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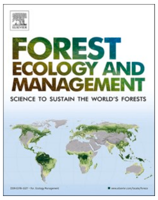

Seasonal differences in day-roost selection by Northern long-eared bats (*Myotis septentrionalis*) in Louisiana and a meta-analytical comparison across North America

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ABSTRACT

Resting-site selection involves some of the most important decisions made by organisms. For forest-dwelling bats, where to roost influences not only resting but also many other activities that affect fitness such as raising young, thermoregulation, communication, and evasion of predators. Across much of North America, many bats roost in trees during summer and hibernate in caves during winter and as such, most of the focus on roosting ecology and forest management has been during summer. Along much of the Atlantic and Gulf coastal plains in the southern portion of North America, winters are relatively warm, few caves exist, and many bat species are active. Herein, we described the tree-roosting ecology of Northern long-eared bats (*Myotis septentrionalis*) in Louisiana in both summer and winter, examined roost selection, compared selection seasonally, and compared various aspects of roosting ecology in Louisiana to other areas across North America. We found that in Louisiana *M. septentrionalis* roosted primarily in pine trees and found no significant differences in roosting characteristics between sexes. Year-round, bats preferred roosts in trees in more advanced stages of decay than available trees. In summer, bats selected for plot level characteristics such as higher density of trees that were large and in more advanced stages of decay. In contrast, in winter, bats selected for tree characteristics such as those with taller, greater diameter and with more exfoliating bark. Comparisons with 21 other studies across North America indicated variation in selected roost characteristics among regions. These results highlight variability in roost selection through space and time and suggest that management strategies that are tailored to specific sites may be most effective for enhancing roosting opportunities of *M. septentrionalis* and ultimately the conservation of this species.

1. Introduction

Roosts, or other day-time resting sites, are key components of the ecology of forest-dwelling organisms such as bats (Kunz, 1982). Day-roosts in particular have many important functions and many bat species prefer to roost in certain forest patches or in trees/structures with different characteristics than others available across the landscape (Kunz and Lumsden, 2003). Indeed, roost selection plays an important role in ecology and evolution of bats (Kunz, 1982, Russo and Ancillotto, 2015) because roosts provide protection from natural elements and facilitate mating, rearing of young, social interactions, hibernation, digestion of food, and provide microclimates necessary for energy conservation (i.e. torpor, Kunz, 1982) to name only a few. Bats use a variety of roosts in both manmade and natural structures depending on their seasonal and reproductive condition and bats may select roosts with specific characteristics to fulfill their seasonal requirements.

Many temperate cave bats overwinter in underground structures, particularly caves, that provide consistent cool temperatures and relative humidity regimes that are conducive to hibernation (Davis, 1970). Unfortunately, such conditions are also conducive to the growth of the invasive pathogen *Pseudogymnoascus destructans* (Johnson et al., 2014) that causes the disease White-Nose Syndrome (WNS). White-Nose Syndrome has decimated populations of tricolored bats (*Perimyotis subflavus*), little brown bats (*Myotis lucifugus*), Indiana bats (*M. sodalis*), and northern long-eared bats (*M. septentrionalis*) over much of eastern Canada and the United States over the last decade (Cheng et al., 2021) and

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recently the US Fish and Wildlife Service has proposed listing of *P. subflavus* as endangered (US Fish and Wildlife Service, 2022). Fortunately, environmental conditions vary across the geographic distributions of these species and relatively warmer conditions in southern portions of their ranges may facilitate sufficient winter activity by these bats that could mitigate effects of WNS. Although some of these bat species overwinter in the Gulf Coastal Plain of the southeastern United States, caves are absent throughout much of this region (Sevenair and Williamson, 1983). In winter, roosts in sites other than caves and abandoned mines may not provide microclimates that are conducive to infection by *P. destructans* and these roosts may not facilitate outbreaks of WNS. Winter roosts of bats across the Gulf Coastal Plain are poorly known yet information on winter roosting behavior in this region would inform predictions of potential WNS effects on bats in this area.

Myotis septentrionalis was historically common in the eastern United States and typically hibernates in caves. Populations of *M. septentrionalis* have experienced dramatic decreases in some areas. For example, across 42 sites in New York, Pennsylvania, Vermont, Virginia, and West Virginia, Turner et al. (2011) reported a 98 percent reduction in the number of *M. septentrionalis* in caves due to effects of WNS and Cheng et al. (2021) found a range-wide decline of 90%. While the species is considered a northern species, *Myotis septentrionalis* was recently discovered in Louisiana (Crnkovic, 2003, Grimshaw et al., 2021) and in coastal North Carolina (Jordan, 2020). *Myotis septentrionalis* will be listed as federally endangered by the US Fish and Wildlife Service under the Endangered Species Act (U. S. Department of the Interior, 2022). Currently, *M. septentrionalis* is known from 4 parishes in Louisiana and has been captured in both summer and winter (Stevens et al., 2017). No caves conducive to hibernation by bats occur in Louisiana (Sevenair and Williamson, 1983), suggesting that this species is limited to roosting in trees or manmade structures in both summer and winter and this southern population may not hibernate through the winter.

In summer, *Myotis septentrionalis* commonly roosts in forests and depends on forest features for both foraging and roosting activities (Broders et al., 2006, Carter and Feldhamer, 2005). This species tends to select foraging areas that are close to roosting sites thereby reducing commuting flight costs (Grindal, 1999) and they roost beneath exfoliating bark of dead trees or hollowed-out cavities within trees (Jung et al., 2004). *Myotis septentrionalis* may prefer deciduous hardwoods over conifers in many places (Sasse and Perkins, 1996, Lacki and Schwierjohann, 2001), but in a more southern population (central Arkansas) pine snags are preferred (Perry and Thill, 2007). Maternity colonies may be located near the tops of larger diameter cavity trees in early stages of decay and surrounded by decaying trees in upper crown (size) classes (Johnson et al., 2009). Male and female northern long-eared bats may select different roost-tree characteristics (Perry and Thill, 2007). Moreover, there appears to be a wide variety of species of trees that are preferred, including oaks (Carter and Feldhamer, 2005, Timpone et al., 2010), maples (Broders and Forbes, 2004, Foster and Kurta, 1999), sassafras (Silvis et al., 2015), black locust (Menzel et al., 2002, Ford et al., 2006), and pine (Perry and Thill, 2007, Alston et al., 2019) and differences among roost tree species appears to vary with geography. In a *meta*-analysis of seven studies involving 230 different roosts from 7 different states, Lacki et al. (2009) found that roost-tree diameter averaged 30 ± 5.4 cm se, average roost height above the ground was 6.95 ± 1.0 m se, and average density of snags was 37.8 ± 3.6 se snags/hectare.

