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Seasonal Shifts in Roosting Strategies of Male Seminole Bats in Coastal South Carolina

Lydia H. Moore[1,*], Samuel J. Holst[2], Kyle E. Shute[3], and Jason B. Robinson[4]

Abstract - Foliage-roosting bats are more exposed to environmental conditions than species roosting under exfoliating bark, in tree cavities, or in caves. To test whether foliage-roosting species alter roosting behavior in response to seasonally changing environmental conditions, we examined roosts of *Lasiurus seminolus* (Seminole Bat) during fall and summer in Beaufort County, South Carolina. We radio-tracked 13 adult males to 64 roosts. Most bats in both seasons roosted in pines that were taller and with greater diameter than surrounding trees. Fall roosts were generally on the south side of dominant trees and in mixed hardwood-pine forests. Summer roosts were primarily in codominant trees in plots composed of pines. Roost selection in both seasons was made at multiple scales, depending on availability of resources. Quantifying variation in roost characteristics between seasons provides a more comprehensive understanding of habitat requirements and aids in more thorough land management.

Introduction

Shifts in seasonal environmental conditions between summer and winter often necessitate corresponding shifts in animal behavior due to energetic requirements. For bats, diurnal roosts are important because they provide shelter and allow individuals to regulate thermal requirements while inactive. Some species use caves, culverts, mines, and tree crevices or cavities that supply stable environmental conditions (Altringham 2011). However, several species forego these stable sites and instead roost in the foliage of trees throughout the year. Previous studies of foliage-roosting species during spring and summer show that bats select warm roosts, reducing energy demands for both adults and pups (Menzel et al. 2000, Monarchino et al. 2020). Although there are several studies of bats in the Southeast roosting in trees in summer (Hein et al. 2008a, Lucas et al. 2015, Miles et al. 2006, Shute et al. 2021) and winter (Hein et al. 2008b, Jorge et al. 2021, Newman et al. 2021), few have occurred in spring and fall (Cryan and Veilleux 2007), during which roosting behavior may be impacted by fluctuating ambient temperature (TA) and other environmental conditions.

Bats select diurnal roosts based on landscape-level variables in addition to thermoregulatory requirements (Jachowski et al. 2016). Individuals may choose to roost near resources that are either important or limited on the landscape, including fresh water and foraging corridors (Hein et al. 2008b, Newman et al. 2021, O'Keefe et al. 2009). Selection of roosts may vary between seasons at multiple spatial scales due to thermoregulatory requirements, or if access to resources becomes increasingly important in cooler months when bats are only briefly active. For example, male *Lasiurus seminolus* (Rhoads) (Seminole Bat) roost farther from edges during winter and closer to edges during summer (Hein et al. 2008a, b). This may be due to increased predation risk and exposure to wind while bats are inactive during colder months (Hein et al. 2008b). Therefore, the effects of multiple spatial scales should be considered when evaluating roost-site selection.

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The Seminole Bat is a medium-sized bat (9–14 g) common to the coastal plains of the southeastern United States (Wilkins 1987). Similar to many other foliage-roosting species in temperate areas, Seminole Bats have thick fur and a completely furred uropatagium that provides increased insulation while roosting (Shump and Shump 1980). Seminole Bats primarily roost in pines but also use hardwoods (Constantine 1958; Hein et al. 2008a, b; Menzel et al. 1998, 2000; Perry and Thill 2007). Typical roost structures include pinecones, pine needles, vines, *Tillandsia usneoides* (L.) L. (Spanish Moss), and leaf clusters in the canopy (Best and Dusi 2014, Hein et al. 2008a), although they also hide under leaf litter during winter (Hein et al. 2005). There are few studies on Seminole Bat roosting habits in the southeastern coastal plains, and none have explored seasonal changes in roosting strategies during fall. Because TA during this time is declining, yet still warm enough for bats to be active, individuals may select different roosts based on varying needs.

Seminole Bats, like many other foliage-roosting bats, have low roost fidelity but high site fidelity (Carter and Menzel 2007, Castleberry et al. 2020, Hein et al. 2008a, Shute et al. 2021), indicating that features of the landscape surrounding the roost may be more important than the roost itself. Therefore, quantifying habitat characteristics at multiple spatial scales provides a more holistic view of roosting requirements—an understanding that is particularly important as coastal areas continue to experience habitat degradation and loss due to high rates of development (Terando et al. 2014). Given this loss of habitat and its impact on the persistence of species, understanding changes in habitat needs between seasons is important. As such, the goal of our study is not to determine which spatial scale (tree, plot, or landscape) is most influential on seasonal roost-site selection by Seminole Bats. Instead, our goal is to identify specific features selected at each scale and how these patterns of selection change between summer and fall. We hypothesized that season-specific environmental conditions would result in differences in roosting behavior, with tree and plot selection focusing on thermoregulatory needs and selection at the landscape scale related to proximity of resources.

Field-site Description

We conducted our study at Palmetto Bluff, an 8094-ha residential community in Bluffton, Beaufort Co., South Carolina. Palmetto Bluff is in the Lower Coastal Plain geographic province, which has characteristically low elevation (8–38 m; South Carolina Department of Natural Resources 2015). The climate is sub-tropical, with mild falls (19.5 ± 0.08 (*SE*) °C, 265 ± 10 mm precipitation) and hot and humid summers (27 ± 0.06 °C, 323 ± 9 mm precipitation; National Oceanic and Atmospheric Administration 2023).

The property was converted from timber production to a residential development in 2001. Palmetto Bluff currently consists of 2044 ha of human-dominated landcover, including low-density neighborhoods, golf courses, man-made freshwater ponds, roads, and parks. Developed land is interspersed with 130 ha of mixed forest, protected in conservation easements, and 2138 ha currently without residential development, including managed forest and wildlife openings. Dominant forest types include maritime, pine-dominated, and mixed hardwood-pine forest. Common tree species include *Quercus virginiana* Mill. (Live Oak), *Q. laurifolia* Michx. (Laurel Oak), *Pinus taeda* L. (Loblolly Pine), *Pinus elliottii* Engelm. (Slash Pine), *Sabal palmetto* (Walter) Lodd. ex Schult. and Schult. f. (Cabbage Palmetto), and *Magnolia grandiflora* L. (Southern Magnolia). Spanish Moss is common in the canopy. Bordered by the May River to the east and the New River to the west, Palmetto Bluff is a peninsula surrounded by ~2226 ha of saltmarsh interspersed with small hammock islands.

