Summer Roosting Ecology of the Northern Yellow Bat and Tri-colored Bat in Coastal South Carolina

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Abstract - *Lasiurus intermedius* (Northern Yellow Bat) and *Perimyotis subflavus* (Tri-colored Bat) are species of conservation concern in South Carolina and are threatened by loss of roosting habitat. To better understand summer roost selection, we radio-tracked individuals to roost trees during May through August of 2018 and 2019. We characterized roost trees, sites surrounding roost trees, and unused but available trees for each roost occasion. We used discrete-choice models to test hypotheses of factors influencing roost-site selection. Tri-colored Bats used foliage and *Tillandsia usneoides* (Spanish Moss) in hardwood trees and selected trees with high densities of Spanish Moss. Northern Yellow Bats used dead palm fronds in *Sabal palmetto* (Cabbage Palm Trees) or Spanish Moss in trees with high densities of Spanish Moss. Our results suggest that conservation of maritime and bottomland forests with trees that have high densities of important roost structures like Spanish Moss and dead palm fronds would benefit these species.

Introduction

Diurnal roosts are particularly important for tree-roosting bats because they provide protection from predators and adverse environmental conditions and sites for rearing offspring during the summer reproductive period (Carter and Menzel 2007). Use of roost structures varies by species of bat, but roosts may occur in foliage, bark of live or dead trees, and tree cavities (Kunz and Lumsden 2003). Tree-roosting bats select roost trees based on structural and landscape characteristics that meet their ecological needs (Kalcounis-Rüppell et al. 2005). Structural characteristics include roost-tree diameter and decay status, canopy closure at the site, surrounding stand characteristics, and density of vegetative clutter around the roost (Carter and Menzel 2007, Lacki and Baker 2003), while landscape characteristics include proximity to water, density of surrounding roost structures, and proximity to foraging areas (Kalcounis-Rüppell et al. 2005, Lacki and Baker 2003). Individuals commonly switch roosts, possibly in response to changes in microclimate, roost availability, and to avoid predators and parasites (Lausen and Barclay 2002, Lewis 1995). Thus, an abundance of potential roosts that meet the needs of a species is important to manage populations.

Forest loss, and the consequent loss of roost trees, is a major conservation threat to bats and results from clear cutting, agricultural expansion, urbanization, and weather events intensified by climate change (Frick et al. 2020). Loss of forests due to human activity coupled with increasing intensity of storm events (e.g.,

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hurricanes) due to climate change (Knutson et al. 2015, Ting et al. 2019) will likely result in an increased loss of roost trees. Loss of forests due to disturbances results in a matrix of varying quality in availability of habitat, separating animals from resources and in some cases leading to direct mortality (McKinney 2008, Russell et al. 2009). Loss of available tree cover also reduces the number of potential roosts that meet the needs of individual bat species, disproportionately impacting habitat specialists that rely on specific roost structures and leading to changes in roost selection (Loeb 2017). Changes in selectivity may cause bats to use suboptimal roosts, potentially leading to decreased fitness, increased exposure to predators, and increased energy expenditure (Chaverri and Kunz 2011, Vlaschenko et al. 2019). The southeastern US in particular is threatened by forest loss due to human disturbance as it is projected to have one of the largest urban expansions in the country (Terando et al. 2014). Given the cascading effects of potential roost loss, southeastern bat species are at risk of losing critical habitat in the region.

Lasiurus intermedius H. Allen (Northern Yellow Bat) and *Perimyotis subflavus* (F. Cuvier) (Tri-colored Bat) are both species of special concern that occur in the Coastal Plain of the southeastern United States. Tri-colored Bats are foliage roosters during summer, roosting in dead hardwood leaves, pine needles, and *Tillandsia usneoides* (L.) L. (Spanish Moss; Menzel et al. 1999, O'Keefe et al. 2009, Perry and Thill 2007, Veilleux et al. 2003). In Nova Scotia, individuals select trees and sites with higher densities of the non-tree foliage structure *Usnea trichodea* Ach. (Beard Lichen; Poissant et al. 2010). Information on the roosting ecology of the Tri-colored Bat in the southeastern Coastal Plain is limited, with only 1 published account of roost use by 1 individual (Menzel et al. 1999). The Tri-colored Bat has also experienced declines in populations due to white-nose syndrome, a disease caused by the fungus *Pseudogymnoascus destructans* (Blehert and Gargas) Minnis & D.L. Lindner. These declines have resulted in a proposal for listing of the species under the Endangered Species Act (USFWS 2017). However, white-nose syndrome is not present in the Coastal Plain, and thus, this area may serve as a refugium for the species.

The Northern Yellow Bat is relatively understudied throughout its range, with few studies documenting roost use (Coleman et al. 2012, Constantine 1958, Hutchinson 2006, Menzel et al. 1999, Socci et al. 2017). Northern Yellow Bats are associated with coastal maritime forests and roost in dead *Sabal palmetto* (Walter) Lodd. ex Schult. & Schult. f. (Cabbage Palm) fronds and Spanish Moss in the canopy of mixed hardwood trees such as *Quercus* spp. (oak) and *Nyssa* spp. (tupelo) (Castleberry et al. 2020, Coleman et al. 2012, Menzel et al. 1999, Socci et al. 2017). Castleberry et al. (2020), who conducted the only published study on roost selection for this species, found that male Northern Yellow Bats select roosts in large trees with low surrounding clutter, as well as sites that are close to freshwater.