Most observations of *M. septentrionalis* roosting in forest have come from studies that focus on more central populations and that are conducted during summer. Nothing is known of the roosting ecology of *M. septentrionalis* in Louisiana and little is known regarding tree-roost characteristics in winter (Jordan, 2020) or if they are different than in summer. Herein, we address 3 issues regarding roost selection by *M. septentrionalis*: 1) does *M. septentrionalis* nonrandomly select certain tree, plot, or landscape characteristics over others when roosting in Louisiana, 2) does this species exhibit differences between summer and winter in its roost preferences, and 3) are roosting preferences different in Louisiana compared to other places across its geographic range?

2. Material and methods

2.1. Study area

Research was conducted in the Kisatchie National Forest in west-central and north-western Louisiana. The Kisatchie National Forest encompassed approximately 414,665 ha, of which 244,337 ha was national forest land and the remainder was private holdings. The forest was comprised of 5 ranger districts: Caney, Calcasieu, Catahoula, Kisatchie, and Winn (Fig. 1; United States Department of Agriculture, 1999). Elevation ranged from approximately 60 to 130 m above sea level and mean annual precipitation is 1500 mm. Within the Kisatchie there were five broad plant or vegetation communities: longleaf pine *(Pinus palustris),* shortleaf pine (*Pinus echinata*), oak-hickory (*Quercus* spp.-*Carya* spp.), mixed hardwood-loblolly pine (*Pinus taeda*), and riparian (United States Department of Agriculture, 1999). Mean temperatures in January and July were 10° and 28 °C in the Catahoula district and 9° and 28 °C in the Calcasieu District, respectively. Average rainfall was 1433 mm in the Catahoula district and 1345 mm in the Calcasieu district (Haywood and Harris, 1999).

2.2. Bat capture and radiotelemetry

We surveyed bats in the Winn and Catahoula ranger districts across two summers and winters (2016–2018). During the summer (April through August) and winter (December through March) seasons, we set 4–16, 12-m mist nets (Avinet Research Supplies, Portland, Maine) at netting sites with a varied combination of single and double high nets totaling 5671 net hours (1695 net nights). Netting sites were set up primarily over ephemeral streams where a bridge was located or over permanent or ephemeral ponds. We followed the guidelines of the American Society of Mammalogists for capture, handling, and care of mammals (Sikes et al., 2016). All animal care and handling were performed following the Texas Tech Institutional Animal Care and Use Protocol Number 15062–09. Details on netting results and seasonality of the bat community can be found in Stevens et al. (2020).

Captured *M. septentrionalis* were fitted with Holohil (Carp, Ontario CA) radio transmitters. In summer, we used LB-2X transmitters with a mass of 0.33 g and had a battery life of 21 days. During winter, we used LB-2XT transmitters with mass of either 0.27 or 0.32 g and had a battery life of 7–10 days. Transmitters were bonded to the mid-scapular region with Skin Bond or Super Glue (Super Glue Corporation) after removing a small portion of hair from the bat. The following morning, we radio tracked each bat to its day roost and continued to track the bat until the battery life of the transmitter ended or until we could no longer hear a signal.

2.3. Tree and plot characteristics

We identified confirmed roost trees to species, recorded their geographic location, and measured 5 tree, 10 plot, and 4 landscape characteristics (Table 1). Height of tree was measured using a clinometer (Suunto PM5/360PC) and its diameter at breast height (dbh) was measured with a diameter tape (Forestry Suppliers model 345D). We also visually estimated percent remaining bark and decay class (stage 1 = live, stage 2 = declining, stage 3 = dead, stage 4 = loose bark, stage 5 = clean, stage 6 = broken, stage 7 = decomposed, stage 8 = down material, and stage 9 = stump; Maser et al., 1979). Plot characteristics were measured in an 18-m radius (~0.1 ha) plot centered on the roost tree used by *M. septentrionalis*. We measured percent canopy closure in the center of the plot with a spherical densiometer. We counted the number of standing dead and alive small (4.5 – 15 cm DBH) and large stems (>4.5 cm DBH) that were ≥ 1 m in height in the plot.