Methods

Capture and telemetry

We captured bats using polyester mist nets with a 38-mm mesh (Avinet Research Supplies, Portland, Maine). Fall netting occurred on 20 nights between 14 September and 28 October 2020, and 12 nights between 23 September and 25 October 2021. Summer netting took place on 12 nights between 22 June and 30 July 2021, and 26 nights between 16 June and 31 August 2022. Nets were erected across trails and small roads, and over natural ponds. Most netting occurred in undeveloped maritime forest due to the desirable flyways created by overhanging canopy.

For each captured bat, we documented weight, right forearm length, sex, age, reproductive condition, and the wing damage index of Reichard and Kunz (2009). Male Seminole Bats were banded on their right forearm with a 2.9-mm aluminum split ring (Porzana Ltd, East Sussex, United Kingdom) and were fitted with either a 0.27-g or 0.31-g radio-transmitter (LB-2X, Holohil Systems, Ontario, Canada). We affixed transmitters to the interscapular region using surgical adhesive (Osto-bond, Montreal Ostomy, Quebec, Canada) and held bats for 30 min to allow the adhesive to set. Transmitters weighed <5% of the body weight of bats (Aldridge and Brigham 1988), and our techniques followed the guidelines of the American Society of Mammalogists (Sikes et al. 2016).

Bats were tracked using a receiver (TRX-2000) and 3-element yagi antenna (Wildlife Materials, Murphysboro, IL) for either 7 consecutive days, until the transmitter fell off, or the bat flew out of range. We attempted to locate the bat in a tree using binoculars and a spotting scope while it roosted or by observing it emerge at dusk. If found in a tree, we determined roost aspect and structure (e.g., Spanish Moss, pinecone, pine needle), measured roost height with a laser rangefinder (Nikon, Melville, NY), and determined the location of the tree using a submeter global positioning system (R1 GNSS, Trimble, Westminster, CO). If we could not verify a specific tree, we marked the area directly below the strongest transmitter signal as plot center, but did not include roost-tree variables in analyses.

Vegetation sampling

We measured habitat variables that influence roost selection of tree-roosting bats (Kalcounis-Rüppell et al. 2005, Nado and Kanuch 2015; Table 1). For each roost tree, we documented species, decay class (Maser and Trappe 1984), and Kraft crown class (Smith et al. 1997). We measured tree height and flight space (height between the subcanopy and first limb of the tree) using a laser rangefinder, and measured canopy closure directly below the roost using a concave spherical densiometer (Model A; Forestry Suppliers, Jackson, MS). We determined diameter at breast height (DBH), distance to nearest tree ≥10 cm DBH, and canopy diameter at its widest point using appropriate measuring tapes. We also counted the number of Spanish Moss clumps on the roost tree that appeared large enough to conceal a bat.

We established a 10-m radius (0.03-ha) plot around each roost tree to quantify vegetation structure surrounding the roost. Within this plot, we measured the DBH and height of trees ≥10 cm DBH to calculate basal area and mean canopy height, respectively. We counted the number of trees in the plot and calculated the proportion of pines. We measured canopy closure and flight space at the center of the plot and 5 m from the plot center in all 4 cardinal directions. The number of Spanish Moss clumps large enough to conceal a bat were counted along these transects from the plot center to 5 m in the 4 cardinal directions.

For each roost tree and plot, we generated 2 random trees and random plots, respectively, in ArcGIS (ArcMap version 10.8.2; ESRI Inc., Redlands, CA). Due to a lack of published

Table 1. Variables measured at the roost, tree, plot, and landscape scale for male Seminole Bat roosts and associated random points during fall and summer 2020–2022 in Beaufort County, South Carolina.

Scale	Variable	Explanation (units)
Roost	Roost height	Height of roost (m)
	Roost structure	Description of roost material
	Roost aspect	Cardinal direction of roost (N, S, E, or W)
Tree	Tree species	Species of roost or random tree
	Tree height	Height of tree (m)
	Tree DBH	Diameter of tree at breast height (cm)
	Spanish moss in tree	Number of Spanish Moss clumps large enough to conceal a bat in roost or random tree
	Canopy closure	Amount of canopy obscured by vegetation (%)
	Flight space below tree	Height of space between the first limb of a tree and the subcanopy (m)
	Canopy diameter	Measure of canopy diameter at its widest point (m)
	Nearest tree	Distance to the nearest tree ≥10 cm DBH (m)
	Decay class	Categorization of living state of trees, ranging 1-9
	Dominance class	Relative position of the roost tree in the canopy: dominant, co-dominant, intermediate, or suppressed
Plot	Plot DBH	Diameter of trees ≥10 cm DBH within the plot at breast height (cm)
	Basal area	Basal Area of the Plot (m^2)
	Mean canopy height	Average height of trees ≥10 cm DBH within the plot (m)
	Number trees	Number of trees within the plot
	Proportion pine	Proportion of trees within the plot that are pine (%)
	Flight space	Average height of space between the lower canopy and the subcanopy, measured at 5 locations within the plot (m)
	Plot canopy closure	Average amount of canopy obscured by vegetation, taken at 5 locations within the plot (%)
	Spanish moss in plot	Average number of clumps of Spanish moss large enough to conceal a bat that intersected transects extending from plot center to 5m in all 4 cardinal directions
Landscape	Forest cover	Hardwood, pine-dominated, mixed hardwood-pine, open (marsh and food plots), or residential area
Distance to Resources[a]	Distance to road	Distance from plot center to the nearest road (paved and unpaved) (m)
	Distance to freshwater	Distance from plot center to the nearest freshwater pond (m)
	Distance to edge	Distance from plot center to nearest edge (m)

Table 1. Continued.

	Distance to residential area	Distance from plot center to the nearest residential area (m)
Near Landscape[b]	Near - Residential area	Amount of residential area (including parks and small forest patches) within the 463-m buffer (ha)
	Near - Freshwater pond	Area comprised by manmade freshwater lagoons within the 463-m buffer (ha)
	Near - Open habitat	Area within the 463-m buffer covered by saltwater marsh and food plots (ha)
	Near - Forest	Amount of forest (combining all forest types) within the 463-m buffer (ha)
Far Landscape[c]	Far - Residential area	Amount of residential area (including parks and small forest patches) within the 1000-m buffer (ha)
	Far - Freshwater pond	Area comprised by manmade freshwater lagoons within the 1000-m buffer (ha)
	Far - Open habitat	Area within the 1000-m buffer covered by saltwater marsh and food plots (ha)
	Far - Forest	Amount of forest (combining all forest types) within the 1000-m buffer (ha)

[a] These variables were modified into principal components Dist1, Dist2, Dist3, and Dist4 (see text).
[b] These variables were modified into principal components Near1, Near2, Near3, and Near4.
[c] These variables were modified into principal components Far1, Far2, Far3, and Far4.

data on Seminole Bat home range size, random points were generated within buffers for each individual bat based on the longest distance traveled by that individual, either between roosts or between the capture location and first roost, whichever was greater. This buffer conservatively estimated the amount of roosting habitat available to individual bats, given nightly movement. Random points were at least 100 m apart to reduce overlap. We designated the ≥10 cm DBH overstory tree closest to the random point as the focal tree and documented the same measurements at the tree and plot level as we did for used roosts.

