on IUCN ecosystem assessment criteria (DellaSala et al., 2022). Forested habitats are at risk of loss due to continued land conversion and habitat degradation (Comer et al., 2022). Remnant forests in eastern North America are present at a fraction of their historical extent, but they exist in a younger and altered state due to their history of exploitation, and ongoing "mesophication" (Nowacki and Abrams, 2008, Pan et al., 2011). This leaves the forest-dependent taxa of highly modified landscapes in a tenuous conservation situation, especially if they show preferences for unharvested or old-growth forests.

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Despite their long history of exploitation, forests of the eastern United States are habitat for many taxa including endangered species. Bats, for example, represent a uniquely imperiled assemblage that depends on key structural and compositional features of forested ecosystems for foraging and roosting habitat (Kalcounis-Rüppell et al., 2005). Of the ~20 bat species that live in the eastern United States, seven are listed as threatened or endangered under the Endangered Species Act (USFWS, 2026) and five additional bat species are classified as endangered, threatened, or vulnerable on the IUCN Red List (IUCN, 2023). Oftentimes, conservation of endangered species relies on understanding the key characteristics associated with their preferred habitat. Once identified, this information can be used to guide management that is aimed at the creation, enhancement, and maintenance of those traits that provide suitable habitat.

Old-growth forests often have features that are attractive to bats, such as an abundance of large snags and large trees (Fan et al., 2003), structural diversity (Zeigler, 2000, Burrascano et al., 2013), and a high abundance of arthropod prey (Chandler, 1987, 1991, Müller et al., 2012). Indeed, several studies have suggested that managing for bats involves managing for old-growth forest (Thomas, 1988, Jung et al., 1999, Krusic et al., 1996, Crampton and Barclay, 1998). While this is a desirable conservation strategy where old-growth forest exists, such forests can be exceedingly rare — e.g., in the eastern U.S. Therefore, it is important to identify key habitat features that may exist in the younger forests that bats currently use (Donato et al., 2012, Knuff et al., 2020). Once identified, managing for these traits offers another reasonable conservation strategy that can be applied across a wide range of younger or cutover forests to increase suitable habitat.

The federally endangered Indiana bat (*Myotis sodalis,* Miller and Allen, 1928) is forest dependent, using trees as daytime refugia during the non-hibernation period (Whitaker et al., 2002, O'Keefe and Loeb, 2017, Bergeson et al., 2020, Watrous et al., 2006), and foraging in forests for arthropod prey (Kniowski and Gehrt, 2014, Divoll et al., 2022a, Divoll et al., 2022b). Pregnant females migrate from hibernacula to summer roosting areas, which are likely to be in landscapes with at least 45–80% forest cover in a 500-m radius area (Watrous et al., 2006, Cable et al., 2021). Preferred maternity roosts across the Indiana bat range are large-diameter snags (36.5–62 cm) of any species that offer suitable height (18–21 m tall) and high solar exposure at the roost (e.g., 33% canopy closure or emergent in the canopy) (Whitaker et al., 2002, O'Keefe and Loeb, 2017, Watrous et al., 2006). Colony sizes vary, averaging ~25 bats in the heavily forested Southern Appalachian Mountain region (range 1–126) (O'Keefe and Loeb, 2017), to > 100 bats in the more fragmented midwestern U.S. (range 16–384) and northeastern U.S. (range 4–270) (as summarized by Whitaker et al., 2002 and Kurta, 2005, respectively). Reproductive females typically roost in larger, solar-exposed trees to reduce costs of thermoregulation and to support larger colony sizes but will occasionally switch to use "secondary" roosts (Callahan et al., 1997), which are more likely to be smaller-diameter snags, live trees (e.g., shagbark hickory, *Carya ovata*; Watrous et al., 2006), or anthropogenic structures like bat boxes (Bergeson et al., 2020). While secondary roosts are sometimes shaded and thus cooler, driving bats to use torpor more, such roosts may offer more stable microclimates during periods of inclement weather (Humphrey et al., 1977, Bergeson et al., 2021).

Given the importance of roosts as a key habitat characteristic for the Indiana bat, we can focus on the questions of how to develop, promote, and maintain suitable roosting habitat, especially if that information can be applied across the wide range of forest types where this species occurs. Previous studies of roost selection by forest-dwelling bats have recommended the retention of old-growth forests as a way to maintain habitat (Callahan et al., 1997, Crampton and Barclay, 1998, Jung et al., 1999). However, some of the character of old-growth forest can be achieved through the retention of large trees and large snags that can become roosts (Callahan et al., 1997, Jung et al., 1999, O'Keefe and Loeb, 2017, Bergeson et al., 2018, Cable et al., 2021). While it has been suggested that Indiana bat habitat can exist in managed forest conditions, and therefore be maintained through forest management (e.g., uneven-aged silviculture, Gumbert et al., 2002, Bergeson et al., 2018), a crucial detail that is lacking is the timeframe necessary to achieve desirable habitat characteristics. Do managers need to wait centuries for old-growth forest characteristics to develop? Is it possible to use forest management to produce suitable quality roost trees within a shorter interval? Ultimately, the question becomes: how long does it take to create a suitable Indiana bat roost?

With this question in mind, our objectives were to: 1) quantify the age and size of roosts used by the Indiana bat to determine the important factors in roost use, 2) quantify the longevity of roosts, and 3) identify factors that influence roost tree size and longevity. We hypothesized that bats would be limited in their ability to perceive tree age and thus any influence of tree age on bat numbers would be a byproduct of age's influence on tree character (i.e., diameter). Because tree diameter is a product of tree life history strategies (e.g., growth rate), we hypothesized that trees of appropriate diameter would develop over different times spans depending upon growth rate and successional characteristics. Further, growth rate and successional status are related to differences in wood densities and may influence longevity, especially of standing dead trees. Therefore, we predicted that older trees with more dense wood would stand longer as snags than younger, less dense snags. Addressing our objectives will inform conservation strategies by providing information to aid in the identification of trees with Indiana bat roosting potential. This investigation will also help us to understand the habitat potential of trees occurring in forests of varying ages and the timeframe necessary for the creation of tree roosts, a key habitat feature for this forest-dependent endangered species.