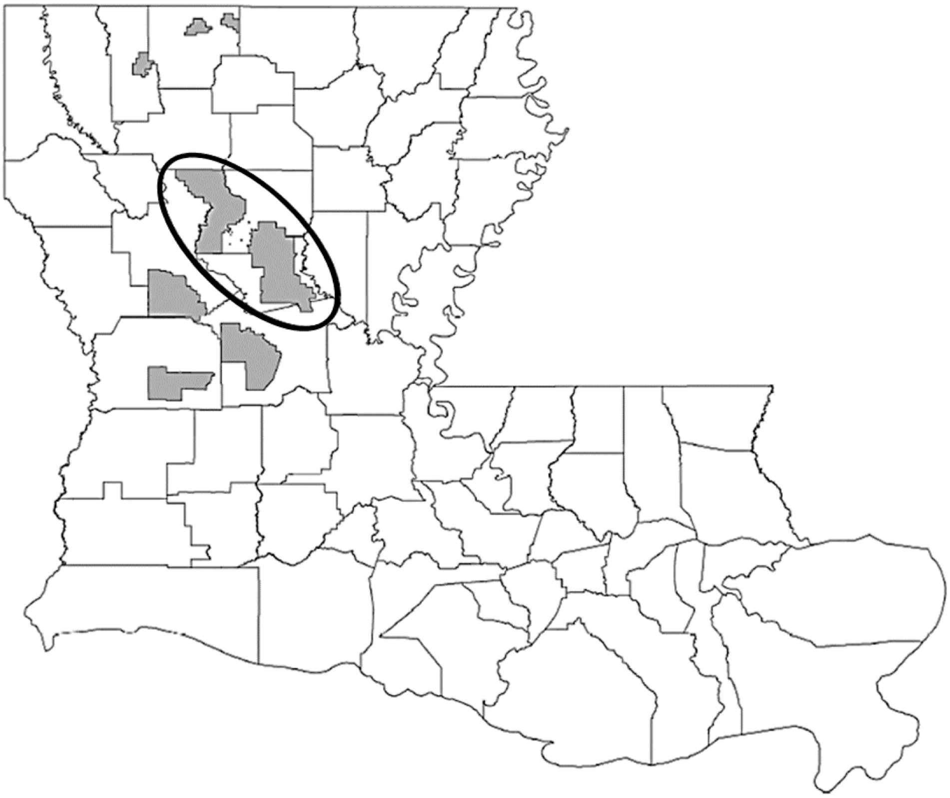

Fig. 1. Location of study areas used to examine roost selection by *M. septentrionalis* in Louisiana, 2016–2018. Shaded gray areas indicate the U.S. Forest Service Ranger Districts and circled areas are the Winn and Catahoula districts where this study was conducted.

Table 1
Summary statistics for each season (summer vs winter) for 19 characteristics of roost (obs) and random (rand) sites of *Myotis septentrionalis* in the Kistachie National Forest Louisiana, 2016–2018. PC1 – PC3 refer to loadings (correlations of each characteristic with the PC) describing the importance of a particular characteristic in defining the kind of variation expressed by each PC. Each of the 19 characteristics are labeled as to whether they were associated with the roost tree (T), plot (P) or landscape (L) characteristics.

Roost Characteristic	$\text{Summer}_{\text{obs}}$	$\text{Summer}_{\text{rand}}$	$\text{Winter}_{\text{obs}}$	$\text{Winter}_{\text{rand}}$	PC1	PC2	PC3
Roost tree diameter (T, cm)	24.09	26.15	40.08	29.15	−0.63	−0.19	0.43
Roost tree height (T, m)	21.65	22.92	26.69	21.17	−0.46	−0.09	0.67
Percent remaining bark (T)	95.59	96.59	85.28	91.58	0.00	0.59	0.36
Roost tree decay class (T)	2.32	1.90	2.44	2.22	0.26	−0.58	−0.48
Distance to nearest tree as tall (T, m)	5.19	4.87	7.80	5.77	−0.32	−0.04	0.27
Percent canopy closure (P)	46.26	47.55	66.82	57.16	−0.60	0.41	0.03
Percent deciduous trees in plot (P)	24.57	28.25	42.55	41.14	−0.64	0.41	−0.22
Understory density (P, no.)	2.36	2.42	2.77	3.47	−0.04	−0.75	−0.02
Snag density (P, no.)	5.36	4.15	2.33	5.84	0.58	−0.31	−0.33
Number trees in decay class ≥ 2 (P, no.)	54.71	40.36	12.10	13.54	0.91	0.21	0.14
Number of small tree stems (P, no.)	50.69	45.48	13.56	11.92	0.77	0.45	0.02
Number of large tree stems (P, no.)	37.53	28.39	18.13	15.68	0.81	0.33	0.12
Distance to nearest snag (P, m)	8.08	10.59	11.32	9.87	−0.52	0.15	0.17
Percent overstory deciduous trees (P)	4.07	5.61	12.95	13.25	−0.29	0.43	−0.44
Number of trees in plot (P, no.)	72.63	57.07	25.82	23.59	0.88	0.39	0.08
Distance to water (L, m)	103.53	98.78	84.95	125.08	0.06	−0.38	−0.16
Total deciduous area (L, m^2)	0.11	0.14	0.19	0.19	−0.35	0.49	−0.49
Total coniferous area (L, m^2)	1.53	1.54	1.46	1.46	0.37	−0.41	0.45
Size of fragment (L, km^2)	0.80	0.71	0.38	0.31	0.41	0.09	0.44

To measure landscape characteristics, we collected digital vegetation data using Earth Explorer via USGS. We used Landsat 8 OLI/TRIS images from February 17, 2017 with a criterion of zero percent cloud cover to classify landscape characteristics. The Landsat 8 sensor records 8 bands of spectral data in the visible, infrared, and thermal ranges of the electromagnetic spectrum with a 30 m resolution. We reclassified images into 6 landscape classes: 1) coniferous forest, 2) highway, 3) bare ground, 4) water, 5) deciduous forest, and 6) grass/forest litter. The reclassified image was imported into a Geographic Information System (GIS; ArcInfo), where we extracted information in a 1 km buffer around each roost. To determine distance to water and to obtain the area of each landscape class within each buffer, we used the attribute table of each roost and used the “calculate geometry” option to quantify the area of each landscape class.

To determine if roost trees were different from neighboring random trees in their tree and plot characteristics, we selected random sites to compare with roost sites by choosing a random bearing from the roost tree and walking 100 m and selecting the nearest random tree. At these random plots, we measured the same characteristics as in roost plots.

2.4. Statistical analysis

We used a chi-square goodness of fit test (Sokal and Rohlf, 1995) to examine if bats were roosting in tree species in frequencies different from expected based on a random sample of trees in the forest, a measure of resource selection (Manley et al., 2002). Frequencies of random tree species came from the list of species measured as random roost trees. Few deciduous tree species were selected as day roosts by bats or occurred in random plots; thus, we pooled all species of deciduous trees. We used chi-square tests to determine if bats roosted in conifers and deciduous trees in the same proportion as found in the forest.

The 19 tree, plot, and landscape characteristics were substantively correlated (mean pearson product moment correlation coefficient, $r = 0.47$, $P < 0.001$, df = 148). Therefore, we conducted a principal components analysis (PCA) on the entire dataset of tree, plot, and landscape characteristics to reduce the 19 variables to a smaller number of derived variables that were uncorrelated with each other. We retained principal components (PCs) that had eigenvalues greater than that based on the broken-stick stopping rule (Jackson, 1993). Retained PC's were then used as independent variables in inferential analyses to examine multivariate differences among roost and random trees. We used substantive correlations ($r > 0.50$) of the original variables with the retained principal components to interpret their identity.