Landscape measurements

Landscape characteristics were measured using ArcGIS. Distance to resources, such as drinking water and travel corridors, were quantified based on digitized aerial imagery (B. Rife, Thomas and Hutton Engineering Firm, Savannah, GA, unpubl. data; Table 1). We calculated distance to nearest road, freshwater pond, edge, and residential area using the Near tool. We consolidated ~20 forest-cover types into 3 forest-cover categories: hardwood, pine, and mixed hardwood-pine. Each random or used roost was assigned a forest cover category. Moran's *I* Index assessed clustering of roosts. Roosting range for each season was calculated using a minimum convex polygon for individual bats with ≥3 roost trees.

We classified landscape characteristics within 2 buffers around used and random roosts. These buffers represent a localized landscape and a broader landscape. We chose a localized landscape buffer of 463 m because the average maximum distance traveled between roosts for all bats in this study was 463 ± 505 m. We chose a larger landscape buffer of 1000 m because this is close to the maximum distance travelled by individual bats in this study (excluding one outlier that travelled >1800 m) and has been used as a buffer in previous

studies (Perry et al. 2007). We quantified area of 4 landscape categories within each buffer: open space, freshwater, forest, and residential. Open space represented undeveloped areas without forest cover and was primarily composed of saltmarsh. Freshwater consisted of human-made retention ponds. Forest was a combination of the 3 forest classifications (pine, hardwood, and mixed hardwood-pine). Residential included neighborhoods and associated green spaces, including parks and small patches of trees.

Statistical analyses

Highly correlated variables (Spearman's correlation coefficient >|0.70|) were not included in the same model. Data were pooled across years, scaled, and centered before inclusion in analyses. Means are reported as ± 1 *SE* unless otherwise specified. All tests were 2-tailed, with alpha set at 0.05. Statistical analyses were performed in R version 4.2.2 (R Core Team 2022).

We developed additive, a priori models for the tree, plot, and landscape scales, based on our knowledge of the ecology of this species (Table 2). Models influencing selection of roost trees emphasized ability to find a roost tree (Ease of Discovery, ED), density of potential roosts (Roost Availability, RA), and the amount of clutter that would impede flight to the roost (Maneuverability, M), as well as all combinations of models, a global model, and a null model, for a total of 8 models. Similarly, the 8 models at the plot level included the ability to locate the plot around the roost (Plot Discovery, PD), abundance of alternative roosts (Potential Future Roosts, PFR), ease of mobility through the plot (Plot Maneuverability, PM), all combinations of these models, and global and null models. Landscape-level selection was modeled on proximity to resources, such as water and foraging corridors (i.e., roads and forest edges; Distance to Resources, DR), and area of surrounding habitat categories within the 463-m buffer (Near Landscape, NL) and the 1000-m buffer (Far Landscape, FL), as well as a global and null model.

Due to correlated variables in the landscape models, we used principal components analyses (PCA) on a variance/covariance matrix to create uncorrelated parameters. Continuous variables were standardized via *z*-scoring so they had the same scale and were dimensionless before PCA (Legendre and Legendre 1998). To aid interpretation, separate PCAs were conducted for each model (Distance to Resources, Near Landscape, and Far Landscape). All principal components

Table 2. Variables included in additive a priori models used in AIC.

Model	Variables
Tree	
Ease of Discovery	Tree height + Tree DBH + Flight space below tree
Roost Availability	Canopy diameter + Spanish Moss in tree
Maneuverability	Canopy closure + Nearest tree
Plot	
Plot Discovery	Mean canopy height + Plot DBH
Plot Maneuverability	Plot canopy closure + Basal area + Number trees + Flight space
Potential Future Roosts	Proportion pine + Spanish Moss in plot
Landscape	
Distance to Resources	PC scores Dist1+Dist2+Dist3+Dist4
Near Landscape	PC scores Near1+Near2+Near3+Near4
Far Landscape	PC scores Far1+Far2+Far3+Far4

were included in the models as covariates, regardless of eigenvalue, due to the ecological importance of components that do not contribute strongly to explanation of variance (Nichols 1977). PCA was completed using the 'psych' package in R.

We used logistic regression to assess selection at each spatial scale, with the binary response being either used or random points for fall and summer sites, or season (fall or summer) for used roosts. This resulted in 3 sets of model comparisons at each spatial scale (used vs. random roosts during fall, used vs. random roosts during summer, and used roosts in fall vs. summer). Models were evaluated using the Akaike Information Criterion corrected for small sample sizes (AICc). We calculated Akaike weights (ω_i) and deemed models ≤ 2 ΔAICc from the top model to be competing models (Burnham and Anderson 2002). Model fit was assessed using Nagelkerke's R^2. Predictive power of the top model was determined by 10-fold cross validation with 80% of the data used to train the model and 20% used to test the model.

We model-averaged parameter estimates and standard errors in top competing models to incorporate model uncertainty into our analyses and calculated 95% confidence intervals. We transformed model-averaged parameter estimates to odds ratios to aid in interpretation. For each parameter, we determined relative importance by summing Akaike weights from all models and examining confidence intervals that did not overlap 0. We repeated these steps for the 3 model sets at each spatial scale.

We used a Fisher's exact test to evaluate the effects of season and condition (used or random) on tree dominance class. Simple linear regressions determined whether tree height and DBH differed between random and used trees in both seasons. Because of the circular nature of roost aspect, we converted degrees to categories north, south, east, and west for analyses, and used a Fisher's exact test to determine whether aspect was significantly associated with season. We used Welch's 2-sample *t*-tests to assess the effect of season on roost height and roosting range. We compared the height and DBH of used trees to surrounding trees in the plot using simple linear regression. We compared tree species (with all non-pines combined into the category hardwood) of used versus random trees using a Pearson's c^2 test. We followed the same procedure to compare tree species of used trees in summer versus fall. A Fisher's exact test was used to evaluate whether season or condition influenced use of forest cover. Climatological data was obtained from the Hilton Head Island Airport weather station (National Oceanic and Atmospheric Administration 2023). We determined whether there was a significant difference in the average of hourly TA over a 24-h period between seasons using a Welch's 2-sample *t*-test.