2. Methods

2.1. Observation of used roosts

To identify Indiana bat roosts, we used mist nets to capture bats at three locations across the species' range: central Indiana, Great Swamp National Wildlife Refuge in New Jersey, and the Southern Appalachian Mountains, USA (Supplemental Figure 1). Our central Indiana study site was located near Indianapolis, Indiana, in Hendricks County. The forests of this site are highly fragmented and within a suburban and agricultural matrix. Dominant overstory species include a mix of hardwood species, such as cottonwood (*Populus deltoides*), black walnut (*Juglans nigra*), oaks (*Quercus* spp.), maples (*Acer* spp.), and shagbark hickory (Kaiser and O'Keefe, 2015). Forest cover at this site is ca. 18% based on Forest Inventory and Analysis estimates in a 16-km radius buffer around the centroid of roosts at the site (USDA Forest Service, Forest Inventory and Analysis Program, 2023). This site is central to a long-term monitoring study of an Indiana bat maternity colony that inhabits lands adjacent to the East Fork of White Lick Creek. Our New Jersey study site was mainly in Morris County but there were a few roosts in adjacent Somerset County. Though the surrounding areas are suburban, most roosts were within a large tract of forest on Great Swamp National Wildlife Refuge, which is managed by U.S. Fish and Wildlife Service. Dominant overstory species include American beech (*Fagus grandifolia*), oaks, hickories (*Carya* spp.), and red maple (*Acer rubrum*; Kitchell, 2008). Forest cover at this site is ca. 26% in a 16-km buffer (USDA Forest Service, Forest Inventory and Analysis Program, 2023). Our Southern Appalachian study site was located at the border of Tennessee and North Carolina, in Blount and Monroe counties, TN, and Cherokee, Graham, and Swain counties, NC. Forests in the areas used by bats were broadly mixed pine (*Pinus* spp.)-hardwood, though other forest types occurred in riparian areas and at high elevations (O'Keefe and Loeb, 2017). This site has the highest forest cover in this study at ca. 91% in a 16-km buffer (USDA Forest Service, Forest Inventory and Analysis Program, 2023). Table 1 summarizes tree species used by Indiana bats at these three study sites.

We captured bats in central Indiana from 2002 to 2014 (Whitaker

Table 1
Roost species and emergence data for 95 Indiana bat (*Myotis sodalis*) roosts organized by three sites. Tree species' successional status was based on its shade tolerance, response to disturbance, and presence in pioneer or climax communities (Huston and Smith, 1987; sourced from https://www.feis-crs.org/feis/).

	Number of roosts and range (mean) of bat emergence counts by site					
	Indiana		New Jersey		Southern Appalachian	
Species (successional status)	# roosts	# bats (mean)	# roosts	# bats (mean)	# roosts	# bats (mean)
Acer rubrum (early)			7	1–7 (3)	1	32
Carya ovata (late)	23	1–83 (16.7)	10	4–214 (61.4)		
Pinus echinata (early)					13	1–75 (19)
Pinus strobus (early)					11	1–84 (34.7)
Pinus virginiana (early)					5	1–39 (10.4)
Populus deltoides (early)	6	20–228 (136.5)				
Quercus palustris (mid)			6	3–252 (80.5)		
Quercus rubra (mid)	1	32				
Robinia pseudoacacia (early)	2	2–14 (8)	2	19–72 (45.5)		
Tsuga canadensis (late)					2	4–37 (20.5)
Ulmus americana (mid)	1	60	5	21–75 (38.8)		
Total or Range & (Mean)	33	1– 228 (40)	30	1– 252 (47)	32	1– 84 (24)

et al., 2008, Whitaker et al., 2011, O'Keefe et al., 2014), in New Jersey from 2006 to 2009 (Kitchell, 2008), and in the Southern Appalachian Mountains from 2008 to 2012 (O'Keefe and Loeb, 2017). Indiana bats were captured via mist net surveys; we attached radio transmitters (<5% of body mass) to bats' skin with non-toxic glue and used radio telemetry to track bats to roost trees daily, as feasible, for the lifespan of the transmitter (usually 7–14 days). Bat handling occurred under appropriate state and federal permits and followed guidelines from the American Society of Mammalogists (Sikes et al., 2026). University studies occurred under approved animal care and use protocols at Clemson University (O'Keefe), Indiana State University (O'Keefe and Whitaker), and William Paterson University (Risley).

Upon locating a roost, we documented the species, live or dead status of the roost, and measured diameter at breast height (DBH) which is a common variable used in studies of Indiana bat roost preference (e.g., O'Keefe and Loeb, 2017, Bergeson et al., 2018). We performed at least one emergence count on each roost tree within the 15 May-to-15 August maternity period recommended by USFWS (2024). An emergence count consisted of observing the roost from 10 min prior to sunset until no bats were observed exiting the roost for at least 10 min, usually 30 or more minutes after sunset (e.g., Hoeh et al., 2018). Many roosts were observed on multiple nights, and we report the maximum number of bats observed emerging from each roost. Roosts containing only one bat or a tracked bat for only one day were not prioritized for observation and were only repeatedly observed as labor allowed.