Because Tri-colored Bats and Northern Yellow Bats face habitat-conservation threats in the Coastal Plain, retention of important summer-roost habitat that facilitates survival and rearing of young is crucial to their persistence on the landscape. Thus, understanding summer-roost selection of these 2 species is important

for conservation and management. Our objective was to determine summer-roost selection at the home-range scale for both species in coastal South Carolina. We hypothesized that roost selection would vary for these 2 species of bats but would be influenced by similar covariates associated with individual tree characteristics such as roost availability, tree permanence, and protection from environmental conditions. Additionally, we hypothesized that roost selection would be influenced by covariates associated with the forest stands and surrounding landscape including ease of movement around the roost, surrounding forest-cover type (e.g., maritime forest, bottomland forest), landscape characteristics, and anthropogenic disturbance (Tables 1, 2).

Our first set of hypotheses related to characteristics of individual roost trees. We predicted Tri-colored Bats would select oaks (Menzel et al. 1999, Veilleux et al. 2003) and Northern Yellow Bats would select oaks and palm trees (Castleberry et al. 2020, Menzel et al. 1999). We also predicted that roost trees selected by Tri-colored Bats and Northern Yellow Bats would have high densities of potential roosting structures such as Spanish Moss and dead palm fronds (Castleberry et al. 2020, Poissant et al. 2010). Because of the importance of roosts in providing protection from the wind and rain, we predicted that both species would select live roost trees that were subdominant to the canopy for protection from wind and rain,

Table 1. Additive a priori models, covariates, and citations for Tri-colored Bat summer roost selection at study areas in Bluffton, SC, 2018 and 2019.

Model	Model Makeup	Citation
Roost-structure availability	Roost tree category Spanish moss density	Veilleux et al. 2003 Menzel et al. 1999
Forest type	Forest type	Perry et al. 2008
Tree permanence and environmental protection	Tree dominance Roost tree dbh Distance to nearest taller tree Canopy closure	Veilleux et al. 2003 Castleberry et al. 2020 Veilleux et al. 2003 Perry and Thill 2007
Movement ability	Midstory stem density Overstory basal area Overstory stem density	Veilleux et al. 2003 Perry and Thill 2007 Perry and Thill 2007
Landscape resources	Distance to freshwater Distance to edge	Veilleux et al. 2004 O'Keefe et al. 2009
Anthropogenic disturbance	Distance to residential cover Distance to roads	Moretto and Francis 2017 O'Keefe et al. 2009
Subglobal roost characteristics	Combination of models: roost structure availability, thermoregulation and tree permanence, and movement ability	
Subglobal landscape characteristics	Combination of models: landscape resources and anthropogenic disturbance	

but also had less canopy closure to provide solar exposure, easing thermoregulatory costs (Coleman et al. 2012, Perry and Thill 2007).

Our next hypotheses were based on various characteristics of the surrounding forest stands and landscape. At the plot scale, we predicted that Northern Yellow Bats would select roost trees with low midstory stem density that allowed ease of access when entering and exiting the roost, but that Tri-colored Bats would use trees with high midstory stem density in the surrounding plot because it is a clutter-tolerant species (Castleberry et al. 2020, Perry and Thill 2007). We also predicted that the Northern Yellow Bat and Tri-colored Bat would select trees within maritime forests (Castleberry et al. 2020, Menzel et al. 1999) and that Tri-colored Bats would additionally select trees within bottomland forests (Menzel et al. 1999). Access to resources like food and water that are spread across the landscape are important to both species. Thus, we predicted both would select roosts close to features such as freshwater, foraging areas, and roads for commuting (Castleberry et al. 2020, O'Keefe et al. 2009, Veilleux et al. 2004). Finally, we predicted that Northern Yellow Bats would roost at sites away from human development because of disturbance and fewer potential roosts in such areas (Moretto and Francis 2017). Although Tri-colored Bats use buildings in the prematernity period, once they transition to the maternity season, they shift to tree roosts (Whitaker et al. 2014). This pattern suggests that Tri-colored

Table 2. Additive a priori models, covariates, and citations for Northern Yellow Bat summer roost selection at study areas in Bluffton, SC, 2018 and 2019.

Model	Model Makeup	Citation
Roost structure availability	Roost tree category	Castleberry et al. 2020
	Roost structure density	Menzel et al. 1999
Forest type	Forest type	Castleberry et al. 2020
Tree permanence and environmental Protection	Tree Dominance	Castleberry et al. 2020
	Roost Tree DBH	Coleman et al. 2012
	Canopy Closure	Castleberry et al. 2020
Movement ability	Midstory stem density	Castleberry et al. 2020
	Overstory basal area	Castleberry et al. 2020
	Overstory stem density	Coleman et al. 2012
Landscape resources	Distance to freshwater	Castleberry et al. 2020
	Distance to edge	Castleberry et al. 2020
	Distance to salt marsh	Castleberry et al. 2020
Anthropogenic disturbance	Distance to residential cover	Moretto and Francis 2017
	Distance to roads	Perry et al. 2008
Subglobal roost characteristics	Combination of models: roost structure availability, thermoregulation and tree permanence, and movement ability	
Subglobal landscape characteristics	Combination of models: landscape resources and anthropogenic disturbance	

bats avoid human disturbance during the pup-rearing period, and we therefore predicted they would also roost away from development. Results of this study will help provide a better understanding of roosting requirements and will inform land managers about critical habitat features for these species.