We evaluated patterns in landscape parameters with a nonmetric multidimensional scaling (NMDS) analysis using Bray-Curtis similarity indices (Borcard et al. 2011, Legendre and Legendre 1998) within the 'vegan' package in R. NMDS orders sites hierarchically based on Bray-Curtis distances to locate the optimal position of *n* entities in *k*-dimensional space and creates a stress value. Stress measures the tradeoff between optimal arrangement of points in their original hierarchy, while reducing distortion with interpretability of the dataset (increased *k*-dimensions decreases stress, but increases difficulty in interpretation; Legendre and Legendre 1998). Final stress in our NMDS after 20 iterations was <0.20 with 2 dimensions, providing an adequate compromise between representation and interpretation of our data. We used the 'envfit' function to assess whether landscape characteristics were associated with NMDS ordination axes after 1000 permutations of the data, and represented these parameters as vectors for which length is proportional to the correlation. We determined parameters to be important if $r^2 \leq 0.50$. We used a permutational analysis of variance (PERMANOVA), based on 1000 permutations of the data via the 'adonis' function, to determine whether season explained a significant

amount of variation in the distance matrix. We repeated this step to determine if the selections of individual bats (BatID) explained significant variation.

Results

We caught and tracked 13 adult male Seminole Bats (fall = 8, summer = 5) to 64 roosts (fall = 42, summer = 22). Although we did not track females, we caught 15 adult female Seminole Bats during summer and zero female Seminole Bats (adult or juvenile) during fall. Males in both seasons switched roosts frequently, with individuals changing every 1.1 ± 0.1 days in both fall and summer. Mean number of roosting occasions was 5.3 ± 0.7 (range = 3–7) and 4.4 ± 1.3 (range = 1–7) for bats in fall and summer, respectively. Bats in both seasons roosted while clasping pinecones, clumps of pine needles, or the petioles of hardwood leaves (Fig. 1). Only 1 individual roosted in Spanish Moss in fall, and none did so in summer.

Summer roosting behavior

Fifty-four percent of roosts were in pine, 14% were in hickory, and 32% were unverified trees. All used trees were alive. Roost trees were taller ($R^2 = 0.36$, $F_{1, 34} = 18.96$, $P = 0.0001$) and had greater DBH ($R^2 = 0.12$, $F_{1, 34} = 4.70$, $P = 0.04$) than surrounding trees in the plot (Table 3). Used trees were taller ($R^2 = 0.06$, $F_{1, 106} = 6.72$, $P = 0.01$), but did not

Figure 1. Male Seminole Bats roosted while clasping pine needles (shown in both images to the left), pinecones, and leaf petioles during fall and summer 2020–2022 in Beaufort County, South Carolina.

have a greater DBH (R^2 = 0.001, $F_{1, 106}$ = 0.12, P = 0.73) than random trees (Fig. 2). There was no evidence of roost-tree selection in summer based on tree species ($c^2_{1, 42}$ = 9.4e-31, P = 1), and there was no difference in dominance class between used and random trees (P = 0.14). Codominant trees comprised 79% of used trees, 7% were intermediate, and 14% were subcanopy trees. No bats roosted in dominant trees. Although most roosts were in mixed hardwood-pine stands, there was no relationship between forest cover of roosts and what was available on the landscape (P = 0.17).

Ease of Discovery was the top model for selection at the tree level, with no competing models and an Akaike weight of 0.56, indicating a 56% chance that this was the best approximating model of all candidates (Table 4). The ED model correctly identified roost trees 57% of the time. Height was important, with individuals 15 times as likely to use a roost tree with every 1 m increase in tree height (Table 5; Fig. 2). The PD model was the only top model at the plot level, with an Akaike weight of 0.83; this model accurately predicted used plots 67% of the time. Mean canopy cover and plot DBH were important, with summer males 4.4 times as likely and 2.9 times as likely to use a plot with each 1 m increase in plot tree height and each 1 cm decrease in plot DBH, respectively. The null model was the top model at the landscape scale, with no competing models, indicating landscape components were not important predictors of roost-site selection.

Fall roosting behavior

Bats roosted in pine (43%), Sweetgum (7%), Spanish Moss on Live Oak (2%), and unverified trees (48%). All used trees were alive. Roost trees were taller (R^2 = 0.58, $F_{1, 63}$ = 88.52, P < 0.001) and with greater DBH (R^2 = 0.42, $F_{1, 63}$ = 45.38, P < 0.001) than surrounding trees in the plot (Table 3). Used roost trees were taller (R^2 = 0.06, $F_{1, 193}$ = 12.49, P < 0.001), but did not have greater DBH (R^2 = 0.002, $F_{1, 193}$ = 0.46, P = 0.49) than random trees (Fig. 2). Bats selected pine trees more frequently than expected given their availability ($c^2_{1, 69}$ = 5.54, P = 0.02). There was a difference in dominance class between used and random trees (P = 0.001), with 39% of roosts in dominant trees and 61% in codominant trees. No bats roosted in subcanopy or intermediate trees. Although most roosts were in mixed hardwood-pine stands, forest cover surrounding used roosts was similar to what was available (P = 0.68).

The top model for roost selection at the tree level was ED, followed by ED+RA as a competing model within 2 units ΔAICc (Table 4). The cumulative Akaike weight of these top competing models was 0.84. The ED model correctly identified roost trees 62% of the time. Tree height was important in model-averaged estimates with confidence intervals that did not overlap 0. Individuals were 4.7 times as likely to use a roost tree with every 1 m increase in tree height (Table 5; Fig. 2). Top models at the plot level included PD+PM, PD, and null, with a cumulative Akaike weight of 0.67. PD+PM accurately predicted used plots 71% of the time. Bats selected plots with fewer trees, with individuals 2.4 times as likely to use a plot with each 1 tree reduction. Far landscape and null were competing models at the landscape scale, with a combined Akaike weight of 0.74. Far Landscape correctly predicted used landscapes 67% of the time. The Far4 principal component, which corresponds with landscapes that have a large proportion of forest cover, was important, with individuals roosting in areas with more surrounding forest.

Comparison of roosting behavior between summer and fall

Average TA over a 24-h period during summer (26.3 ± 0.1 °C) was warmer than fall (21.7 ± 0.3 °C; t_{111} = -14.53, P < 0.001). There was an association between roost aspect and season (P < 0.001), with individuals more likely to roost on the south side of the tree

Table 3. Means and standard errors of continuous variables measured at male Seminole Bat roosts and associated random points during fall and summer 2020–2022 in Beaufort County, South Carolina. Parameter units are in Table 1.