In studies of roost selection, statistical comparisons are often made between random trees and those utilized as roosts, yet each unique roost does not necessarily represent an independent observation. Individual bats may exhibit particular and unique preferences and thus create nonindependence among roosts they choose. Therefore, when the number of roosts is larger than the number of individuals, individuals should be considered a random effect to account for such nonindependence (Ashrafi et al., 2013). We conducted linear mixed-effects models using the R package NLME (Pinheiro et al., 2020) based on Restricted Maximum Likelihood (REML). We began by examining significant differences between sexes regarding PC scores that reflected variation in roost characteristics. If this was non-significant, we then pooled data across sexes to evaluate differences between roost types (random or used), seasons (summer versus winter), and their interaction (roost type by season). We compared goodness of fit of the fixed-effects model with a mixed-effects model, whereby individual bats were random effects and seasons and roost type were fixed effects. Significantly better fit of the mixed effects model over the purely fixed effect model was determined based on a log-likelihood ratio test (Zuur et al., 2009). If fit was significantly better, we proceeded with mixed-effects models thereafter. We conducted inferential analyses on PC's and not the original 19 variables so as to reduce the number of comparisons and thus experiment wise error rate (Sokal and Rohlf, 1995). Application of mixed effects models to PC's provided for a pseudo-multivariate test of differences between roost and random trees.

To examine seasonal differences in occupied roosts and differences between random and occupied roosts and their interaction, we modeled two-way mixed effects as a pseudo multivariate test based on each of the PC's separately. We refer to these as pseudo multivariate because mixed models involved only a single dependent variable (a particular PC axis). Nonetheless, PC axes were multivariate descriptors of variation in all 19 roost characteristics. Pseudo multivariate tests based on PC's were inferential and addressed whether trees selected by bats were different from a neighboring randomly selected tree in the forest. Since these were inferential, we determined significance based on a Bonferroni sequential adjustment (Rice, 1989). Upon determining significance of pseudo multivariate statistical models with PC's as dependent variables, we modeled mixed effects on each of the tree, plot, and landscape characteristics separately as a more direct comparison of differences between random and roost trees to determine selection of important roost characteristics. These tests were exploratory to determine which of the roost characteristics likely contributed to the significant overall pseudo multivariate test with PC's. Accordingly, we made no adjustments for experiment-wise error rate for these contrasts.

To compare the roosting ecology of *M. septentrionalis* in Louisiana to other studies in North America, we compiled information on five roosting characteristics (most frequent tree species, mean number of roosts, mean DBH of roost tree, mean roost tree height, and mean decay class of roost tree) from 21 other studies found in the literature. We used one-sample t-tests (Sokal and Rohlf, 1995) to determine statistical significance of differences between our study and the population of others. We adjusted alpha based on a Bonferroni sequential adjustment (Rice, 1989) to reduce experiment-wise error rate.

3. Results

Twenty-nine *M. septentrionalis* were tagged with a transmitter and released. Eighteen bats in the summer were tracked to 59 roosts, 51 (86%) of which were in live trees. *Myotis septentrionalis* in summer roosted in pine trees (*Pinus* spp., 53 observations), oaks (*Quercus* spp., 3), fragrant snowbell (*Styrax obassia*, 2), and other unidentified deciduous trees (4). In winter, 11 bats were tracked to 39 roosts, 28 (72%) of which were in live trees. Roost trees were of pine (26), oaks (4), sweetgum (*Liquidambar styraciflua*, 3), bald cypress (*Taxodium distichum*, 1), American beech (*Fagus grandifolia*, 1), hickory (*Carya tometosa*, 1), sourwood (*Oxydendron arboretum*, 1), and other unidentified deciduous trees (2). For both seasons combined, *M. septentrionalis* roosted in pine trees with a greater frequency than expected given a random sample of trees ($X^2 = 3.90$, $P = 0.048$, df = 1). This was true in summer (Fig. 2, X2 = 4.50, $P = 0.034$, df = 1) but pine trees were used as roosts in winter at a frequency no different than expected compared to a sample of random trees (Fig. 2, X2 = 0.01, $P = 0.906$, df = 1).

Bats were highly variable regarding characteristics of the trees that they roosted in (Table 1). The first three principal components derived from the 19 roost characteristics had associated eigenvalues that were larger than expected from a broken stick model and were retained as dependent variables in subsequent analyses. The first principle component (PC1) accounted for 29.08%, PC2 accounted for 15.71%, and PC3 accounted for 11.26% of the variation among characteristics of roost and random trees. Principal component 1 was most positively correlated with number of trees in decay class 2 or above, number of trees in the plot, number of large tree stems, number of small tree stems, and snag density (Table 1). This PC was negatively correlated mostly with percent deciduous trees in a plot, roost tree diameter, percent canopy closure, and distance to nearest snag. This axis likely represents forest structure whereby as you move from negative values to positive values, plots have relatively more open canopies with more small-diameter trees but plots also have more declining trees and snags. The second PC was most positively correlated with percent remaining bark and most negatively correlated with density of the understory and decay class of trees. This axis is likely related to snags having less decay and more residual bark in areas with fewer understory stems and the fact that trees of small diameter were primarily in the understory. The third PC was most positively correlated with tree height and most negatively correlated with total deciduous area measured at the landscape scale. This axis likely reflects taller trees in areas with fewer deciduous trees.

We found no significant differences between females and males for roost-tree characteristics on PC1 ($t = 0.267$, $P = 0.791$, df = 27), PC2 ($t = -1.48$, $P = 0.149$, df = 27), or PC3 ($t = 0.400$, $P = 0.692$, df = 27). Therefore, we pooled data across sexes for all subsequent analyses. In the analysis of differences due to sex, for all three principal components, the random intercept mixed-effects model fit the data significantly better (all three $P < 0.001$) than a standard ordinary least squares model based on only fixed effects, suggesting a random effect of bats on individual preferences in roosting characteristics existed (Fig. 2). Accordingly, we used mixed-effects models for all subsequent analyses.