Field- Site Description

We conducted this study at 3 sites in the southern Coastal Plain of Beaufort County, SC: Palmetto Bluff, Pickney Island National Wildlife Refuge, and Victoria Bluff Heritage Preserve (Fig. 1). During the survey period (May–August) the average temperature was 26.2 °C with an average total precipitation of 52 cm (20-year average; NOAA 2020). Palmetto Bluff (8093 ha) is a multi-use property made up of scattered suburban development, golf courses, maintained fields, freshwater ponds, undeveloped land, and areas under conservation easement (132 ha). Forests were predominantly upland including *Pinus* (pine)-dominated forests, mixed pine–hardwood forests, and maritime forest, with patches of bottomland forest. Victoria Bluff (470 ha) is an undeveloped state heritage preserve bordered by a suburban housing development and salt marsh. Dominant forest types at this site were bottomland hardwood and mixed hardwood–pine forests. Pinckney Island is a National Wildlife Refuge (1640 ha) surrounded entirely by salt marsh and in proximity to
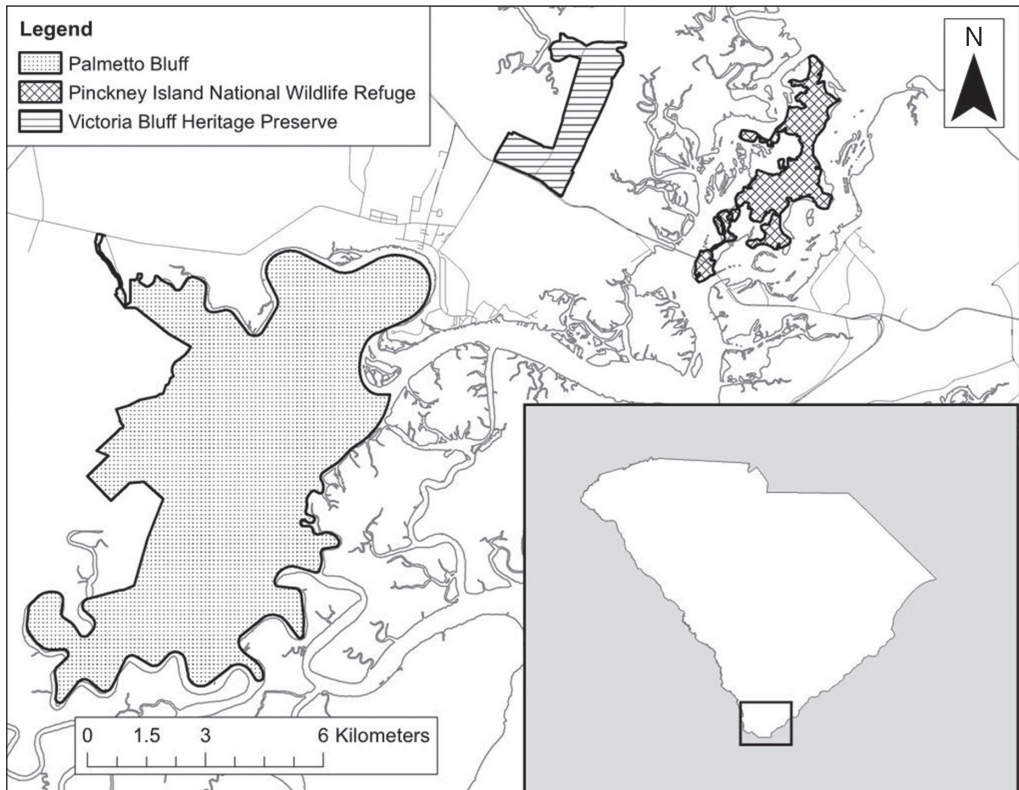

Figure 1. Map of 3 sites where Northern Yellow Bats and Tri-colored Bats were captured and tracked in Bluffton, SC, 2018 and 2019.

suburban development on the adjacent Hilton Head Island. Maritime forests made up most of the forest cover at this site with patches of bottomland forest, fields, and ponds across the island.

Methods

Bat capture

We captured bats in mist-nets from May to August 2018 and 2019 on Palmetto Bluff, Victoria Bluff Heritage Preserve, and Pinckney Island National Wildlife Refuge. In 2018, we placed triple-high nets along flight corridors including closed-canopy roads, trails, and ephemeral wetlands. In 2019, we used the same triple-high set up and opportunistically placed double-high mist-net sets when possible. We used 38-mm polysester mist-nets that were 6 m, 9 m, or 12 m wide by 2.6 m tall (Avinet Research Supplies, Portland, ME) and selected sites based on previous capture records to increase the probability of capturing the target species. We opened nets 10 minutes after sunset and kept them open for at least 4 hours unless inclement weather prevented netting. We checked nets every 8–10 minutes and recorded species, sex, age class (adult or juvenile based on knuckle joint ossification; Anthony 1988), reproductive condition (Racey 1988), injury, mass, forearm length, and presence of any parasites for each bat captured. We banded all individuals with the exception of bats that appeared highly stressed or injured, and affixed radio transmitters to the interscapular region of Tri-colored Bats during 2019 and Northern Yellow Bats during 2018 and 2019. We used 0.27 g LB-2X 7-day transmitters on Tri-colored Bats and 0.52 g LB-2 21-day transmitters on Northern Yellow Bats (Holohil Systems, Carp, ON, Canada). We trimmed fur and cleaned the area with alcohol, then used surgical adhesive (OSTO-BOND, Montreal Ostomy, Montreal, QC, Canada) to attach the transmitter. Transmitters were ≤5% of bat body mass, and all handling and tagging procedures were conducted in accordance with the American Society of Mammalogists' guidelines (Sikes 2016) and approved by the Clemson University IACUC (#2017-072) and US Forest Service IACUC (#2018-002).