	Fall males				Summer males			
	Roost		Random		Roost		Random	
Variable	Mean	*SE*	Mean	*SE*	Mean	*SE*	Mean	*SE*
Tree	*n* = 23		*n* = 46		*n* = 14		*n* = 28	
Roost height[a]	23.0[b]	0.9			23.8[c]	1.5		
Tree height	25.9	0.5	20.8	1.0	26.6	1.2	23.0	1.2
Tree DBH	48.6	2.7	46.4	5.1	40.6	3.2	42.2	3.5
Spanish Moss in tree	8.4	7.2	23.5	8.8	0.7	0.6	13.9	8.0
Canopy closure	78.1	3.1	79.6	3.4	79.9	7.5	81.3	4.7
Flight space below tree	1.0	0.9	10.9	1.0	15.3	1.9	12.9	1.3
Canopy diameter	12.0	0.8	11.1	0.9	9.4	0.6	10.0	1.0
Nearest tree	2.0	0.3	2.1	0.2	3.2	0.8	2.9	0.3
Plot	*n* = 42		*n* = 84		*n* = 22		*n* = 44	
Plot DBH	31.8	1.1	29.8	0.9	33.6	1.6	34.1	1.6
Basal area	1.1	0.2	1.0	0.1	0.8	0.1	0.9	0.1
Mean canopy height	17.9	0.6	16.1	0.5	20.8	0.8	18.1	0.8
Number trees	9.8	0.6	12.4	0.9	8.5	0.8	8.7	0.8
Proportion pine	42.5	4.2	37.6	3.2	65.7	5.4	50.7	5.3
Flight space	13.0	0.6	12.2	0.5	15.9	1.1	14.3	0.7
Plot canopy closure	83.1	1.8	84.1	1.9	81.0	4.4	84.8	2.6
Spanish Moss in plot	0.7	0.2	0.6	0.1	0.2	0.1	0.4	0.1
Landscape	*n* = 42		*n* = 84		*n* = 22		*n* = 44	
Distance to road	58.5	8.6	63.5	5.3	54.7	12.4	75.5	12.7
Distance to freshwater	171.7	14.2	200.1	15.0	212.4	54.3	247.3	48.1
Distance to edge	41.4	4.6	45.9	3.7	34.3	6.9	50.0	6.8
Distance to residential area	704.4	176.9	734.1	123.8	231.8	92.1	311.2	74.9
Near – Residential area	9.9	1.2	9.3	0.8	15.3	4.1	18.7	3.4
Near – Freshwater pond	3.4	1.4	1.4	0.3	0.4	0.3	0.4	0.2
Near – Open	35.2	2.7	37.6	1.8	28.5	2.8	29.3	2.1
Near – Forest	44.9	2.9	45.2	2.3	49.7	3.2	45.1	3.4
Far – Residential area	55.1	4.6	52.5	3.7	87.3	14.2	86.5	10.6

Table 3. Continued

Far – Freshwater pond	6.3	1.1	6.5	0.8	6.9	1.9	5.9	1.2
Far – Open	125.5	6.1	125.1	4.9	106.6	8.6	114.8	6.4
Far – Forest	254.3	10.2	253.2	7.8	236.9	14.2	229.9	14.0

[a] Only available when the bat could be identified in the tree.
[b] Fall males $n = 10$
[c] Summer males $n = 10$

during fall. There was no difference in roost height between summer (23.8 ± 1.5 m) and fall (23 ± 0.9 m; $t_{15} = -0.45$, $P = 0.66$; Table 3). There was no difference in roosting range between summer (3.1 ± 2.6 ha) and fall (1.9 ± 1.2 ha; $t_3 = -0.41$, $P = 0.71$). Season had an association with dominance class ($P = 0.002$), with bats more likely to roost in a dominant tree during fall. There was no relationship between season and species of used trees ($c^2_{1, 37} = 2.56e\text{-}31$, $P = 1$). Roosts used during fall were more likely to be in mixed hardwood-pine forests ($P = 0.03$). We found clustering of roost trees in both fall ($I = 0.60$, $z = 2.36$, $P = 0.02$) and summer ($I = 0.77$, $z = 2.14$, $P = 0.03$).

Top competing models comparing used trees between seasons included ED, ED+M, and RA, with a combined Akaike weight of 0.69 (Table 4). ED correctly identified roost trees to season 67% of the time. Tree DBH was an important predictor, with larger trees used during fall. For every 1 cm increase in DBH, a roost tree was 8.8 times as likely to be used in the fall than the summer (Table 5; Fig. 2). PD + PM and PFR were top competing models at the plot level, with a cumulative Akaike weight of 0.56. PD + PM correctly identified used plots to season 58% of the time. Flight space and proportion of pines were important parameters in top competing models, and both had a positive relationship with plots used in summer versus fall. For every 1 m increase in vertical distance and for every 1% increase in proportion of pines, plots were 2.8 and 2.3 times as likely to be used in summer, respectively. Use of landscapes between seasons was best predicted by the Near Landscape model, with an Akaike weight of 0.96. Our top model accurately predicted whether a landscape was used during fall or summer 83% of the time. Two principal components were important parameters in the model and both had a positive relationship with use during fall: Near3, which represents landscapes with a large availability of water, and Near4, which represents landscapes with a small amount of forest cover and open salt marsh.

The NMDS ordination had a final stress value of 0.12 with 2 dimensions (linear fit $R^2 = 0.96$). Season did not explain a significant amount of variation in ordination space (Permutation ANOVA, $F_{1, 62} = 1.95$, $R^2 = 0.03$, $P = 0.13$). Selection by individual bats explained 92% of the variation in ordination space (Permutation ANOVA, $F_{12, 51} = 48.01$, $R^2 = 0.92$, $P = 0.001$). Increased distance to residential areas and large amounts of freshwater and hardwood-pine forest at both near- and far-landscape scales were associated with roosts used during fall (Fig. 3). Summer roosts were associated with residential areas in both near and far landscapes.

Discussion

Seminole Bats in both seasons frequently switched roosts within a small area. This is consistent with previous research on male Seminole Bats (Hein et al. 2008a, b), as well as other foliage-roosting species, such as *Lasiurus borealis* (Müller) (Eastern Red Bat),