On PC1, but not PC2 or PC3, there was a significant interaction

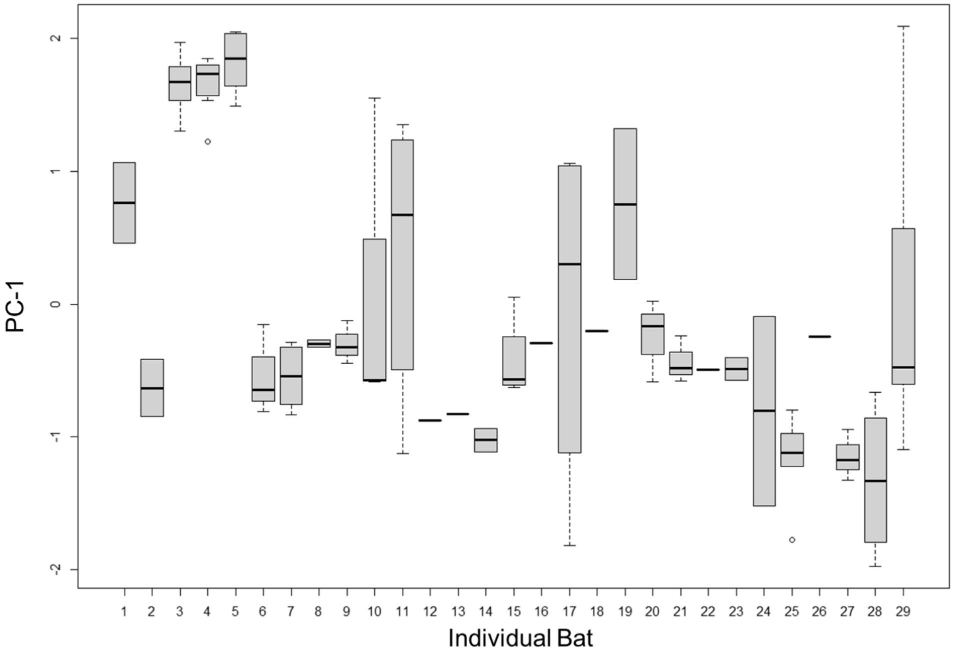

Fig. 2. Illustration of the random effect of individual bats on characteristics of day roosts utilized by *M. septentrionalis* in the Kisatchie National Forest in Louisiana, 2016–2018. Lines represent box plots characterizing the distribution of roost characteristic values (PC1 scores) for each of 29 individuals (1–29). Note the variability that can be attributed to individual bats.

between roost type and season indicating the difference between random and occupied roosts was dependent on season (Table 2). For PC2 and PC3, the main effects of season, roost type, and the interaction were not significant. Because of the significant difference and interaction on the primary multivariate axis (PC1), we examined differences between seasons for occupied roosts and differences between random and occupied roosts for each season separately based on the original nineteen variables. For used roosts, seasonal differences involved roost trees of larger diameter in plots with fewer trees (total trees, large trees, and trees in decay class ≥ 2) in winter than in summer (Table 3). In summer *M. septentrionalis* preferred roost trees that were more decayed in plots with more trees (total trees, large trees, and trees in decay class ≥ 2) than neighboring random trees (Table 3). In winter, *M. septentrionalis* preferred trees of larger diameter and greater height with less remaining bark and of a greater decay class than neighboring random trees (Table 3).

Based on our synthesis of 21 other studies across its geographic range, *M. septentrionalis* is highly variable with regards to roost-tree characteristics and they use both coniferous and deciduous trees as roosts (Table 4). Mean number of roosts was significantly greater in both seasons in Louisiana when compared to other studies (t = -6.59, P < 0.001, d.f. = 19, winter; t = -2.98, P < 0.008, d.f. = 19, summer). Mean diameter at breast height of roost trees was no different than in other studies in winter (t = -1.59, P = 0.127. d.f. = 21) and smaller than in other studies in summer (t = 4.74, P < 0.001, d.f. = 21, summer). *Myotis septentrionalis* used trees that were significantly taller than those in other studies in both winter and summer (t = -11.1, P < 0.001, d.f. = 18 winter; −6.04, P < 0.001, d.f. = 18, summer). Mean decay class of roost trees appears to be similar to other studies, but no statistical test was performed due to different methods used across studies.

Table 2
Results of Linear Mixed Effects Models conducted on each PC axis to examine influence of roost characteristics and season on roost selection by *Myotis septentrionalis* in the Kistachie National Forest of Louisiana, 2016–2018.

	PC1	PC2	PC3
$Roost_b$	−0.200	−0.046	0.056
$Roost_p$	0.042	0.604	0.685
$Roost_{df}$	219	219	219
$Season_b$	−0.803	−0.320	−0.158
$Season_p$	0.009	0.368	0.586
$Season_{df}$	27	27	27
RxS_b	0.348	0.254	−0.375
RxS_p	0.022	0.065	0.081
RxS_{df}	219	219	219

A Bonferroni sequential adjustment reduced alpha to 0.013, 0.025, and 0.050 for the three tests ranked from most to least significant. Subscripts $_b$, $_p$, and $_{df}$ refer to the beta coefficient, p-value, and degrees of freedom of the analysis, respectively. $_b$ – beta coefficient; $_p$ – p-value; $_{df}$ – degrees of freedom.

4. Discussion

4.1. Differences between seasons

This study is the first to demonstrate differences between summer and winter in tree-roost characteristics used by *Myotis septentrionalis*. During winter in Louisiana, *M. septentrionalis* selected trees that were significantly larger (DBH and height), more decayed, and had less remaining bark than those in surrounding forest. During summer, *M. septentrionalis* preferred pine trees in plots with a greater number of trees, greater number of large stems, and in plots with more declining trees/snags. Therefore, *M. septentrionalis* may select for tree characteristics in winter and plot characteristics in summer.