2.2. Effects of roost age and diameter on use and bat group size

We extracted increment cores (standing trees) or cross-sections (downed trees) from 95 roost trees (72 snags, 23 live) from our three sites to estimate roost age from tree-ring data. Roost tree-ring samples were collected from Indiana in 2012 (33 roosts), New Jersey in 2014 (30), and the Southern Appalachian Mountains in 2013 (32). These cores and cross-sections were sanded and visually crossdated against local master chronologies to assign calendar years to each tree-ring. Crossdating ensures that the calendar year assigned to a ring is verified based on the matching patterns of growth of surrounding trees (Speer, 2010). Local master chronologies were built by collecting cores from 5 to 10 trees of the same species as the roost from each region or sometimes each roost location. Rings were measured on a Velmex measuring machine to the nearest 0.001 mm and crossdating was verified using the program COFECHA (Holmes, 1983). For each roost, we calculated the mean ring width of all rings present in the sample (Table 2). The mean ring width can be used to infer tree growth rate (Fritts, 1976), which is often related to other life history traits like life span and successional status (Loehle, 1988).

For snag roosts, death date (i.e., "year of death") was assigned as the final year showing growth of the cambium. For all roosts (live and dead), establishment year was assigned as the pith year with the caveat that pith year does not represent the true establishment but the year that the tree reached the height at which the core was taken. Depending on tree species, the true establishment is often 5–15 years prior to our estimate as it took the tree time to reach our sampling height (DesRochers and Gagnon, 1997, Gutsell and Johnson, 2002). To limit this uncertainty, all samples were taken as close to 30 cm above the ground as possible to balance the tradeoff between accurately estimating tree establishment and ease of crossdating. Previous studies have shown that samples taken closer to the root collar more accurately reflect the true age but do not crossdate as well and, thus, make assigning a death date more difficult (DesRochers and Gagnon, 1997). Due to sampling restrictions (only one core sample was allowed for standing trees within Great Smoky Mountains National Park as per permit GRSM-2013-SCI-2292) and the occasional tree with a rotten center, we were not always able to identify a pith year. In these instances where pith was not present on a sample, we estimated the number of rings missing from the sample based on a transparency overlay with concentric rings which were matched to the curvature and size of our sample's inner rings (Applequist, 1958).

We used a Kruskal-Wallis rank-sum test to determine if roost ages varied across the three sites. To determine if snags at all sites were used as roosts at similar time spans after tree death, we used an ANOVA and a post-hoc Tukey test to compare difference in years before use among sites. We used three linear regression models and their associated Akaike Information Criterion (AIC) values to assess which of the three following hypotheses was best supported: 1) maximum emergence of bats from a roost was best predicted by tree DBH (diameter at breast height, cm); 2) maximum emergence of bats from a roost was best predicted by age at use (years); 3) the null hypothesis (a model with no explanatory information). Analyses were conducted in the R statistical language (R core team, 2026). We assumed statistical significance at $\alpha = 0.05$ for all significance tests. Means ±1 SD were reported.

2.3. Snag roost longevity

We were able to confidently crossdate 53 of 72 snags sampled in this study (14 in Indiana, 17 in New Jersey, and 22 in the Southern Appalachian Mountains) and, thus, we know the calendar year of each annual ring on these trees including the year of death. Some species were too variable in growth (e.g., *Ulmus americana*), or certain patches of trees were too complacent in growth (i.e., every ring was similar in width, e.g. *Ulmus americana* and *Pinus strobus* trees, especially in valley bottoms) to accurately crossdate. Trees that could not be crossdated were removed from analyses where date of death was needed for calculation of a variable of interest.

To determine how long roosts stood dead before falling, we collected data on the year a snag roost fell. For 7 roosts, we knew the exact year they fell because we observed the roosts every year from first

observation of use until the fall occurred. In these instances, time dead before falling was calculated as "year of falling" minus the "year of death" observed through crossdating (hereafter, "time dead before falling", see definitions in Table 2). However, the exact year in which a roost fell was not known for 11 snag roosts that were found on the ground upon resurvey after a lapse in annual monitoring. Thus, when a tree was observed fallen but the exact date of the fall was unknown, we approximated the time dead before falling as the year a tree was observed on the ground, "year of survey," minus the "year of death." Because the year of survey was either the exact year the tree fell or later, this estimation method artificially increased the estimated time dead before falling. Because of this inflation, we removed one estimated date outlier from this dataset. We used a Mann Whitney U-test to compare the values for time dead before falling for trees with estimated versus known dates for year of death to test for inflated estimates. This test showed no significant difference.

Because only 18 of the 53 crossdated snag roosts had fallen when we conducted our study, we also calculated the "time observed standing dead" of all crossdated snags that never fell during the study period (n = 35). Time observed standing dead was calculated as "year of survey" minus "year of death" for these roosts. To determine how long snag roosts stand on the landscape, we tallied the numbers of snags standing and those that had fallen in 5-year intervals after tree death. This analysis examined the depreciation of standing roosts and the accumulation of fallen roosts over time.

2.4. Effects of roost tree successional status on longevity

To determine if growth strategies of trees impact the speed with which they become available as potential bat roosts and their longevity (e.g., age at use, time dead before falling, time observed standing dead), we assigned the successional status of each roost species. Tree successional status is a life history characteristic that describes how a tree is likely to germinate and reach canopy status. Tree species that are intolerant of shading by an existing forest canopy are considered early-successional. These trees usually grow quickly early in stand development due to abundant access to light; however, they are relatively short-lived (Loehle, 1988). Tree species that are very tolerant of shading and that almost exclusively germinate and grow under a closed-canopy forest are considered late-successional. These grow slower compared to early-successional species because competition for light and other resources is higher under a closed canopy and these species are relatively long-lived (Loehle, 1988). Mid-successional species exhibit a life history that is intermediate between early- and late-successional species with respect to shade tolerance or canopy accession strategy (Millet et al., 1999). We assigned successional status of the roost trees into three groups based on species' characteristics including shade tolerance, response to disturbance, and presence in pioneer or late-successional communities (Table 1; Huston and Smith, 1987). These traits have been previously assessed for U.S. species in the USDA Fire Effects Information System (https://www.feis-crs.org/feis/). To determine if successional status and average ring width were related, as expected, we used a Kruskal-Wallace and post-hoc Dunn's test. Then, to determine if mean ring width and successional status respectively influenced the age a tree attained before being used by bats, we used a correlation analysis and a Kruskal-Wallace test with an accompanying post-hoc Dunn's test. Mean ring widths were used in linear regression models as predictors of two tree-longevity metrics: time dead before falling and time observed standing dead. Mean ring widths could not be reliably obtained from two fallen roosts and two standing snag roosts due to large portions missing from samples. Thus, for this analysis, there were 16 fallen roosts and 33 standing dead roosts.

