Research Article

Seasonal Shifts in Nocturnal Habitat Use by Coastal Bat Species

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ABSTRACT Sensitivity of bats to land use change depends on their foraging ecology, which varies among species based on ecomorphological traits. Additionally, because prey availability, vegetative clutter, and temperature change throughout the year, some species may display seasonal shifts in their nocturnal habitat use. In the Coastal Plain of South Carolina, USA, the northern long-eared bat (*Myotis septentrionalis*), southeastern myotis (*Myotis austroriparius*), tri-colored bat (*Perimyotis subflavus*), and northern yellow bat (*Lasiurus intermedius*) are species of conservation concern that are threatened by habitat loss. Our objective was to identify characteristics of habitat used by these species during their nightly active period and compare use between summer and winter. We conducted acoustic surveys at 125 sites during May–August and at 121 of the same 125 sites December–March 2018 and 2019 in upland forests, bottomland forests, fields, ponds, and salt marsh and used occupancy models to assess habitat use. The northern long-eared bat and southeastern myotis (i.e., myotis bats) used sites that were closer to hardwood stands, pine stands, and fresh water year-round. We did not identify any strong predictors of tri-colored bat habitat use in summer, but during winter they used bottomland forests, fields, and ponds more than salt marsh and upland forests. During summer and winter, northern yellow bats used sites close to fresh water and salt marsh. Additionally, during summer they used fields, ponds, and salt marsh more than upland and bottomland forests, but in winter they used bottomland forests, fields, and ponds more than upland forest and salt marsh. Our results highlight important land cover types for bats in this area (e.g., bottomland forests, ponds, and salt marsh), and that habitat use changes between seasons. Accounting for and understanding how habitat use changes throughout the year will inform managers about how critical habitat features may vary in their importance to bats throughout the year. © 2021 The Wildlife Society.

KEY WORDS habitat use, northern long-eared bat, northern yellow bat, season, South Carolina, southeastern myotis, summer, tri-colored bat, winter.

Globally, many bat species are threatened by a variety of anthropogenic disturbances to the landscape. Land use change as a result of these disturbances includes concerns such as forest loss due to tree harvesting, removal of natural features for agriculture, and urban development, which rank as some of the most pressing threats to bat species (Frick et al. 2020). Specifically, these changes cause habitat fragmentation and degradation, which leaves a mosaic of habitat of varying quality (Bennett and Saunders 2010) and can negatively affect bats' abilities to acquire resources, reproduce, and ultimately sustain populations (Russo and Ancillotto 2014). This poses a concern for already at-risk bat species as human disturbance continues to expand across vast portions of the landscape.

The northern long-eared bat (*Myotis septentrionalis*), southeastern myotis (*M. austroriparius*), tri-colored bat (*Perimyotis subflavus*), and northern yellow bat (*Lasiurus*

intermedius) are species of conservation concern and year-round residents of the South Carolina, USA, Coastal Plain. These species face a variety of threats throughout various parts of their range. The northern long-eared bat and tri-colored bat can be infected by the fungal pathogen associated with white nose syndrome (WNS), which affects cave-hibernating and mine-hibernating bat species. Northern long-eared bat and tri-colored bat populations have experienced severe declines in numbers in parts of their range due to WNS and consequently are threatened and proposed for listing, respectively, under the Endangered Species Act (U.S. Fish and Wildlife Service [USFWS] 2015, 2017). The Outer Coastal Plain of South Carolina is a region devoid of caves and mines; thus, conditions are likely not amenable for fungal growth. Consequently, this region may provide a refugium from WNS for resident individuals of these species. The southeastern myotis is a highest priority threatened species in South Carolina (Kindel 2017) and the most pressing threat to the species is habitat loss (Bat Conservation International and Southeastern Bat Diversity Network 2013). Although

not federally listed, the northern yellow bat is a species of greatest conservation need in South Carolina. The species has experienced mortality associated with strikes at wind turbines and communications towers (Crawford and Baker 1981, Arnett and Baerwald 2013); however, major sources of mortality are still mostly unknown. The northern yellow bat's range in the United States overlaps with many populated areas; consequently, loss of habitat is likely a concern. Ultimately, all 4 of these species face a variety of threats across their range, but in the Coastal Plain of South Carolina, the most pressing threat appears to be habitat loss. Thus, understanding habitat use and conservation of habitat for each species is important to sustain populations in this region.