In winter, trees selected by *M. septentrionalis* were taller than random trees. This is a common characteristic of *M. septentrionalis* roosts and many other species of North American bats during summer (Lackie and Baker, 2003, Kalcounis-Ruppell et al., 2005, Lacki et al., 2009, Nad'o and Kanuch, 2015, Drake et al., 2020). Taller trees may extend above the canopy and absorb more solar energy and thus heat faster (Owen et al., 2002). Larger-diameter trees also provide greater insulation and are less affected by fluctuating ambient conditions, enabling roosts to maintain more stable microclimates than those in trees with smaller diameters (Coombs et al., 2010, Nicolai, 1986, Vonhof and Barclay, 1996). Large snags in advanced stages of decay have characteristics that promote cavity formation (Alston et al., 2019). Lastly, larger snags tend to remain standing longer than smaller snags (Bull et al., 1981, Chambers et al., 1997) and roosts that persist for longer periods of time may be preferred

Table 3

Results of Linear Mixed Models examining effects of roost and season on individual variables selected by *Myotis septentrionalis* in the Kistachie National Forest of Louisiana, 2016–2018. Abbreviations P and df refer to p-values and degrees of freedom, respectively whereas subscripts SE, S, and W refer to season, summer and winter, respectively.

	Coefficient$_{SE}$	P$_{SE}$	df$_{SE}$	Coefficient$_{S}$	P$_{S}$	df$_{S}$	Coefficient$_{W}$	P$_{W}$	df$_{W}$
PC1	See Table 2								
PC2	See Table 2								
PC3	See Table 2								
Roost tree diameter	**15.385**	**<0.001**	**27**	0.776	0.690	119	**−11.261**	**<0.001**	**100**
Roost tree height	3.657	0.143	27	1.021	0.344	119	**−5.235**	**0.006**	**100**
Percent remaining bark	−12.802	0.056	27	1.001	0.722	119	**11.940**	**0.005**	**100**
Roost tree decay class	0.136	0.683	27	**−0.420**	**0.019**	**119**	**−0.596**	**0.011**	**100**
Distance to nearest tree as tall	2.605	0.183	27	−0.353	0.722	119	−2.045	0.181	100
Percent canopy closure	12.962	0.253	27	−0.648	0.723	119	−1.664	0.443	100
Percent deciduous trees in plot	13.872	0.203	27	3.673	0.317	119	5.357	0.209	100
Understory density	0.402	0.397	27	0.085	0.456	119	0.254	0.123	100
Snag density	−1.438	0.259	27	−0.732	0.226	119	1.764	0.078	100
Number of trees in decay class ≥ 2	**−27.803**	**0.009**	**27**	**−10.280**	**0.014**	**119**	1.562	0.524	100
Number of small tree stems	−20.508	0.066	27	−0.380	0.911	119	−0.163	0.953	100
Number of large tree stems	**−14.388**	**0.018**	**27**	**−7.237**	**0.003**	**119**	−1.872	0.357	100
Distance to nearest snag	1.036	0.624	27	−0.500	0.611	119	−0.722	0.560	100
Percent overstory deciduous trees	9.278	0.151	27	1.189	0.670	119	2.027	0.707	100
Number of trees in plot	**−29.178**	**0.026**	**27**	**−10.085**	**0.017**	**119**	−0.701	0.825	100
Distance to water	−29.462	0.213	27	−5.132	0.628	119	27.208	0.149	100
Total deciduous area	0.018	0.853	27	−0.019	0.529	119	0.008	0.587	100
Total coniferous area	−0.066	0.666	27	0.017	0.630	119	−0.001	0.984	100
Size of fragment	−0.398	0.043	27	−0.099	0.199	119	−0.047	0.559	100

Table 4

Summary statistics and quantitative analyses comparing roosting characteristics of *M. septentrionalis* across 22 different studies. Numbers in parentheses indicate the number of decay classes characterized.

Study	Location	Roosts	DBH	Height	Decay	Roost Tree Species
Carter and Feldhamer, 2005	Illinois	1.9	37.3	15.8	1.4 (4)	Quercus palustris (Pin Oak)
Bergeson et al., 2021b	Indiana	2.5	30.4	18.2	2.0 (7)	Sassafras albidum (Sassafras)
Lacki and Schwierjohann, 2001	Kentucky	3.8	21.9			*Pinus echinata* (Short-Leaf Pine) *Oxydendrum arboretum* (Sourwood)
Thalken and Lacki, 2018	Kentucky	3.2	32.0	18.3	2.7 (9)	*Acer rubrum* (Red Maple)
Menzel et al,. 2002	West Virginia	1.7	29.2	18.7	4.0 (9)	Robinia pseudo-acacia (Black Locust)
Perry and Thill, 2007	Arkansas	2.2	16.9	8.3		*Pinus echinata* (Short-Leaf Pine)
Sasse and Perkins, 1996	New Hampshire	2.2	40.9	14.8	2.8 (5)	*Fagus grandifolia* (Beech)
Johnson et al., 2009, Ford et al., 2006	West Virginia	2.0	28.5	15.4	4.0 (7)	Robinia pseudo-acacia (Black Locust)
Silvis et al., 2015[a]	Kentucky	1.2	32.2	13.4		Sassafras albidum (Sassafras)
Silvis et al., 2015[b]	Kentucky	4.4	32.8	18.0		Sassafras albidum (Sassafras)
Timpone et al., 2010	Missouri	3.0	43.0	15.7		*Quercus rubra* (Northern Red Oak)
Broders and Forbes, 2004	New Brunswick	3.5	37.8			*Acer saccharum* (Sugar Maple) *Betula alleghaniensis* (Yellow Birch)
Park and Broders, 2012	New Foundland	2.6	26.0			*Picea glauca* (Balsam Fir)
Garroway and Broders (2008)	Nova Scotia		42.0	17.8		
Foster and Kurta, 1999	Michigan	2.9	64.6	23.3		Acer saccharinum (Silver Maple)
Fabianek et al. 2015	Quebec	5.0	20.2	9.3		*Picea glauca* (Balsam Fir)
Cryan et al. 2001	South Dakota	2.3	39.0	9.10		*Pinus ponderosa* (Ponderosa Pine)
Owen et al. 2002	West Virginia		27.2	17.8		Robinia pseudo-acacia (Black Locust)
Rojas et al. 2017	Tennessee	1.8	58.2	20.50		*Pinus strobus* (White Pine)
Alston et al. 2019	South Dakota	2.4	35.7	8.53	4.95 (9)	*Pinus* spp. (Pine)
Burrell and Bergeson, 2022	Indiana	3.0	51.4	20.7		Acer saccharinum (Silver Maple)
Andersen and Geluso, 2022	Nebraska	1.2	46.7	14.0	2.10 (6)	
Average			2.6	36.1	15.7	
Standard error			0.22	2.53	1.00	
This study winter	Louisiana	4.1	40.1	26.7	2.4 (9)	*Pinus* spp. (Pine)
This study summer	Louisiana	3.3	24.1	21.7	2.3 (9)	*Pinus* spp. (Pine)

[a] 2011 data.