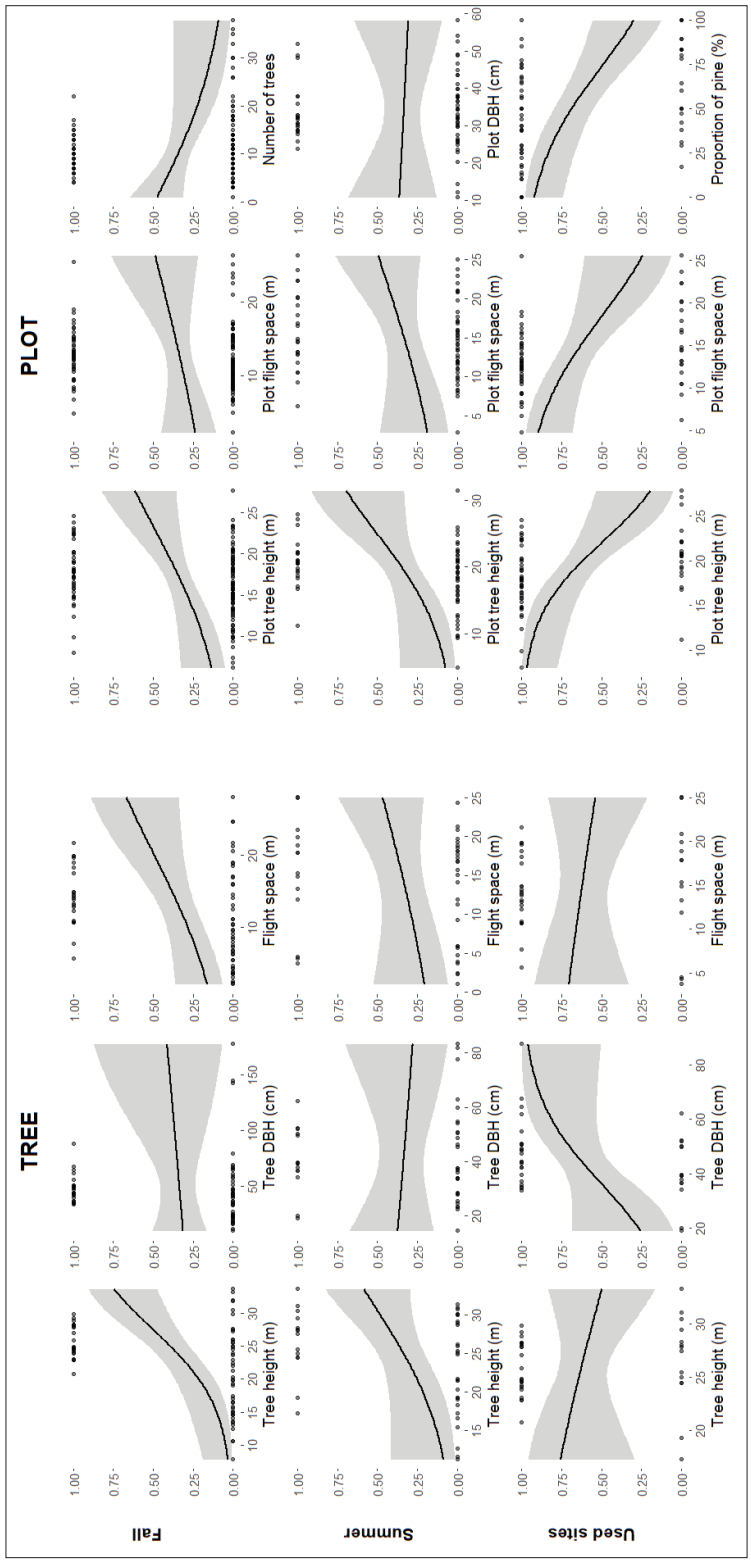

Figure 2. Probability plots showing use of sites during 2020–2022 in Beaufort County, South Carolina, by male Seminole Bats as a function of tree and plot characteristics. Binary response for fall and summer sites is 1 = used and 0 = random. Binary response for used sites is 1 = fall and 0 = summer. Dots represent binary samples. Shaded areas are 95% confidence intervals.

Table 4. Best approximating models for Seminole Bat roosts during fall and summer 2020–2022 in Beaufort County, South Carolina, as determined by the Akaike Information Criterion corrected for small samples (AIC_c). ω_i is the Akaike weight of the model. R^2 is Nagelkerke's pseudo- R^2. ED = Ease of Discovery. RA = Roost Availability. M = Maneuverability. PD = Plot Discovery. PM = Plot Maneuverability. PFR = Potential Future Roosts. NL = Near Landscape. FL = Far Landscape. DR = Distance to Resources. See text for description of models.

Model	K	ΔAIC_c	ω_i	R^2
Fall Males[a]				
Tree				
Ease of Discovery	4	0.00	0.52	0.25
ED+RA	6	1.04	0.31	0.31
ED+M	6	4.44	0.06	0.25
Plot				
PD+PM	7	0.00	0.30	0.15
Plot Discovery	3	0.38	0.25	0.06
Null	1	1.89	0.12	-3.08e-16
PM+PFR	7	2.02	0.11	0.13
Landscape				
Far Landscape	5	0.00	0.42	0.10
Null	1	0.52	0.32	-3.08e-16
NL+FL	9	2.42	0.13	0.16
Summer Males[a]				
Tree				
Ease of Discovery	4	0.00	0.56	0.30
Roost Availability	3	2.76	0.14	0.16
Plot				
Plot Discovery	3	0.00	0.83	0.21
PD+PFR	5	4.61	0.08	0.21
Landscape				
Null	1	0.00	0.84	0.00
NL+FL	9	5.52	0.06	0.26
Used Sites[b]				
Tree				
Ease of Discovery	4	0.00	0.31	0.32
ED+M	6	0.97	0.19	0.44
Roost Availability	3	1.06	0.19	0.21
RA+M	5	2.06	0.11	0.34
Plot				
PD+PM	7	0.00	0.41	0.41

Table 4. Continued.

Potential Future Roosts	3	1.96	0.15	0.22
PM+PFR	7	2.05	0.15	0.38
Landscape				
Near Landscape	5	0.00	0.96	0.50
DR+NL	9	6.90	0.03	0.55

[a] Used versus random sites
[b] Fall versus summer used sites

Perimyotis subflavus (F. Cuvier) (Tricolored Bat), and *Dasypterus intermedius* (H. Allen) (Northern Yellow Bat), which have low fidelity to individual roosts, yet high fidelity to a specific site (Castleberry et al. 2020; Menzel et al. 1998, 2000; Shute et al. 2021; Veilleux and Veilleux 2004). Although previous authors observed that low TA (below ~4 °C) decreases frequency of roost-switching (Hein et al. 2008b), TA did not drop below 14 °C during our study, potentially explaining continued roost-switching behavior during fall.