Table 2
Terms and factors defined for a study of Indiana bat (*Myotis sodalis*) roost characteristics in relation to use by bats.

Term	
Roost age at use	Number of crossdated tree rings on sample from bark to pith during the first year of use
DBH (cm)	Diameter of a tree measured at breast height (1.3 m above ground)
Mean ring width (cm)	Mean of all crossdated ring widths of a roost from bark to pith
Standing dead	A tree that has died but a portion of the stem remains upright as it has not yet fallen
Successional status	Categorization of tree based on shade tolerance of seedlings
Time dead before falling (yrs)	For trees that fell in this study, number of years before fall
Time observed standing dead (yrs)	For trees that did not fall in this study, number of years observed standing
Years before use (yrs)	Time a tree stood dead before use by Indiana bats was observed

3. Results

We sampled 95 Indiana bat roosts from 11 tree species across three regional sites (Table 1). Maximum nightly emergence at these roosts varied from 1 to 252 bats ($\bar{x} = 36.5 \pm 52.0$). Most roost trees were snags (n = 72) but 23 live *Carya ovata* roosts were observed (19 in Indiana, 4 in New Jersey). No live trees were used by bats in the Southern Appalachian Mountains. DBH of roost trees varied from 14.2 to 137.5 cm ($\bar{x} = 44.9 \pm 21.3$).

Ages of roosts ranged from 31 to 283 years ($\bar{x} = 97.8 \pm 49.1$). Roost ages at time of use did not vary significantly among the three sites ($\chi^2 = 2.4$, df = 2, p = 0.30, Fig. 1A). Nine roosts were < 50 years old and every site had at least one young roost tree. Young roost tree species were *Acer rubrum, Pinus strobus, Pinus virginiana, Robinia pseudoacacia,* and *Ulmus*

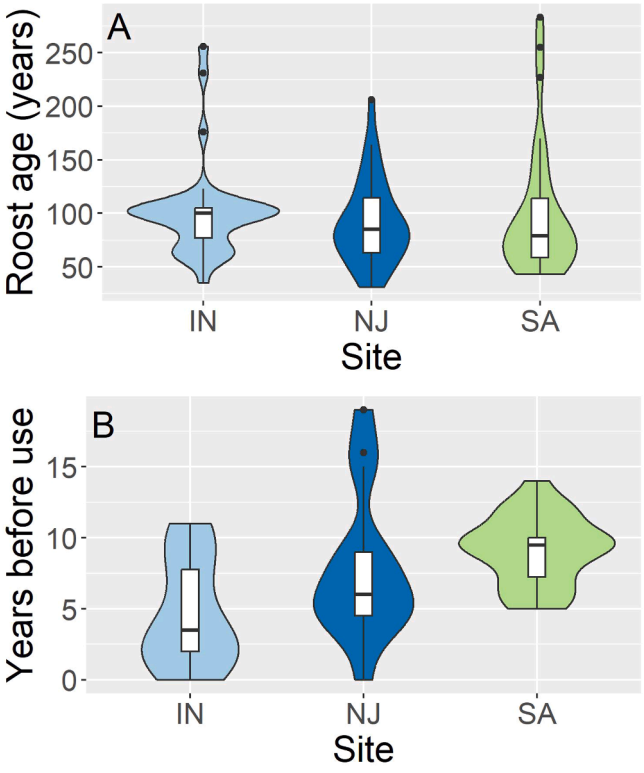

Fig. 1. Violin plots showing A) age at use of roost trees (n = 95) and B) years before use after the death of snag roosts (n = 53) for three different sites across the Indiana bat (*Myotis sodalis*) range (IN = central Indiana, NJ = New Jersey, SA = southern Appalachian Mountains). Violin plots are a way of visualizing the frequency of data along the y-axis. Violins are colored by site and colors are maintained for all relevant plots below.

americana. The youngest individual species was *Ulmus americana* ($\bar{x}$ = 52.5 years, n = 6 at 2 sites). Eleven roosts were older than 150 years, represented by *Carya ovata* in Indiana and New Jersey and *Pinus echinata* and *Tsuga canadensis* in the Southern Appalachian Mountains (Supplemental Figure 2). The oldest species were *Tsuga canadensis* ($\bar{x}$ = 269 years, n = 2 at 1 site) and *Carya ovata* ($\bar{x}$ = 121 years, n = 33 at 2 sites); most of the latter were living while used by bats.

Across the three study sites, 7.4 ± 4.2 years passed after tree death before we observed use by Indiana bats (Fig. 1B). Site was a significant predictor of years before use of snags (F = 5.5, p < 0.01, df = 2, 47). A post-hoc pairwise comparison (Tukey test) showed that trees were used earlier in Indiana ($\bar{x}$ = 4.6 years before use) versus the Southern Appalachians ($\bar{x}$ = 9.1 years before use).