Bat tracking

On the day following radio-tagging and all subsequent days, we attempted to track individuals to their roost tree using a radio receiver (Trx-2000; Wildlife Materials, Murphysboro, IL) and 3-element, 5-element, and unidirectional antennae. We stopped looking for an individual if we could not detect it for 5 days. If a roost was located on private property, we gained permission from the landowner to access their property. We marked each roost tree and recorded its location using a Trimble GeoExplorer 2008 Series Global Positioning System unit (Trimble, Inc., Sunnyvale, CA) and attempted to visually confirm the roost structure. When we could not visually confirm a roost, we determined the most likely roost tree and conducted emergence surveys, when possible, to locate the roost structure. Although we did not visually confirm the structure on every roost occasion, we only included roost trees that we were confident the bat was in based on radio-telemetry signals.

Tree characterization

To characterize roost trees, we identified each roost tree to species, measured the diameter at breast height (DBH), tree height, and determined its canopy position (above or below canopy) (Kalcounis-Rueppell et al. 2005). For analysis, we grouped roost-tree species into categories based on similar structural characteristics (pines, oaks*,* and other for Tri-colored Bats and oaks, Cabbage Palm, and other for Northern Yellow Bats). At each tree, we established a transect along a randomly selected bearing from one edge of the roost-tree canopy to the opposite edge, intersecting the middle of the plot. We measured canopy diameter along this transect and counted number of dead palm fronds on the tree and Spanish Moss clumps that intersected the transect and were estimated to be large enough to conceal a roosting bat based on average size of the target species (Tri-colored Bat: 85.1 mm, Northern Yellow Bat: 126.8 mm; Menzel et al. 2003). We calculated density of roost structures per meter by taking the total number of dead palm fronds or Spanish Moss divided by the diameter of the canopy. To characterize surrounding plot features, we created a 0.05-ha (radius = 12.5 m) circular plot around each roost tree and measured DBH of all trees ≥10 cm DBH and identified each to genus. Additionally, we measured canopy closure at the roost tree and 6 m from the tree in each cardinal direction using a spherical densiometer (Model-A; Forest Densiometers, Forestry Suppliers Inc., Jackson, MS) and averaged these to obtain a canopy-closure value for the plot. We also measured distance to nearest tree and distance to nearest tree taller than the roost tree (Kalcounis-Rüppell et al. 2005). To characterize midstory stem density, we established a 25-m transect through the plot center along the same randomly selected bearing as used to quantify Spanish Moss and counted all stems ≥4 cm DBH and <10 cm DBH within 1 m of either side of the transect. We used ArcMap (10.5.1) to calculate distance between subsequent roosts, distance to the nearest freshwater pond, distance to the nearest road (paved or unpaved), distance to salt marsh, distance to forest edge, distance to residential area, and forest cover type based on the SCGAP raster (SCDNR 2001). Even though this is an older database, we used it because, when checked with actual forest characteristics, it more accurately classified observed land-cover types compared to other databases. Specifically, it provided more accurate representation of forest-stand types that were grouped together or merged into 1 type in larger databases like the National Land Cover Database.

Defining availability

In order to assess availability and compare it to use, we used ArcMap to create a buffer around each roost tree with a radius equal to either the farthest distance an individual of the species moved between roosts or from the capture site to first roost tree, whichever was greater (Northern Yellow Bat radius = 1.08 km and Tri-colored Bat radius = 4.25 km). This method gave us an estimate of the area potentially available to a bat during nightly movement. We took this approach because of limited information on home-range size or nightly movements of these species in this region. Within each buffer, we generated 10 random points using the ArcMap

extension Alaska Pak version 3.0.0 (NPS 2010). For each roosting occasion (i.e., day that a bat used a tree), we selected 2 random trees (1:2). To select these trees, we randomly ordered the available points and selected the first 2 points. If more than 1 roosting occasion occurred at a tree, we progressively selected 2 random points until we had chosen enough available trees for the number of roosting occasions. When random points fell in salt marshes or ponds where there were no trees, we removed the point and used the next one. At each selected random point, we searched for the closest available tree to the point (usually within 10 m) and collected all habitat measurements outlined above for the used roost tree. For Northern Yellow Bats, we defined available trees as (1) live broadleaved hardwood trees ≥10 cm DBH that possessed at least 1 clump of Spanish Moss, and (2) live cabbage palm trees ≥6 m in height that possessed at least 1 dead frond. For Tri-colored Bats, we defined available trees as (1) live hardwood trees ≥10 cm DBH that possessed Spanish Moss, and (2) live pine trees ≥10 cm DBH that possessed Spanish Moss or dead clusters of leaves. If a random tree did not meet these criteria, we did not include it as available and instead selected the next nearest tree to evaluate. We based these criteria for available trees on previous literature (Castleberry et al. 2020, Coleman et al. 2012, Menzel et al. 1999, Socci et al. 2017, Veilleaux et al. 2003) and observed use at our study area.

Analysis

From potentially important factors mentioned in previous literature, we developed 6 additive a priori models based on roost availability, forest cover type, tree permanence and protection from environmental conditions, movement ability around the roost, surrounding landscape resources, and anthropogenic disturbance to assess roost selection by Tri-colored Bats (Table 1) and Northern Yellow Bats (Table 2). We also fit a sub-global roost-characteristics model and sub-global landscape-characteristics model for both species, as global models were overparameterized and did not converge. We scaled all continuous covariates prior to analysis and screened for correlation. To analyze our data, we used discrete-choice models in R package 'mlogit' (Version 1.1-1; Croissant 2019) where response variables were choice sets made up of 1 used tree and 2 available trees for each choice event. We ranked models using Akaike's information criterion corrected for small sample size (AIC_c) to assess relative support for our models and to account for the small sample size of our study. We defined the confidence set of top models as those with $\Delta AIC_c \leq 4$, and only discuss those models because models have considerably less support at higher ΔAIC_c values (Burnham and Anderson 2002). We defined important covariates by 85% confidence intervals that did not overlap zero (Arnold 2010). Following this step, we used our top model for each species to conduct 10-fold cross validation using 80% of our data to train the model and the remaining 20% to test the model (Boyce et al. 2002). We present the proportion of test-data choice sets for which the model correctly identified the used tree, where 1.0 indicates perfect performance of the model and 0.50 indicates that the model performed no better than random. We used Program R (Version 3.6.2; https://www.R-project.org) for all analyses and present descriptive statistics as mean ± SD.