During their nightly active period, these bat species search for food, fresh water, nocturnal roosts, and diurnal roosts. Species use forests and landscapes differently based on their ecomorphological traits such as echolocation call characteristics and wing loading (Aldridge and Rautenbach 1987, Audet 1990). Small and maneuverable species like the southeastern myotis and northern long-eared bat exploit cluttered forests (areas with dense vegetation), where they can take advantage of gleaning foraging strategies, which are especially important during cool periods (Patriquin and Barclay 2003). Cluttered bottomland forests are important features for the southeastern myotis, which uses them for foraging and roosting (Menzel et al. 2005, Medlin and Risch 2008, Clement and Castleberry 2013). Tri-colored bats, although also small in size, tend to exploit edges between forests and open areas during the nocturnal activity period because insects are abundant along such features (Morris et al. 2010). Finally, although no research has been conducted on northern yellow bat nocturnal habitat use, based on their size and morphological characteristics, they likely exploit open areas where there is less clutter, similar to other lasiurine species (Norberg and Rayner 1987, Jantzen and Fenton 2013).

Landscape features are also important for facilitating bat habitat use during nocturnal periods. Linear corridors including low-use forest roads and forest edges, or tree lines provide areas that some bats use for foraging and commuting (Morris et al. 2010, Amelon et al. 2014). Such features are especially important for large species, similar to the northern yellow bat, that require open areas for foraging and movement (Ford et al. 2006). Water features such as freshwater ponds and streams also provide important resources like drinking water sources and abundant insects (Ford et al. 2006, Moore and Best 2018, Ancillotto et al. 2019). The loss or addition of forests, corridors, and freshwater sources can affect bat species' habitat use by causing changes in resource availability (Owen et al. 2003, Ethier and Fahrig 2011, Parker et al. 2019). Further, nightly foraging and commuting habitat may vary across or within seasons (Vasko et al. 2020) because of changes in vegetative clutter, temperature, and resource availability; however, research into bat habitat use typically occurs in summer (Loeb 2020). Although there are studies that compare summer and winter activity (Grider et al. 2016) for

some of these target species, no data exist on winter foraging habitat use. This lack of information precludes understanding variation in habitat associations across seasons (Weller et al. 2009), which is particularly important for bats that are active and forage during winter.

Our objective was to determine habitat characteristics associated with nocturnal habitat use during summer and winter for the southeastern myotis, northern long-eared bat, tri-colored bat, and northern yellow bat in coastal South Carolina. We hypothesized that habitat use would vary based on morphology of each species or species group (Norberg and Rayner 1987). Specifically, we predicted that in summer, myotis bats would use interior forest sites, whereas tri-colored bats and northern yellow bats would use sites near forest edges and non-forested sites, respectively (Ford et al. 2006, Morris et al. 2010, Jantzen and Fenton 2013). Because landscape characteristics like commuting corridors, freshwater resources, and foraging areas are important for a variety of species (Henderson and Broders 2008, Amelon et al. 2014, Starbuck et al. 2015), we predicted that all species or groups would use sites near such features. In addition, we hypothesized that habitat use by some species would vary across seasons because of changing resource availability, environmental conditions, and loss of vegetative clutter like leaves on deciduous trees, midstory shrubs, and vines. Because of their association with interior forest and their ability to glean insects in cold weather (Burles et al. 2009), we predicted that there would be no difference in myotis bat habitat use between seasons. In contrast, we predicted that tri-colored bats and northern yellow bats would shift from using open sites during the summer to using upland and bottomland forests during winter because of decreased vegetative clutter and the possibility of higher insect abundance due to warmer interior forest temperatures (Li et al. 2015).

STUDY AREA

The study took place at 3 areas in Beaufort County in the southern Coastal Plain of South Carolina: Palmetto Bluff (8,093 ha), Pickney Island National Wildlife Refuge (1,640 ha), and Victoria Bluff Heritage Preserve (470 ha). The study areas were located within the southeastern climate region (Karl and Koss 1984). Average temperature during winter (Dec–Mar) was 11.8°C and average total precipitation was 33 cm; average temperature during the summer survey period (May–Aug) was 26.2°C with an average total precipitation of 52 cm (20-yr average; National Oceanic and Atmospheric Association 2020). The 3 study areas are approximately 7–9 km from one another and are slightly above sea level (7 m) with small changes in elevation resulting in low-lying areas where most bottomland forests occur. Land cover types in all 3 study areas included upland forests (pine [*Pinus* spp.] savannas, mixed hardwood-pine forests, and maritime forests), bottomland forests, ponds, maintained fields, and salt marshes. Pine savannas had been previously thinned and were made up predominately of even aged slash pine (*Pinus elliottii*) and loblolly pine (*P. taeda*). Mixed hardwood-pine stands consisted of sweet gum