3.1. Effects of roost tree age and diameter on use and bat group size

Roost age was not a good predictor of the number of bats using the roost and the hypothesized age model was not plausible (Age model: Δ AIC = 22.3, Null model: Δ AIC = 20.8, Supplemental Table 1); rather, we observed relatively equal counts of bats in roost of all ages (Fig. 2A). Tree size (DBH) was the top model (Δ AIC = 0, R^2 = 0.21) and a positive predictor of number of bats (Fig. 2B).

3.2. Snag roost longevity

For 18 roosts that we observed after they fell, including trees where the fall year was known and those that were observed down but fall year was unknown, trees stood dead for an average of 10.8 ± 4.2 years. When we considered all 72 snag roosts, only 19% had fallen within 10 years post death. Of the 18 roosts observed 15 years post death, 77.8% had fallen (Fig. 3).

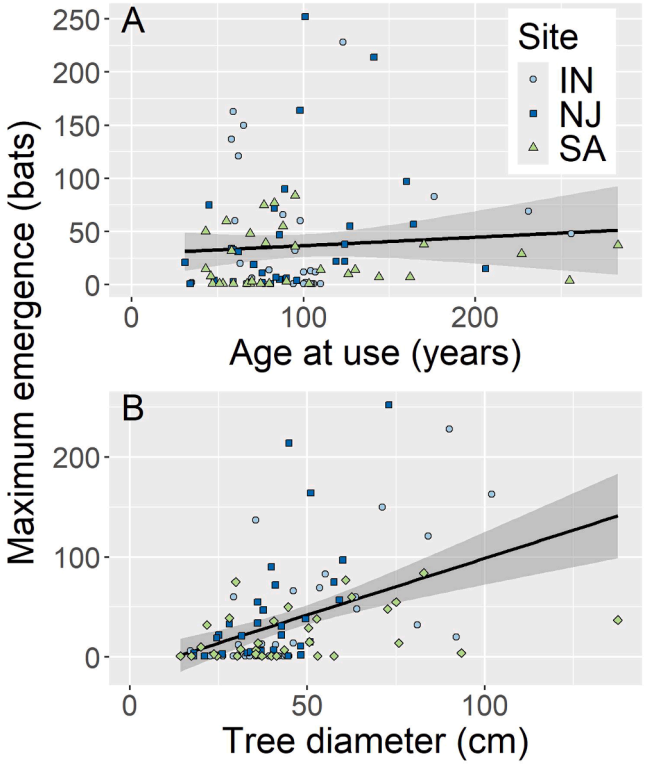

Fig. 2. Linear regression plots predicting maximum emergence counts of Indiana bats (*Myotis sodalis*) from trees for three different sites across the Indiana bat range (IN = central Indiana, NJ = New Jersey, SA = southern Appalachian Mountains) based on either A) age at use of a roost tree (n = 95) or B) diameter at breast height (DBH) (n = 95). Gray-shaded bands represent a 95% confidence interval of the linear models with data from all sites pooled.

3.3. Effects of roost tree successional status on longevity

Species' successional status was a strong predictor of roost age at use (Fig. 4A). Roost age at use differed significantly across the three successional categories (Dunn tests; early – mid, Z = -0.98, p < 0.01; early – late, Z = 5.4, p < 0.01; late – mid, Z = 4.7, p < 0.01). Early-successional species were the youngest group of roost trees (72 ± 22 years old when used by bats). Mid-successional species were intermediate in age (85 ± 41 years old when used) and late-successional species were the oldest (130 ± 54 years old when used). Mean ring width was negatively correlated with roost age at use (df = 81, r = -0.41, p < 0.001; Fig. 4B) and differed significantly among the three successional groups (Dunn tests; early – mid, Z = 5.11, p < 0.01; early – late, Z = 3.3, p < 0.01; late – mid, Z = -1.7, p < 0.01). Early-successional trees had larger mean ring widths (3.5 mm) than mid-successional trees (2.0 mm), which in turn were larger than late-successional species (1.5 mm; Fig. 4C).

Mean ring width was negatively correlated with snag roost longevity. Trees with larger rings (i.e., > 2.5 mm) stood dead for less time than those with smaller rings (trees that fell during the study: df = 14, r = -0.74, p < 0.01; Fig. 5A; trees that did not fall during the study: df = 31, r = -0.39, p = 0.02, Fig. 5B).

4. Discussion

We aimed to address whether tree age was a strong predictor of group sizes for the federally endangered Indiana bat. Maximum emergence counts were best predicted by tree diameter and not by roost age. Successional status of roosts and mean ring width, a related life history attribute, were significantly related to tree age at death or when used as a roost. Furthermore, mean ring width was significantly related to the length of time that roosts stood dead on the landscape. These results, taken together, show that bat group sizes are not influenced by roost age but by characteristics that are associated with roost tree size. Among the roost tree species we observed in this study, we expected each successional grouping to reach a sufficient roost size at different rates. Though early-successional trees can grow to a desirable size quickly, slow-growing, late-successional roosts lasted longer on the landscape, a highly desirable trait in areas where roosts are limited. Thus, to promote bat roosting habitat, forest managers could employ silvicultural strategies that promote the unique properties of fast-growing and slow-

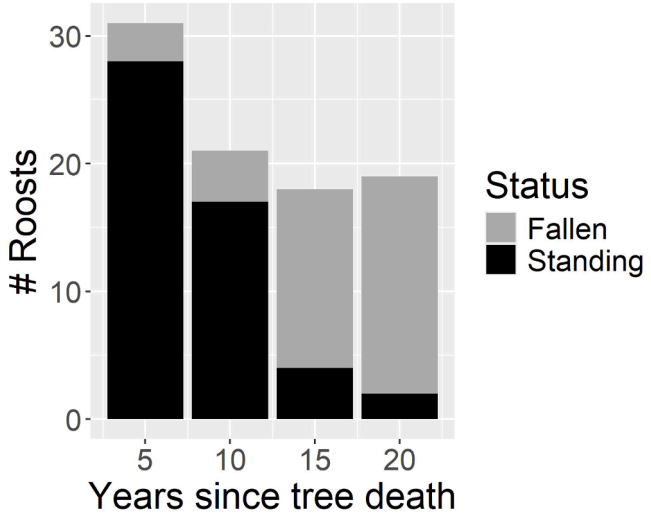

Fig. 3. Number of Indiana bat tree roosts observed fallen or that remained standing in 5-year intervals after tree death for three different sites across the Indiana bat (*Myotis sodalis*) range.