Results

We mist-netted 32 nights in 2018 and 26 nights in 2019. In 2018, we captured 170 bats: 46 Tri-colored Bats, 41 *Nycticeius humeralis* (Rafinesque) (Evening Bat), 39 *Lasiurus seminolus* (Rhoads) (Seminole Bat), 29 *Eptesicus fuscus* (Palisot de Beauvois) (Big Brown Bat), 8 *L. borealis* (Müller) (Eastern Red Bat), 5 *Myotis austroriparius* (Rhoads) (Southeastern Myotis), 1 *M. septentrionalis* (Trouessart) (Northern Long-eared Bat), and 1 Northern Yellow Bat. In 2019, we captured 151 bats: 36 Tri-colored Bats, 35 Evening Bats, 32 Seminole Bats, 32 Big Brown Bats, 6 Eastern Red Bats, 5 Northern Yellow Bats, 3 Northern Long-eared Bats, and 2 Southeastern Myotis.

We radio-tagged and tracked 7 Tri-colored Bats (1 juvenile female, 2 juvenile males, 3 non- reproductive adult females, and 1 adult male) for an average of 4.5 ± 2.5 days (min–max = 1–9). Although we captured the most individuals of this species, we were unable to tag more because they were not added to the research objectives until the second year of the study, and due to limited transmitter availability. Five individuals were captured and tracked at Palmetto Bluff and 2 at Pinckney Island National Wildlife Refuge. We tracked bats to 25 roost trees (3.8 ± 2.3 roost trees per bat, min–max = 1–8). Tri-colored Bats spent 1.3 ± 0.5 days (min–max = 1–3) in a roost and average distance between subsequent roosts was 107 ± 84 m (min–max = 6–294 m). All roost trees were live, and species used were *Liquidambar styraciflua* L. (Sweetgum; *n* = 7), *Quercus virginiana* Miller (Southern Live Oak; *n* = 7), *Celtis laevigata* Willdenow (Sugar Hackberry; *n* = 3), *Q. laurifolia* Michaux (Laurel Oak; *n* = 2), *Q. nigra* L. (Water Oak; *n* = 2), *Acer rubrum* L. (Red Maple; *n* = 1), *Magnolia grandiflora* L. (Southern Magnolia; *n* = 1), *M. virginiana* L. (Sweetbay Magnolia; *n* = 1), and *Pinus taeda* L. (Loblolly Pine; *n* = 1). The average Tri-colored Bat roost tree was a relatively large (52.4 ± 6.7 cm) hardwood tree in hardwood-dominated stands with a high degree of canopy closure (85%; 1.2 times higher than available) (Table 3). Distances to landscape features were highly variable. Compared to roosts, available trees were on average 1.1 times farther from water and residential cover and 1.4 times farther from roads. We visually confirmed use of Spanish Moss and dead foliage roosts for this species and did not find evidence that Tri-colored Bats used roosts other than foliage. Of the 25 roosts, we confirmed that 13 were in Spanish Moss and 2 were in dead foliage, whereas 9 were in unidentified roosts that we presumed were Spanish Moss because of high density of Spanish Moss on the tree and the absence of other apparent roost structures, and 1 roost was in unknown foliage (presumed dead foliage). For all individuals that we visually observed, bats were roosting alone.

We modeled Tri-colored Bat roost-tree selection from 32 choice sets. The roost-structure–availability model was the top model and carried 94% of model weight (Table 4). Important covariates in this model were pines and Spanish Moss density (Table 5). Relative probability of selection was negatively related to pines and positively related to Spanish Moss density (Fig. 2a). The proportion of test cases where the model correctly identified the true roost was 0.83.

Table 3. Mean and standard deviations (SD) of characteristics of summer roost trees used by Tri-colored Bats (2019) and Northern Yellow Bats (2018 and 2019) in Bluffton, SC.

Covariate	Tri-colored Bat		Northern Yellow Bat	
	Mean	SD	Mean	SD
Tree height (m)	19.3	6.7	14.3	4.8
Distance to nearest taller tree	5.8	3.5	5.5	3.1
DBH (cm)	52.4	21.3	44.8	25.1
Canopy closure (%)	85	8	88	7
Site basal area (m^2)	1.8	0.7	1.8	0.6
Overstory stem count (# of stems)	14.4	8.2	17.7	7.7
Spanish moss density (structure/m)	1.4	1.1	1.7	1.0
Midstory stem density (# of stems)	2.7	2.3	2.0	1.7
Distance to freshwater (m)	475.9	243.9	282.3	230.8
Distance to road (m)	135.2	94.0	246.9	167.0
Distance to residential cover (m)	766.4	507.9	99.8	127.3
Distance to salt marsh (m)	-	-	196.5	156.5
Distance to hard edge (m)	89.5	63.9	72.8	63.8
Proportion pine in surrounding plot	0.24	0.28	0.34	0.28
Proportion oak in surrounding plot	0.43	0.33	0.34	0.28
Proportion other in surrounding plot	0.33	0.22	0.22	0.24
Proportion Cabbage Palm in surrounding plot	-	-	0.10	0.24

Table 4. Discrete choice models, number of parameters (K), model Log liklihood, Akaike's information criterion corrected for small sample size (AICc), difference between model AICc and lowest AICc value (ΔAICc), model weight, and cumulative model weight of summer roost selection models for Tri-colored Bats (2019) and Northern Yellow Bats (2018 and 2019) in Bluffton, SC.