(*Liquidambar styraciflua*), slash and loblolly pine, and a variety of oak (*Quercus* spp.) species (e.g., water oak [*Q. nigra*], laurel oak [*Q. laurifolia*]). Maritime forests were composed mostly of mature southern live oak (*Q. virginiana*) and cabbage palm (*Sabal palmetto*). Bottomland forests consisted of mainly water tupelo (*Nyssa aquatica*) with sporadic sweet gum and bald cypress (*Taxodium distichum*). Palmetto Bluff was an 8,093-ha multi-use property that consisted of low-density housing, areas that were zoned for future low-density housing, and 132 ha under conservation protection or easement, which cannot be developed. The areas we surveyed at Palmetto Bluff were predominately upland forest (Table S1, available online in Supporting Information). Victoria Bluff was an approximately 470-ha state-owned heritage preserve surrounded by suburban development and was composed mostly of upland and bottomland forest (Table S1). Pinckney Island National Wildlife Refuge was on a 1,640-ha island without significant development and composed of scattered ponds and fields within upland forest, which dominated the island (Table S1). Neither Pinckney Island nor Victoria Bluff contained significant urban cover on their property, but both were bordered by varying degrees of residential or high intensity commercial development. Twelve bat species occupied the Lower Coastal Plain of South Carolina (Menzel et al. 2003, White et al. 2018): the big brown bat (*Eptesicus fuscus*), Brazilian free-tailed bat (*Tadarida brasiliensis*), eastern red bat (*Lasiurus borealis*), evening bat (*Nycticeius humeralis*), hoary bat (*L. cinereus*), northern long-eared bat, northern yellow bat, Seminole bat (*L. seminolus*), silver-haired bat (*Lasionycteris noctivagans*), southeastern myotis, tri-colored bat, and Rafinesque's big-eared bat (*Corynorhinus rafinesquii*).

METHODS

Acoustic Sampling
We used Anabat Express acoustic detectors (Titley Scientific, Columbia, MO, USA) to record bat passes during winter and summer of 2018 and 2019 in the 3 study areas. We stratified our sampling among 5 land cover types: upland forest, bottomland forest, open field, salt marsh edges, and freshwater ponds. We used ArcMap (version 10.5.1; Esri, Redlands, CA, USA) to create tessellation grids over all study areas where each cell was 0.4 ha to allow for flexibility of detector placement. We removed cells that contained >1 land cover type to reduce the likelihood that we were recording bats using a different land cover type than that associated with the cell. From the remaining grid, we selected cells based on a generalized random tessellation stratified (GRTS) sampling design using R package spsurvey (Kincaid et al. 2018). We restricted salt marsh cells to those that had 1 edge touching land to assure access and to avoid loss of detectors due to high tide. Because ponds are discrete landscape features, we did not include them in the GRTS sampling framework. Instead, we assigned each pond a number, randomly ordered them, and selected the first 25 ponds to survey. We surveyed 125 sites (25 in each land cover type) once over the course of the 2 summers. In winter, we surveyed 121 of these same 125 sites once each; we were not able to survey 4 sites at Palmetto Bluff because of time constraints. In winter, we surveyed 24 sites in bottomland forest, 23 in fields, 25 at ponds, 25 in salt marsh, and 24 in upland forests. We surveyed 81 sites at Palmetto Bluff (77 in winter), 30 at Pinckney Island, and 14 at Victoria Bluff to distribute our sampling effort relative to the size of each property.

During summer, we surveyed sites for 4 nights and during winter we surveyed sites for 5–10 nights to account for potentially lower activity related to lower temperatures (Grider et al. 2016). During both seasons, acoustic recording began 30 minutes before sunset and ended 30 minutes after sunrise. We set detectors to a data division ratio of 8 and a sensitivity of 115. We placed acoustic units on 3.5-m-high poles as close to the center of sample cells as possible (within forests always ≥25 m away from the nearest edge), in low clutter locations that would maximize our ability to record bats. We also faced microphones in the direction with the least amount of vegetative clutter. For field and salt marsh sites, we faced detectors toward open areas and away from edges. At ponds, we selected locations where detectors faced the pond but were not blocked by dense vegetation that surrounded many ponds. Although standardizing detector sensitivity may have influenced detection in different land cover types, we accounted for variation in detection probability in our models by including metrics of clutter.

Site and Observation Covariate Measurements
At each site, we characterized the vegetation structure by creating a 0.05-ha circular plot (radius = 12.5 m) around each detector. We confirmed land cover type derived from the geographic information system (GIS) layer (upland forest, bottomland forest, field, pond, and salt marsh) and estimated tree basal area using a variable plot method and angle gauge with a basal area factor (BAF) of 10. We measured canopy closure at the plot center and 6 m from the center in each cardinal direction using a spherical densiometer (Model-A; Forest Densiometers, Forestry Suppliers, Jackson, MS, USA). We averaged all 5 measurements to obtain a canopy closure value for the plot. To characterize midstory stem density, we created a transect through the plot center along a randomly selected bearing and counted all stems ≥4 cm diameter at breast height (DBH) and <10 cm DBH within 1 m of either side of the transect.