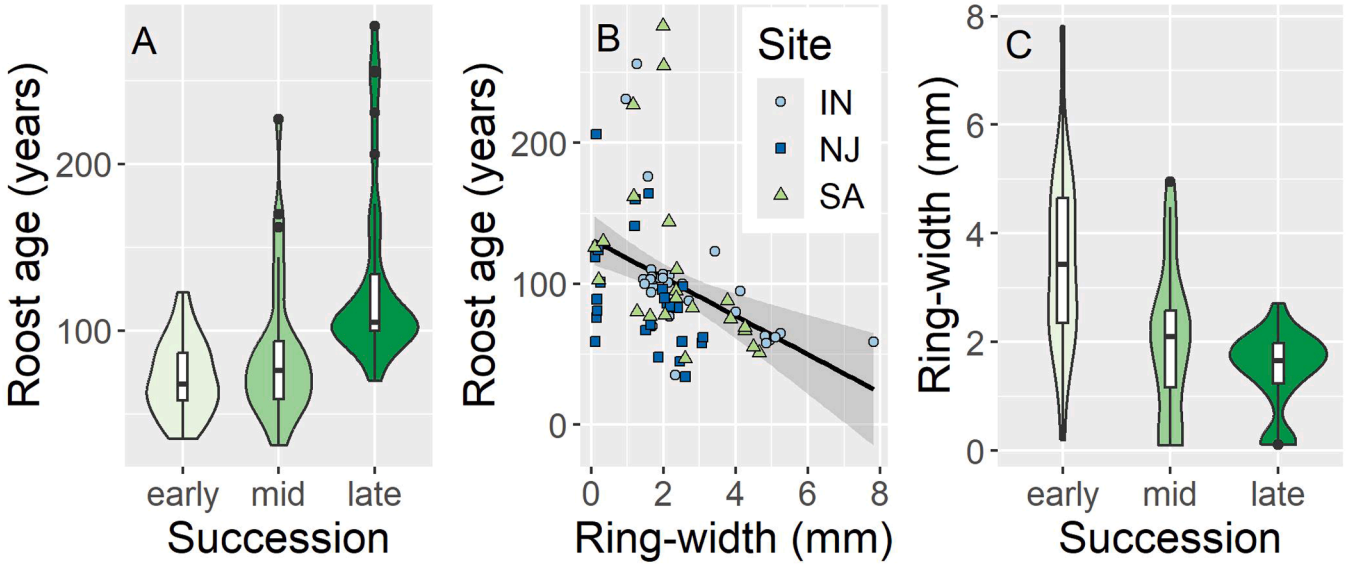

Fig. 4. Roost tree age when used by Indiana bats (*Myotis sodalis*) was influenced by A) successional status (n = 95 roosts) and B) growth rate (i.e. ring width, n = 82). Black line in panel B shows the linear regression of growth rate and age at use pooled for three different sites across the Indiana bat range (IN = central Indiana, NJ = New Jersey, SA = southern Appalachian Mountains). Gray-shaded ribbon is the 95% confidence interval for the model. C) Violin plot of successional status and growth rate of roost trees (n = 82), where larger rings indicate faster growth.

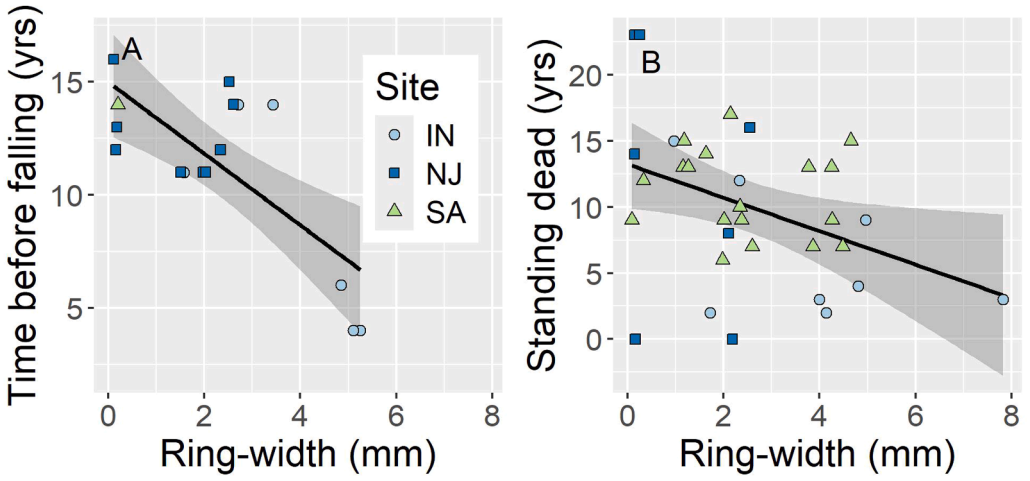

Fig. 5. Ring width (i.e., growth rate) as a predictor of time Indiana bat (*Myotis sodalis*) roost trees stood dead before falling (A; for 16 roosts that fell within the survey period) and time standing dead (B; for 33 roosts that never fell during the survey period). Gray-shaded ribbons are 95% confidence intervals of the line of best fit. Data are for three different sites across the Indiana bat range (IN = central Indiana, NJ = New Jersey, SA = southern Appalachian Mountains).

growing tree species, but ideally a mixture of both when possible.