Model	K	Log Likelihood	AICc	ΔAICc	Weight	Cumulative weight
Tri-colored Bat						
Roost structure availability	3	-10.50	27.80	0.00	0.94	0.94
Roost characteristics sub-global	8	-6.00	34.30	6.50	0.03	0.97
Tree permanence and environmental protection	3	-13.90	34.70	6.90	0.03	1.00
Movement ability	3	-24.00	54.90	27.10	0.00	1.00
Forest type	2	-29.40	63.20	35.50	0.00	1.00
Anthropogenic disturbance	2	-33.10	70.70	42.90	0.00	1.00
Landscape resources	2	-34.80	74.10	46.30	0.00	1.00
Landscape characteristics sub-global	4	-32.90	75.20	47.50	0.00	1.00
Northern Yellow Bat						
Roost structure availability	3	-14.20	35.10	0.00	0.93	0.93
Roost characteristics sub-global	9	-7.90	40.40	5.30	0.06	0.99
Tree permanence and environmental protection	3	-19.20	45.10	10.00	0.01	1.00
Movement ability	3	-34.10	75.00	39.90	0.00	1.00
Anthropogenic disturbance	2	-35.80	76.00	40.90	0.00	1.00
Landscape characteristics sub-global	5	-33.80	79.00	44.40	0.00	1.00
Landscape resources	3	-36.90	80.60	45.50	0.00	1.00
Forest type	2	-40.30	85.00	49.90	0.00	1.00

We radio-tagged 6 adult male Northern Yellow Bats and tracked them to 27 trees (1 bat to 7 trees in 2018 and 5 bats to 20 trees in 2019) for an average of 4.5 ± 2.9 (min–max = 1–12) trees per bat. We tracked Northern Yellow Bats for an average of 9.2 ± 5.4 days (min–max = 1–12) and they spent 1.3 ± 0.6 days (min–max = 1–3)

Table 5. Estimates, standard errors, and 85% confidence intervals for covariates in top models for Tri-colored Bat (2019) and Northern Yellow Bat (2018 and 2019) summer roost selection in Bluffton, SC. * indicates important covariates given 85% confidence intervals that do not overlap zero.

Covariate	Estimate	SE	Lower CI	Upper CI
Tri-colored Bat				
Pines*	-2.07	1.16	-3.74	-0.41
Oaks	-1.09	1.20	-2.82	0.65
Spanish Moss density*	2.52	0.86	1.28	3.77
Northern Yellow Bat				
Oaks	1.44	1.02	-0.03	2.91
Cabbage Palm*	1.82	0.22	0.07	3.58
Roost structure density*	2.11	0.55	1.32	2.91

Figure 2. (a) Relative probability of summer-roost selection for Tri-colored Bats based on Spanish Moss density in *Quercus* (oaks), *Pinus* (pines), and other trees, and for (b) Northern Yellow Bats based on roost structure density in oaks, *Sabal palmetto* (Cabbage Palm), and other trees in Bluffton, SC, 2018 and 2019.
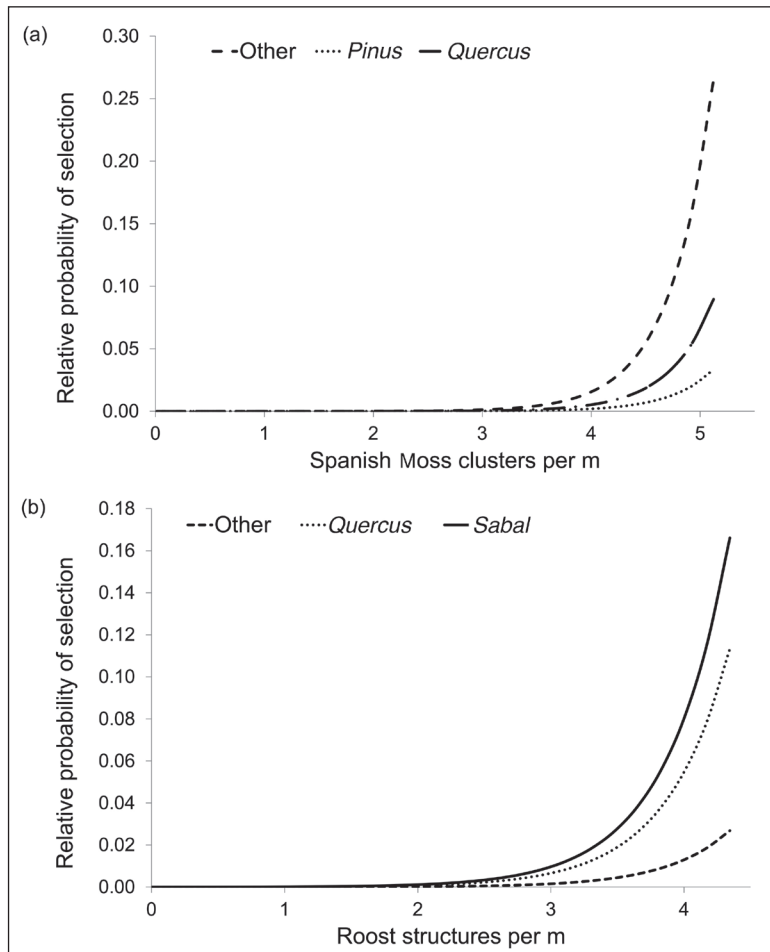
in a roost tree. Average distance between subsequent roosts was 299 ± 284 m (min–max = 52–1078). Used trees were live Cabbage Palm (n = 12), Live Oak (n = 6), *Nyssa aquatica* L. (Water Tupelo; n = 3)*,* Laurel Oak (n = 3)*,* Water Oak (n = 2)*,* and *Q. chapmanii* Sarg. (Chapman Oak; n = 1)*.* The average roost tree used by Northern Yellow Bats was 44.8 ± 25.1 cm dbh, had high canopy closure (88%; 1.2 times higher than available), and was in pine- and oak-dominated stands (Table 3). Distance to landscape features was variable, but compared to used trees, available trees were, on average, 1.3 times farther from freshwater, 1.5 times farther from the salt marsh, and 1.8 times farther from residential cover. We visually confirmed use of Spanish Moss for 3 individuals and dead palm fronds for 2. Of the 27 roosts, 12 were in dead Cabbage Palm fronds, 7 were in Spanish Moss, and 8 were in canopy roosts that we presumed were in Spanish Moss because of density of Spanish Moss on the tree and the absence of other roost structures. All bats appeared to roost alone. Individuals were consistent in use of 1 type of roost tree, with no individuals switching between Spanish Moss and foliage roosts in hardwood trees and dead fronds in palm trees.