Roost trees were taller than surrounding trees within the plot in both seasons, which is consistent with other studies (Hein et al. 2008a, b; Menzel et al. 1998, 2000). Foliage-roosting species may select taller roost trees because they provide solar exposure for amenable thermoregulatory conditions, are easy to find and access, and provide increased protection from terrestrial predators (Castleberry et al. 2020, Hein et al. 2008b, Kalcounis-Rüppell et al. 2005, Perry and Thill 2007). However, height is not the only parameter worth considering. For example, roosts used were significantly more likely to be in dominant trees during fall than during summer, when 14% of roosts were in subcanopy trees. These subcanopy roosts were in a forest gap with a large amount of solar exposure and the bats roosted on the same side of the tree as the canopy gap. This indicates dominance class is less important than how it affects solar exposure, the resulting TA, and its effect on metabolic requirements of resting bats. This is similar to findings in Canada where reproductive female *Lasiurus cinereus* (Palisot de Beauvois) (Hoary Bat) did not roost in the tallest trees on the landscape, but did roost on the side of the tree with the least amount of surrounding clutter, resulting in more solar exposure and a warmer microclimate (Willis and Brigham 2005). Additionally, Seminole Bats were more likely to roost on the south side of a tree during fall than summer, consistent with roost aspect selected by male Seminole bats during winter in South Carolina (Hein et al. 2008a). However, other research shows there is no pattern in roost aspect used by Seminole Bats (Menzel et al. 1998, Perry and Thill 2007), and there are inconsistencies in roost aspect in a variety of foliage-roosting species (Carter and Menzel 2007).

Forest cover surrounding roosts differed between seasons. Summer roosts were primarily in pine stands, which is consistent with previous studies, while fall roosts were mostly in hardwood and mixed hardwood-pine stands. On Sapelo Island, Georgia, 88% of Seminole Bat roosts were in pine-dominated forests, even though 54% of the study area was hardwood forest (Menzel et al. 1998). Over 95% of roosts used by male Seminole Bats in Arkansas were in pine trees, despite pines constituting only 33% of random trees, leading researchers to conclude that this species is a pine-forest obligate (Perry and Thill 2007). Roosting in areas with a large amount of forest cover composed of semi-evergreen hardwood trees that retain leaves throughout the year could be beneficial when TA decreases, simply because the canopy is more cluttered, allowing heat retention below the canopy and reducing heat loss due to wind (Hein et al. 2008b).

Previous studies on foliage-roosting bats emphasize the selection of roosts with no vegetation directly below them, making it easier for bats to maneuver while approaching and departing the roost (Castleberry et al. 2020, Mager and Nelson 2001, Perry et al. 2007). Our study differed from previous studies in that flight space was not important in differentiating used versus random trees or plots in either season. However, flight space was important for distinguishing used plots between seasons, with fall plots having less flight space than summer plots. However, the top model differentiating fall and summer plots could correctly predict season only 58% of the time, and these results may more accurately reflect the type of forest cover surrounding roosts during each season. Less space between canopy and subcanopy is indicative of the forest cover surrounding fall roosts, which had more mixed hardwood-pine forests with many intermediate and subcanopy hardwood trees. Additionally, used plots during both seasons had a mean canopy height greater than random plots, perhaps suggesting bats select roosting areas that are easier to find.

Although patterns of landscape selection did not differ between used and random roosts during either season, we found that landscape-scale parameters influenced selection in used roosts between seasons. Used roosts during fall had a larger amount of water in the Near Landscape—but not the Far Landscape—compared to summer. Previous studies have shown evidence of bats roosting close to freshwater (Castleberry et al. 2020, Miles et al. 2006, Perry et al. 2008), and proximity to water within a smaller landscape buffer (i.e., Near

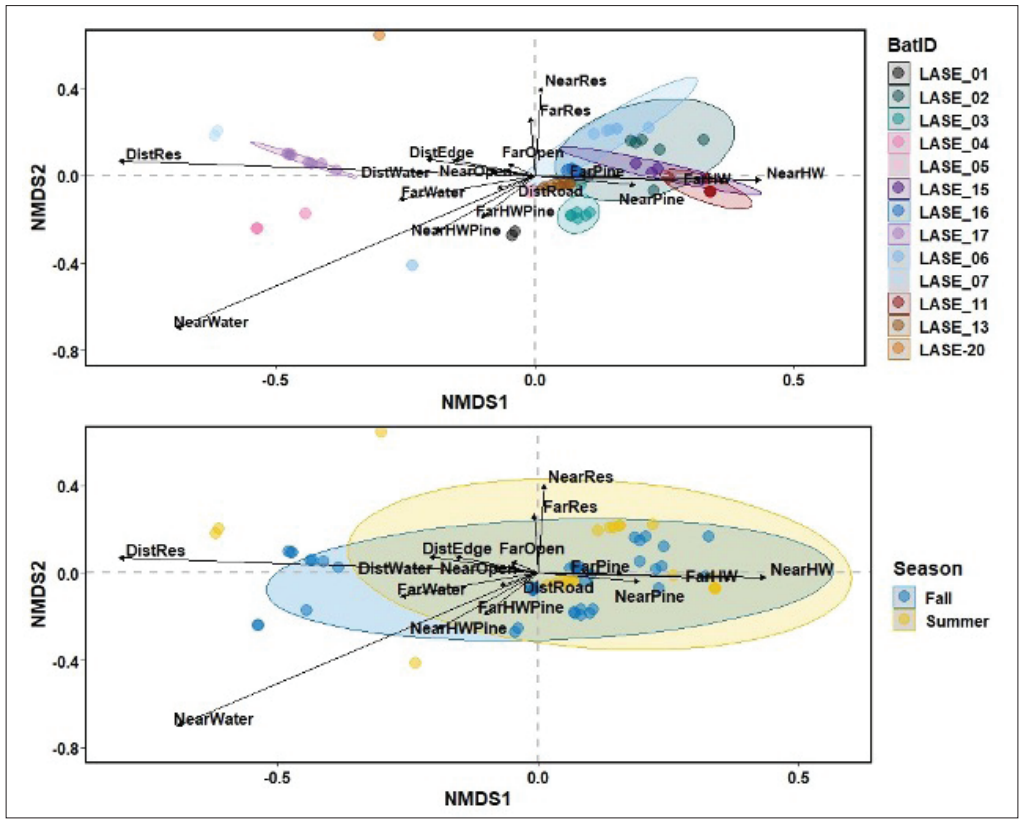

Figure 3. Non-metric multidimensional scaling of landscape characteristics of used roosts for Seminole Bats in summer and fall 2020–2022 in Beaufort County, South Carolina. Model parameters are displayed as vectors and roosts are color-coded by individual bat (top) and season (bottom). Ellipses represent 95% confidence intervals.

Table 5. Model-averaged estimates, unconditional standard errors, 95% confidence intervals, odds ratios, and summed Akaike weights ($\sum\omega_i$) of parameters included in top competing models evaluating Seminole Bat roosts in fall and summer 2020–2022 in Beaufort County, South Carolina.