It is not surprising that larger groups of Indiana bats chose roost trees based on their size rather than their age. Tree characteristics like large diameter, and associated traits like thick bark, are apparent to bats, whereas tree age may only be inferred from tree character. Many studies have shown that bats tend to select large-diameter trees as roosts (Kalcounis-Rüppell et al., 2005). For example, in southern Michigan, Indiana bat roosts averaged 42 cm in diameter, whereas similar trees within 17 m of the roost were only 27 cm (Kurta et al., 2002). In this same study, the most-used roosts (maximum emergence count of $\geq$ 10 bats) were consistently larger in diameter and less-used roosts (maximum emergence count of $<$ 10 bats) were more variable in diameter (Kurta et al., 2002). Just because a tree is large, however, does not necessarily mean that the tree is old (Odom and Ford, 2021). Species-specific, age-diameter relationships tend not to hold across sites when factors such as proximity to edge, light availability, and other environmental factors differ (Odom and Ford, 2021). Thus, managers may consider tree diameter, rather than focusing on tree or stand age when determining habitat suitability for the Indiana bat.

Successional status determined the range of ages that a given tree was likely to reach, with late-successional species growing older before dying compared to early-successional species. We have long known that fast growing, early-successional species can reach large diameters more quickly than slower growing, late-successional species (Bazzaz, 1979). However, slow-growing trees may live longer than fast-growing trees (Black et al., 2008), which allows them to eventually reach sufficient diameter to become a preferred roost. Promoting rapid growth is a desirable strategy for managers interested in providing habitat for Indiana bats. Early-successional roost trees of sufficient diameter could develop within decades of planting when thinning is used to release some trees from competition. In contrast, slower-growing, late-successional species needed ~130 years to become suitable roost trees. Regenerating late-successional species may be challenging; for example, *Carya ovata* can remain suppressed as seedlings in excess of 40 years

(Lefland et al., 2018). However, the developmental timespan of a late-successional tree could be sped up to just under a century if thinning or gap creation is used to reduce competition and increase solar radiation after seedlings have established. These observations have direct implications for mitigation projects aimed at supporting tree-roosting bats. In forest-limited areas, early-successional trees may provide a bridge to creating appropriate habitat sooner while later-successional trees become established and grow to a desirable size.

We did not assign causes of death for most roosts in this study; however, by examining the list of tree species that died and housed bats at a young age, we see evidence of various pathogens and disturbances. In the Southern Appalachian Mountains, most of the young pines died in the early 2000s coincident with a southern pine beetle (*Dendroctonus frontalis* Zimmerman) outbreak and *Adelges tsugae* (Annand) attacked over-mature eastern hemlocks (Jenkins, 2007). Elms in Indiana and New Jersey likely suffered increased stress and mortality due to Dutch elm disease (*Ophiostoma ulmi* (Buisman) Nannf.) (Hubbes, 1999). No sign of disease was observed for the maple trees in our study, but many were dead in groups in New Jersey, which may be a sign of prolonged flooding at the Great Swamp National Wildlife Refuge. In Indiana, multiple cottonwood roosts between 50 and 70 years in age had been girdled by beaver (*Castor canadensis* Kuhl). Regardless, the various mortality agents observed in our study suggest that bats are relatively indifferent to what killed the tree when choosing a snag roost and are opportunistically using the snags present around them. However, this does make the case for managing for stand heterogeneity. Disturbances like fungal disease or insect outbreaks often act at the species level, and fire, wind, and climate often act at the stand level. Heterogeneity of tree species and age classes in stands and forests reduces the risk of losing all quality roost trees in a single disturbance event. That said, trees are facing multiple stressors, and tree mortality is accelerating as these stressors increase and interact (Dietze and Moorcroft, 2011, McDowell et al., 2020).

Once dead, roosts in Southern Appalachian forests were dead longer before use than those in Indiana. We interpret this to be due to differences in tree species decay rates and relative abundance of snags. In the Southern Appalachian Mountains, most roosts were pines and pine snags were abundant (O'Keefe and Loeb, 2017), meaning there was high availability relative to the bats' needs. Pines are slightly more resistant to decay than many of the hardwood species we encountered in Indiana (Forest Products Laboratory, 1967), though decay in this sense is a measure of wood decay and not bark retention. Studies of decay class that incorporate bark retention do not show significant differences in decay rates between hardwoods and softwoods of most North American species (Harmon et al., 2008). O'Keefe and Loeb (2017) discussed how greater snag abundance in the Southern Appalachian Mountains resulted in lower roost fidelity and smaller colony sizes. Likewise, Kitchell (2008) suggested that snag abundance at Great Swamp National Wildlife Refuge may have been the reason for observed high switching rates. Greater roost abundance allows bats to choose the most suitable roost from among a larger pool, and one byproduct may be that bats do not use roosts as soon after death in this circumstance.

Indiana bats are likely already choosing roosts that will persist longer on the landscape compared to an average tree. We determined that snags in this study stood on the landscape for an average of 10.8 years prior to falling and only ca. 22% stood dead for at least 15 years. Russell and Weiskittel (2012) observed that *Picea* spp., *Abies* spp., *Acer* spp. and *Fagus* spp. snags in the Acadian Forest in Maine, USA had a 20% chance of standing dead for $>$ 10 years, which was slightly shorter than roosts in this study. Quick decay of roosts may have prevented us from including some roosts in this study, thus biasing our results toward greater longevity (see also Hoppenworth, 2025). Previous studies have also shown that tree diameter, a variable known to be correlated with bat group size, is positively correlated with snag longevity (Russell and Weiskittel, 2012, Onodera and Tokuda, 2015, Fassnacht and Steele, 2016, Oberle et al., 2018). Tree durability, a measure of resistance to wood decay, was also found to influence snag longevity; species with dense wood tend to decay more slowly (Fassnacht and Steele, 2016, Oberle et al., 2018). While we do not have data on decay rates across all species in our study, our results were consistent with previous work in that the trees standing the longest in this study were slow-growing, late-successional species, which would have the densest wood due to their lower average ring width and relative abundance of dense latewood (Vargas-Hernandez, Adams, 1992). We found that some roosts which had been dead for $>$ 10 years were still in use by Indiana bats and, thus, retained sufficient roosting habitat. Other factors may have also contributed to superior decay resistance, though these vary by species (Scheffer and Morrel 1998).