[b] 2012 data.

by bats such as *Myotis septentrionalis.* This may be because females return to the same areas and even the same roost trees in consecutive years thereby facilitating and even enhancing the stability of fission/fusion social networks (Johnson et al., 2012), although these networks have not been examined in winter because these bats hibernate across much of their geographic range during this season.

In summer, *M. septentrionalis* selected plots with greater density of large trees of more advanced stages of decay and with more large stems. These plots may provide higher density of potential roosts in summer than in winter. In summer, *M. septentrionalis* switches roost frequently (e.g., Johnson et al., 2012) and females roost colonially (e.g., Foster and Kurta, 1999), behavior that is associated with fission–fusion dynamics (Silvis et al., 2014). During summer females are more likely to move from highly decayed roosts on warmer days and to less decayed trees of smaller diameter on windy and rainy days (Patriquin et al., 2016). In fact, many bats may use a variety of roosts to facilitate flexibility in the use of torpor to enhance energy budgets (Bergeson et al., 2021a). Therefore, roosting in plots with a greater variety of trees with larger stems and plots with more declining trees/snags may facilitate numerous aspects of roosting ecology such as thermodynamics, colonial roosting and ultimately fission–fusion dynamics.

4.2. No difference between sexes

We found no significant differences between males and females regarding day-roost characteristics in Louisiana. Because most studies examining roost characteristics of *M. septentrionalis* have been conducted in summer, one possibility is that differences between sexes may be more evident during the breeding season in summer. However, we found no significant interaction between sex and season with respect to differences in roost characteristics. Most studies of roosting ecology of *M. septentrionalis* have focused on a single sex. For example, of the 22 (ours included) studies listed in Table 4, twelve focused on females, two focused on males, four studies characterized roost use for both sexes but did not explicitly test for a sex effect, and one study did not distinguish between sexes. Only 3 studies actually tested for a difference between sexes. Weak yet equivocal differences (some ANOVA's were significant but post-hoc tests were not) were reported in Kentucky (Thalken and Lacki, 2018). Strong and significant differences in roost characteristics between male and female *M. septentrionalis* have been reported in two studies whereby females tended to roost in larger trees (Broders and Forbes, 2004, Perry and Thill, 2007) or in plots with larger trees and greater numbers of overstory trees (Perry and Thill, 2007) and differences were obvious and unequivocal. For example, in New Brunswick Canada, females roosted in shade tolerant deciduous trees while males roosted in coniferous trees (Broders and Forbes, 2004). Similarly, females often preferred to roost in snags whereas males roosted in live trees in Arkansas (Perry and Thill, 2007). Even differences between Broders and Forbes (2004) and Perry and Thill (2007) in term of the qualitative nature of the sex difference (deciduous and coniferous trees versus pine snags and live pine trees) suggests geographic variability in sex differences of roost characteristics. Thus, no difference found in Louisiana may simply reflect one position on this spectrum of geographic variability. Generalizations on roosting behavior may be difficult given the wide distribution of this species in North America and sexual differences found in some studies and not in others. Lack of a sexual difference in roost characteristics in Louisiana during both summer and winter suggests that separate management strategies may not be necessary for males and females in this region.

4.3. Individual differences

Differences among individual bats may represent an important form of variation in roost-selection studies and individual differences contributed to significant improvement in model fit. Individual differences have two important effects. First, when not treated as a random effect, individual differences create nuisance variability that may reduce power and repeated observations from individuals that have particular preferences introduce a lack of independence into the dataset and ultimately the analysis (Hurlbert, 1984). In addition, individual specialization may be a common phenomenon and better appreciation may enhance our understanding of roosting ecology. For example, in yellow-shouldered bats (Phyllostomidae: *Sturnira lilium*), individual fruit preferences were demonstrated in laboratory experiments (Muylaert et al., 2014) and manifested as individual spatial patterns of foraging that had consequences for seed dispersal and ultimately, connectivity across the landscape (Kerches-Rogeri et al., 2020). Similar findings of individual specialization in diet have been demonstrated for *Eptesicus fuscus* (Cryan et al., 2012). Bats have also been demonstrated to have individual preferences for environmental conditions that initiate use of torpor (Fjelldal et al., 2021, McGuire et al., 2021). Although the statistical challenges of individual specialization can be accounted for by using mixed-models that treat individual as a random effect, effects of individual specialization on our perception of resource selection may influence the accuracy of management and conservation plans.

4.4. Geographic differences and generalizations on roosting behavior

Myotis septentrionalis is well-studied in terms of tree-roost use, having been studied in at least 20 other sites in 13 different states or provinces in the United States and Canada. Across its range, preferred roost-tree species varies geographically and includes both pine and hardwoods. The preferred roost tree typically is the most dominant species at the plot level. Moreover, across studies, species of trees most commonly used are highly variable. For example, the number of tree species used as roosts ranged from 1 in South Dakota (Cryan et al., 2001) to 24 in Kentucky (Thalken and Lacki, 2018). Across its geographic distribution it is clear that *M. septentrionalis* does not select roosts based on tree species identity per se. There could be a number of reasons for such variability in tree species used as day-roosts. First, because the distribution of *M. septentrionalis* is so large in North America, it is possible that different kinds of trees provide protection from different extremes of climate across its range. For example, trees that emerge out of the canopy may warm more rapidly (Owen et al., 2002) in colder environments whereas those in the midstory may provide shade in hotter environments (De Frenne et al., 2019). Given that *M. septentrionalis* often prefers snags, selection of individual tree species may be more related to the kind of disturbance that has affected species composition of a particular plot (Diskin et al., 2011). For example, outbreaks of pine beetles may create pine snags whereas in older, even-aged stands, most dying trees may be midstory hardwoods in decline because of overshading. Lastly, the most dominant tree species is statistically more likely to be represented by more snags across the landscape. If a roosting bat species was simply selecting for snags then that particular dominant tree species would likely be selected. Thus, roost-tree species is likely most related to the species composition of the local tree species pool or past land use that determine which species is the most dominant in a particular region (Silvis et al., 2014). While *M. septentrionalis* may select for particular tree species in particular systems, tree species used varies across their range, suggesting that these bats are roost generalists (Drake et al., 2020) and more likely select particular characteristics that enhance roosting at these particular sites.