We modeled Northern Yellow Bat roost selection from 37 choice sets. The roost-structure–availability model was the top model holding 93% of model weight (Table 4). Important covariates in this model were Cabbage Palm and roost-structure density (Table 5), and relative probability of selection was positively related to both covariates (Fig. 2b). The proportion of test cases where the model correctly identified the true roost was 0.84.

Discussion

We found that roost-structure abundance and tree species group were the most important factors in determining roost selection for both Tri-colored Bats and Northern Yellow Bats. Across bat species, various tree characteristics, especially those associated with roost structures, are important in determining selection (Kalcounis-Rüppell et al. 2005, Poissant et al. 2010, Rhodes and Wardell-Johnson 2006). When sites have high densities of roost structures, individuals have multiple options to choose from, providing the opportunity to select structures that best suit their ecological needs. It is possible that landscape features are important for these species, but only when roost structures are evenly distributed or abundant across the landscape (Castleberry et al. 2020, Miles et al. 2006). Our roost-selection results suggest that roost structure availability superseded plot or landscape characteristics, which were not important in our analyses.

Tri-colored Bats in our study did not select oak trees over other species as observed by Veilleux et al. (2003). Instead, they avoided pine trees and selected roost trees that had high densities of Spanish Moss, in line with our predictions. A diversity of broadleaved trees not only provide adequate structure for Spanish Moss to grow (Garth 1964), but they also provide dead foliage clumps, both of which can be used for roosting (Menzel et al. 1999, Veilleux et al. 2003). Tri-colored Bats in Nova Scotia select roost trees and roost areas that have high densities of Beard Lichen, which provides similar structure to Spanish Moss (Poissant et al. 2010).

Although we did not quantify the amount of Spanish Moss in trees surrounding roosts, it was likely present in stands surrounding colonized trees because it spreads to neighboring ones (Garth 1964). Similarities in roost structures between our study and others (Menzel et al. 1999, Poissant et al. 2010) highlight the importance of non-leaf roost structures for this species even across broad geographic areas.

Tree and site characteristics used by Tri-colored Bats in our study varied from those used in other parts of the species' range. Individuals that we tracked used trees with higher percent canopy closure (85%) and larger DBH (52.4 cm) than those reported by other studies (58% and 24.3–26.5 cm, respectively; O'Keefe et al. 2009, Poissant et al. 2010). Sites with high canopy closure may better insulate roosting bats from sun exposure (Veilleux et al. 2004). Therefore, Tri-colored Bats at low latitudes where temperatures are high may roost at sites with high canopy closure because they do not need to optimize thermal exposure to stay warm and it may even prevent over-heating. However, we were unable to measure canopy closure directly above the roost location. Future research is needed to evaluate the extent to which Tri-colored Bats select high canopy cover for thermoregulatory benefits.

As we predicted, relative probability of selection by Northern Yellow Bats was higher for Cabbage Palm trees compared to other tree groups and increased with density of Spanish Moss or dead palm fronds. While relative probability of selecting oak trees was not different than other trees, oaks may still be important because they accounted for 44% of used trees and were used the majority of the time in other study areas (Castleberry et al. 2020, Coleman et al. 2012, Menzel et al. 1999). Oaks, other hardwoods, and Cabbage Palms provide roost structures like Spanish Moss and dead palm fronds that may benefit this species in a number of ways. First, dead Cabbage Palm fronds and Spanish Moss match the coloration of the Northern Yellow Bat and thus, may provide camouflage from predators and allow for safe refugia during the day. These structures may also protect individuals from storms by repelling rain (Castleberry et al. 2020, Hutchinson 2006) and decreasing likelihood of bats becoming wet and cold. While it is still unclear why some individuals used only Spanish Moss or hardwood foliage roosts and others used only dead palm fronds, it is of note that individuals never used both palm trees and hardwoods with Spanish Moss. Our results differed in some ways from the other roost-selection study on Northern Yellow Bats in Georgia. While we did not find that DBH was an important covariate, likely because of high variability in used trees (16.4–164.1 cm), Castleberry et al. (2020) found that DBH of roost trees was higher than surrounding trees. Northern Yellow Bats in Georgia also selected trees with more clearance below the roost compared to available trees. We did not measure clearance directly below roosts, but midstory density, which may reflect similar open flight space around the roost tree, was not an important covariate. However, conditions surrounding the roost tree are likely not reflective of those immediately surrounding the roost structure, and it is important to recognize that our understanding of roost selection is thus limited.