Roosts in this study were found by radiotracking bats and use was typically documented only when a radio tagged bat was present, so we may have an incomplete picture of roost tree use. Furthermore, Indiana bats show dynamic fission-fusion behavior when selecting daytime roosts (Kurta et al., 2002), meaning that use of a single roost is inconsistent and that maternity colonies may view a group of roosts as a unit (Callahan et al., 1997). We acknowledge that we analyzed each tree as an individual, that these roosts are clumped in areas where we have collected Indiana bat roost data (Supplemental Table 2), and that roosts were used for different timespans across our study areas. Certain roosts were used for multiple years in Indiana and New Jersey (Kitchell, 2008, Whitaker et al., 2008), whereas in the Southern Appalachian Mountains most roosts were used within only one year (O'Keefe and Loeb, 2017). Despite this, we showed that there are predictable characteristics of trees associated with large groups that span a large regional gradient.

4.1. Management implications

Multiple studies have shown that Indiana bat roost trees are ephemeral (Britzke et al., 2003, O'Keefe and Loeb, 2017), and this study is no exception. If a snag must decay for ~7 years prior to becoming a roost, and stands dead for 10–15 years, then a new roost must be created every ~3–4 years to maintain a constant amount of habitat. Without the stable recruitment of new roost trees, the number of suitable roosts would decline. Therefore, forest management practices that aim to create a continuous supply of roosts are desirable. The fastest path to *creating* roost trees is through short-term actions taken now (e.g., thinning or snag creation). For example, the use of judicious thinning to encourage growth of large-diameter trees already on the landscape (Dey et al., 2012) may be effective for promoting Indiana bat roosting habitat. Two methods for creating snags suitable for bat roosts are herbicide application (frilling) and double chainsaw cuts to the trunk; however, these approaches produce desirable roosting characteristics for only 1–3 years after treatment (Schroder and Ward, 2022). In Missouri, Timpone et al. (2010) found Indiana bats roosting in girdled trees in managed stands 1–2 years after treatment. Any chosen short-term actions must be guided by longer-term strategies for *maintaining* desirable, large diameter trees that can become roosts in the future.

While preservation of old-growth character trees is an important element of maintaining roosting habitat, previous work shows that Indiana bats will use managed forest habitat, even roosting in snags within or near even-aged silvicultural systems such as clearcuts and shelterwood cuts (Timpone et al., 2010, Bergeson et al., 2018). While even-aged approaches are desirable for regenerating early-successional species that may eventually become roosts, leaving reserve trees during harvests would maintain potential roost habitat in the short-term. Alternatively, the use of uneven-aged silvicultural systems (e.g., single-tree selection, group selection) would ensure that trees of sufficient size are always present within the stand. However, careful control of stocking is required within these systems if the establishment of early-successional, shade-intolerant species is desired (Powell, 2018, Kenefic et al., 2021). Ensuring Indiana bat habitat in perpetuity through forest management will require careful consideration of the diversity of tree sizes and species on landscape, and the establishment of approaches to augment, improve, and maintain suitable roost trees over the

long-term.

Finally, in areas where Indiana bat habitat is lacking, promoting early-successional trees would yield habitat in the shortest amount of time. Within the range of Indiana bats, there are early-successional trees that are fairly rot-resistant (e.g., *Robinia pseudoacacia* and *Pinus* spp.) that may stand as snags for a decade or more (Scheffer and Morell, 1998). However, which species of trees to promote as roosts should be given thoughtful consideration from among the *locally* available species that Indiana bats use. Species' successional status, on the other hand, lends itself to a wider-ranging interpretation because species from all successional statuses exist and are used across the range of the Indiana bat. By promoting early-successional tree species, roosts of suitable diameter can be developed in a relatively short timeframe. However, it is imperative that managers recognize that late-successional species may remain standing dead for three times as long as early-successional tree species. A prudent habitat management approach would recognize the importance of maintaining a combination of fast-growing, early-successional trees, and slow-growing, but more durable, mid- and late-successional trees.

5. Conclusion

Habitat loss, fragmentation, and degradation pose serious challenges for the conservation and management of forest-dependent species like the endangered Indiana bat. Large roost trees, which are almost always snags, are a key habitat component on which the Indiana bat relies. By disentangling the relationships between tree age, size, and growth rate on roost tree development, we improve our understanding of this key limiting feature of Indiana bat habitat. The recognition that group sizes increased with roost size but not roost age, presents opportunities for habitat development in shorter time frames. Given the extensive length of time necessary for Indiana bat roost trees to develop naturally, our results suggest that conservation planning and management should balance the relative amount of early-successional and late-successional species in the planning area over the long-term. It is likely that such an approach to conservation planning will also benefit other forest-dependent species of conservation concern imperiled by habitat loss and other threats.

CRediT authorship contribution statement

Joseph L. Pettit: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **R. Justin DeRose:** Writing – review & editing, Writing – original draft. **James H. Speer:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Marilyn Kitchell:** Writing – review & editing, Writing – original draft, Resources. **Dale Sparks:** Writing – review & editing, Writing – original draft. **Susan C. Loeb:** Writing – review & editing, Writing – original draft. **Joy M. O'Keefe:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Formal analysis, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123942.

Data availability

Data will be made available on request.

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