Myotis septentrionalis in Louisiana differed from those in other regions based on a greater number of roosts, greater Tree DBH and lower tree height in summer. These differences were likely related to geographic variation in forest structure as opposed to differences among populations of bats in how they select roosts. Other important roosting characteristics also vary geographically. For example, in some places *M. septentrionalis* selects trees that are taller than random trees (this study, Fabianek et al., 2015; Perry and Thill, 2007; Sasse and Perkins, 1996) but not in other places (Cryan et al., 2001, Menzel et al., 2002, Carter and Feldhamer, 2005, Rojas et al., 2017). Similarly, some studies have found roost-tree DBH larger than random trees (Cryan et al., 2001; Fabianek et al., 2015; Ford et al., 2006; Rojas et al., 2017; Sasse and Perkins, 1996, Thalken and Lacki, 2018) but not in other studies (Foster and Kurta, 1999, Menzel et al., 2002, Broders and Forbes, 2004, Carter and Feldhamer, 2005). Sexual differences in roosting characteristics are also geographically variable. All of this geographic variability makes generalization of important roost characteristics difficult.

4.5. Consistent difference in decay class between roost and random trees

Although decay class of roost trees in Louisiana was on average low (average = 2.38)*,* *M. septentrionalis* consistently selected trees in greater degrees of decay than those randomly occurring in the forest. Among 22 (ours included) studies on *M. septentrionalis* we reviewed, 7 (Lacki and Schwierjohann, 2001, Ford et al., 2006, Perry and Thill, 2007, Timpone et al., 2010, Park and Broders, 2012, Rojas et al., 2017, Thalken and Lacki, 2018) qualitatively indicated use of decaying trees or snags, 3 (Broders and Forbes, 2004, Carter and Feldhamer, 2005, Johnson et al., 2009, this study) found roost trees were more decayed than a random sample of surrounding trees, 3 (Cryan et al., 2001, Fabianek et al., 2015, this study) statistically determined that stands where roosts occurred had more snags than a sample of random stands from the forest, and 1 (Sasse and Perkins, 1996) found roost snags were larger and less decayed than random snags. More decayed trees may offer a greater number of cavities and greater amounts of exfoliating bark from which to roost. While *M. septentrionalis* roosts in a variety of structures including live trees (Sasse and Perkins, 1996, Foster and Kurta, 1999) and artificial roosts (Brandon, 1961, De La Cruz et al., 2018), use of decayed trees is one of the few ubiquitous roosting characteristics of this species.

4.6. *Management considerations*

Management strategies to enhance roosting opportunities at particular sites and based on studies from other locations must be based on generalities, for which there are few for *M. septentrionalis*. One consistent finding among studies is the use of roost trees that are in more advanced stages of decay. Snags are frequently removed because they can be hazardous to humans and their structures. Nonetheless, retention of snags is beneficial to *M. septentrionalis* and retaining snags is an easy management strategy to implement. In areas of low density of dead or declining trees, snags can also be created on the landscape via removal of the crown by explosives (Bull et al., 1981) or saw-topping (Chambers et al., 1997), inoculation with heart rot fungi (Connor et al., 1983), limbing, or by girdling (Lewis, 1998). Girdling creates taller snags than the other approaches (Lewis, 1998) and may be an effective tool to create roosting substrates for *Myotis septentrionalis* and other bats of conservation concern.

In regions like Louisiana where *M. septentrionalis* is active year-round, management strategies may be more complicated by seasonal differences in roost characteristics. In summer, we found roost selection by *M. septentrionalis* was based more on plot level characteristics, whereas selection in winter was based more on characteristics of particular trees. Thus, one specific management recommendation for areas such as the Kisatchie National Forest in Louisiana where bats are active year-round would be to retain a large number of decaying large trees that would have effects at both the individual tree and plot level, thereby benefiting *M septentrionalis* in both summer and winter.

The geographic variability in preferred roost characteristics of *M. septentrionalis* reported here suggest this species is a generalist, which also has important management implications. Because of its recently imposed federal protections, generalist roosting preferences and large geographic range, *M. septentrionalis* has been described as an umbrella species whereby management practices designed to benefit this species may benefit a number of other species as well (Drake et al., 2020). *Myotis septentrionalis* is a generalist of the "dead tree roosting guild" that exhibits considerable overlap in roosting preferences with other important bat species such as *Eptesicus fuscus*, *Myotis lucifugus*, *Myotis sodalis*, *Lasionycteris noctivagans*, and *Nycticeius humeralis* as well as others (Drake et al., 2020).

More generally, in Louisiana (Andersen et al., 2022) and other coastal environs where *M. septentrionalis* is active during winter (Jordan, 2020, Parker et al., 2020) forest could be managed to enhance abundance given the rarity of this winter behavior across their range. These areas where *M. septentrionalis* does not appear to hibernate during winter are likely to be less affected by WNS and these regions may provide future sources for either natural dispersal or assisted dispersal into areas where the species has been extirpated by WNS. Moreover, management in areas where this species is active during winter could focus on enhancing persistence of *M. septentrionalis* to prevent its global extinction.

CRediT authorship contribution statement

Carlos J. Garcia: Investigation, Methodology, Writing – original draft, Writing – review & editing. **David A. Ray:** Investigation, Project administration, Writing – review & editing. **Roger W. Perry:** Conceptualization, Funding acquisition, Investigation, Project administration, Writing – review & editing. **Richard D. Stevens:** Conceptualization, Data curation, Formal analysis, Investigation, Project administration, Writing – review & editing.

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.

Data availability

Data will be made available on request.

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