Parameters	Coefficient Estimate	*SE*	Lower 95% *CI*	Upper 95% *CI*	$\sum\omega_i$	Odds Ratio
Fall Males[a]						
Tree						
Intercept	-0.91	0.31	-1.53	-0.30		
Tree height[b]	1.54	0.60	0.37	2.72	0.93	4.66
Tree DBH	-0.45	0.56	-1.54	0.64	0.93	0.64
Flight space below tree	-0.52	0.49	-1.48	0.44	0.93	0.59
Spanish Moss in tree	-0.89	0.61	-2.09	0.32	0.41	0.41
Canopy diameter	0.96	0.63	-0.27	2.19	0.41	2.61
Plot						
Intercept	-0.76	0.21	-1.17	-0.35		
Mean canopy height	0.55	0.30	-0.04	1.13	0.67	1.73
Plot DBH	-0.35	0.53	-1.39	0.68	0.67	0.70
Plot canopy closure	0.28	0.27	-0.25	0.80	0.57	1.32
Flight space	0.04	0.25	-0.44	0.52	0.57	1.04
Basal area	0.63	0.44	-0.22	1.49	0.57	1.88
Number trees[b]	-0.88	0.41	-1.68	-0.08	0.57	0.41
Landscape						
Intercept	-0.70	0.20	-1.09	-0.32		
Far1	0.14	0.41	-0.66	0.94	0.58	1.15
Far2	0.29	0.60	-0.88	1.46	0.58	1.34
Far3	-0.16	0.27	-0.69	0.38	0.58	0.85
Far4[b]	0.64	0.27	0.11	1.18	0.58	1.90
Summer Males[a]						
Tree						
Intercept	-1.39	1.01	-3.37	0.60		
Tree height[b]	2.71	1.11	0.54	4.87	0.73	15.03
Tree DBH	-1.74	1.02	-3.73	0.26	0.73	0.18
Flight space below tree	-1.16	0.68	-2.50	0.18	0.73	0.31
Plot						
Intercept	-0.89	0.32	-1.51	-0.27		
Mean canopy height[b]	1.49	0.57	0.38	2.61	0.94	4.44
Plot DBH[b]	-1.07	0.51	-2.07	-0.07	0.94	0.34
Landscape						
Intercept	-0.71	0.27	-1.24	-0.18		

Table 5. Continued.

Used Sites[c]						
Tree						
Intercept	0.95	0.66	-0.35	2.25		
Tree height	-1.39	0.76	-2.88	0.1	0.55	0.25
Tree DBH[b]	2.17	1.00	0.20	4.14	0.55	8.76
Flight space below tree	-0.08	0.50	-1.05	0.90	0.55	0.92
Spanish Moss in tree	2.82	4.38	-5.76	11.40	0.34	16.78
Canopy diameter	1.04	0.65	-0.22	2.31	0.34	2.83
Nearest tree	-1.03	0.54	-2.10	0.03	0.39	0.36
Canopy closure	-0.82	0.57	-1.95	0.30	0.39	0.44
Plot						
Intercept	1.35	0.64	0.10	2.60		
Mean canopy height	-0.26	0.76	-1.75	1.23	0.68	0.77
Plot DBH	-1.84	1.72	-5.22	1.54	0.68	0.16
Plot canopy closure	-0.78	0.47	-1.70	0.13	0.68	0.46
Flight space[b]	-1.01	0.45	-1.89	-0.14	0.68	0.36
Basal area	6.28	3.97	-1.51	14.07	0.68	533.79
Number trees	-1.85	1.41	-4.62	0.92	0.68	0.16
Spanish Moss in plot	0.36	0.55	-0.73	1.45	0.47	1.43
Proportion pine[b]	-0.83	0.42	-0.01	-1.65	0.47	0.44
Landscape						
Intercept	0.90	0.42	0.17	2.11		
Near1	-0.27	0.35	-0.95	0.61	0.99	0.76
Near2	0.70	0.53	-0.62	2.13	0.99	2.01
Near3[b]	1.48	1.01	0.43	5.42	0.99	4.39
Near4[b]	1.92	0.58	0.94	3.23	0.99	6.82

[a] Used versus random sites; random is reference
[b] Indicates important parameters where the confidence interval does not overlap 0
[c] Fall versus summer used sites; summer is reference

vs Far) may be more important during colder months when bats are only active for brief periods each night and are presumably not traveling far from roosts.

Selection may be made at multiple levels, depending on availability of resources at each scale, resulting in a hierarchy of selection. Frequently switching roosts within the same landscape may indicate that roost selection is made at the stand or landscape scale instead of the tree (Hein et al. 2008a). Alternatively, frequent roost switching could indicate that bats are selecting areas that have abundant potential roosts that meet specific criteria, suggesting that tree characteristics are still being selected (Lewis 1995, Shute et al. 2021). Low roost fidelity and high site fidelity may be due to the lack of a constraint on where bats can roost, assuming there are several equally ideal roosts in the same area (Lewis 1995). If future potential roosts are ubiquitous and are not a limiting factor, bats can select roosts based on ideal landscape-

level characteristics, such as proximity to drinking water or foraging areas, resulting in a hierarchy of selection (i.e., landscape first and then roost; Shute et al. 2021). Previous research on landscapes with and without abundant roosts found that bats made selections at the landscape scale when roosts were abundant and at the tree scale when roosts were infrequent or clustered, forcing a tradeoff between using an ideal roost tree and increased commuting time to water and foraging corridors (Castleberry et al. 2020, Miles et al. 2006).

Distribution and abundance of roosts is influenced by urbanization's effect on size and connectivity of forest patches. Increased urbanization leads to increased habitat loss and degradation, resulting in altered roosting behavior. For example, Eastern Red Bats in a fragmented, developed landscape in Illinois had a home range of 90 ha (Mager and Nelson 2001), but only 2.6 ha in the forested South Carolina Coastal Plain (Menzel et al. 1998), indicating bats have to travel farther to acquire enough resources to meet their needs within a fragmented landscape (Mager and Nelson 2001). Urbanization in the Southeast is projected to increase 101–192% by 2060 (Terando et al. 2014) with subsequent habitat loss and fragmentation. However, development could occur in a way that mitigates or minimizes impacts to foliage-roosting species, such as retaining forest patches, preserving tall trees, and providing corridors that facilitate movement between forest patches (Hein et al. 2008a). There may be a species-specific minimum threshold in forest patch size, as well as adequate connectivity between patches, that is required for these forest patches to be effective. Small, isolated forest patches may look suitable, but not serve the same ecological function as connected forests of appropriate size (Dobson et al. 1999, Lovejoy et al. 1986). Seminole Bats are a common species in the South Carolina Coastal Plain, yet there is a dearth of knowledge about foliage-roosting bats despite evidence that their populations are in decline (Carter and Menzel 2007, COSEWIC 2023). It is unclear how further habitat loss and the introduction of wind farms into this species' range will impact population stability. At a minimum, understanding nuances of how Seminole bats select roosts is requisite to developing species-specific management strategies.

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