Counter to our predictions, we found that landscape features were not important in determining roost-site selection for either species. Other studies indicate that proximity to landscape features such as freshwater, roads, and nearby roosts, are important in roost selection of these species (Castleberry et al. 2020, O'Keefe et al. 2009, Perry et al. 2008, Poissant et al. 2010, Veilleux et al. 2004). Freshwater, salt marsh, and various forest stands are necessary for drinking water, foraging areas, and alternate roosts, but access to them may have been secondarily important to roost structures and specific roost trees, explaining why we did not detect landscape-scale patterns (Miles et al. 2006). Castleberry et al. (2020) suggested that landscape features may only be important when roost structures are ubiquitous across the landscape. The importance of roost structures relative to surrounding characteristics may also explain why our landscape model did not receive support in the selection analysis. If specific roost structures (e.g., Spanish Moss or palm fronds) are not available equally across the landscape, individuals may not have the flexibility to select sites close to important landscape features, highlighting that selection is a hierarchical process (Johnson 1980). In our study area, features like freshwater and fields for foraging were distributed relatively homogenously and in some cases in close proximity to one another. This distribution may limit the need for bats to select roosts close to these features. Finally, it is also possible that the buffers we used to measure availability did not capture large distances of available trees to landscape features. Other studies on the Northern Yellow Bat quantified availability at the landscape scale by placing points across the whole study area (Castleberry et al. 2020), likely capturing more variation in the landscape and as a result, were able to detect patterns of landscape-scale roost selection. However, this interpretation assumes that availability is constant for all individuals (Alldredge et al. 1998), which may not be true.

Counter to our prediction, we did not find evidence that individuals of either species avoided residential development when selecting roosts. Individuals of both species roosted in residential yards or even in proximity to ongoing construction. Tri-colored Bats have been documented using human structures, which may indicate tolerance and use of anthropogenic disturbance (Whitaker et al. 2014). The lack of an effect of development on roost selection by either species may indicate that low-density housing that retains forest patches may leave appropriate roosts for some species even within suburbanized areas (Rhodes and Wardell-Johnson 2006), something that future researchers may consider. However, roost selection that occurs within a gradient which includes a more developed urban area may be impacted by the degree of development because urbanization can negatively impact bats (Frick et al. 2020).

Both the Northern Yellow Bats and Tri-colored Bats in our study switched roosts more frequently than in other studies (Coleman et al. 2012, O'Keefe et al. 2009). Roost switching is a tactic that may reduce parasite loads and predation risk and allow access to more-suitable microclimates (Lausen and Barclay 2002, Lewis 1995). In addition, switching roosts frequently may relate to roost permanence and potential loss of roosts (Lausen and Barclay 2002). If some roost structures are

impermanent (e.g., like Spanish Moss or dead foliage), adaptations that facilitate the ability to use multiple roosts would benefit individuals by allowing them to be flexible when roosts are lost to either anthropogenic or natural disturbances. While multiple uses of a single roost tree occurred sporadically in our study, Northern Yellow Bats and Tri-colored Bats typically used new trees in proximity to old ones, displaying fidelity to an area as opposed to a specific tree. This fidelity has been documented in foliage-roosting species, and specifically in other Tri-colored Bat and Northern Yellow Bat populations (Castleberry et al. 2020, Veilleux and Veilleux 2004). Frequent roost switching in our study highlights the importance of the conservation of forests that provide many suitable roost trees with adequate foliage and Spanish Moss roost structures. Bats switch roosts when their physiological or ecological needs are not being met (Lewis 1995), thus the presence of many roost options nearby is important to their survival.

In our study, we were limited by several factors that may have impacted our ability to detect patterns. First, we only included male Northern Yellow Bats, and we analyzed Tri-colored Bat demographic groups together. Different demographic groups, like sexes and age classes, select habitat differently (Perry and Thill 2007, Veilleux et al. 2004). Given this, future studies on Northern Yellow Bats and Tri-colored Bats in this region may consider focusing on how selection varies by demographic group to better understand habitat associations. Further, the sample sizes of our study required us to include the first roosts after capture, which may not be reflective of typical selection events. Finally, although the response variable in discrete-choice models is the selection event, and it is therefore appropriate to include multiple choice sets for single individuals (Cooper and Millspaugh 1999), our models risk bias toward selection patterns of individuals that we tracked for longer periods of time. Thus, it is important to conduct additional studies with larger sample sizes and across broader spatial scales and habitat conditions.

In the Coastal Plain of South Carolina, one of the predominate threats to bats is forest loss due to human disturbance. Loss of forests resulting from land-use change removes critical roosting structures, directly impacting tree-roosting species (Russo and Ancillotto 2014). By identifying features used by Tri-colored Bats and Northern Yellow Bats, we provide information for managers making decisions about how to manage land for these species. First, retention of dead palm fronds which are often removed for aesthetic purposes, will leave more roost structures on the landscape for Northern Yellow Bats. Further, forests with a diversity of hardwood trees that foster the growth of Spanish Moss (Garth 1964), and dead foliage will allow roost structures for both species. As forest loss and climate change continue to threaten bat habitat, management activities in this region that favor the conservation of bottomland and maritime forests will likely favor these species.

Acknowledgments

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