We obtained GIS data layers from the Palmetto Bluff Conservancy, USFWS, the South Carolina Department of Natural Resources, and the Beaufort County Geographic Information Systems Office. We used ArcMap to calculate distance to forest edge, distance to residential cover, distance to paved and dirt roads, distance to fresh water, distance to nearest hardwood stand, distance to nearest pine stand, and percent forest cover within a 250-m buffer for the northern yellow bat and a 200-m buffer for myotis bats and the tri-colored bat. We chose these buffers based on the foraging ranges of northern long-eared bats (Broders

et al. 2006), and scale of response or foraging ranges of other bats with similar ecology to tri-colored bats and similar morphology to northern yellow bats (Moretto et al. 2019). We obtained weather data from the nearest weather station (the Beaufort Merritt Field Airport Weather Station, elevation = 11.3 m) in Beaufort, South Carolina (~38 km from Palmetto Bluff, 26 km from Pinckney Island, and 26 km from Victoria Bluff) using the R package riem (Salmon and Anderson 2019) and calculated average nighttime temperature and total nightly rainfall. Ranges for all occupancy covariates are provided in supplemental material (Table S1).

Analysis

We used Analook (version 4.2n 2017; Titley Scientific) and 2 custom filters to remove recorded call files containing only background noise and non-search phase calls such as feeding buzzes and social calls (Table S2, available online in Supporting Information). The first filter removed files containing only background noise and low frequency interference, and we used the remaining files as an estimate of overall bat activity. The second filter removed passes that were low quality or had <4 pulses. We identified filtered passes using Kaleidoscope Pro (version 4.2.0, Wildlife Acoustics, Maynard, MA, USA) and vetted all call files regardless of species identification to verify that we did not miss target species' calls that were classified as another species. We grouped northern long-eared bat and southeastern myotis together, big brown bats and silver haired bats together, and eastern red bats and Seminole bats together because of similarities in their call structures and tallied total passes of all recorded species or species group.

We developed nightly detection histories for myotis bats, tri-colored bats, and northern yellow bats for each site and season to assess hypothesized factors influencing habitat use for each species or species group. We used Program R (version 3.6.2; R Core Team 2020) to conduct single-season occupancy analyses for each species and each season in package unmarked (Fiske and Chandler 2011). We chose to take a single-season occupancy approach instead of multi-season for 2 reasons. First, one of the assumptions of multi-season occupancy is that covariate values cannot change over seasons. One of our covariates, canopy closure, decreased at some sites during winter months. Second, we wanted to evaluate if bats used habitat differently between seasons. For example, we hypothesized that when conditions like vegetative clutter, temperature, and food availability change between seasons, the northern yellow bat and tri-colored bat may shift from using open- and edge-associated cover types to more forested sites. If this was the case, multi-season occupancy models would be difficult to interpret. Instead, comparing the same candidate sets analyzed separately allowed us to directly compare covariates that changed between seasons. We conducted the occupancy analysis in a 3-step process where we tested for overdispersion using our most parameterized model for each candidate set, modeled detection based on 8 a priori models while using a global model for occupancy (Mackenzie et al. 2018; Table 1) and

retained important detection covariates to include in the additive single-season occupancy models (Table 2). We scaled all continuous covariates prior to analysis and screened for correlation. We found evidence of correlation ($|r| > 0.60$) between canopy closure and basal area. Therefore, we did not include these 2 covariates in the same models for myotis bats and tri-colored bats and did not include canopy closure in any models for the northern yellow bat because of differing species morphology and ecology (Table 2).

For each species or species group, we tested model fit of the most parameterized detection and occupancy models (MacKenzie and Bailey 2004) in package AICcmodavg (Mazerolle 2020) with 1,000 simulations. We ranked models using Akaike's Information Criterion corrected for small sample size (AIC_c) if there was no evidence of overdispersion, or Quasi Akaike's Information Criterion corrected for small sample size ($QAIC_c$) when goodness of fit tests indicated overdispersion ($\hat{c} > 1.0$, $P < 0.05$). We used adjusted standard errors ($SE \times \sqrt{\hat{c}}$) where $\sqrt{\hat{c}}$ is the square root of the overdispersion parameter ($\hat{c}$), when there was evidence of overdispersion.

We defined confidence sets of top models as those possessing ΔAIC_c or $\Delta QAIC_c \leq 4$ and important covariates in top models as those with 85% confidence intervals that did not overlap zero (Arnold 2010) for the detection and occupancy models. In cases where there were multiple models in the confidence set that contained overlapping covariates, we obtained conditional model-averaged estimates using R package AICcmodavg and used those model-averaged estimates for inference. If models in the confidence set contained no common covariates, we present those models with their weights and interpreted each model separately. Finally, foraging bats are highly mobile, and their behavior can cause a violation of the assumption of site closure because they do not constantly occupy a site. Therefore, although we used occupancy modeling, given the violation of this assumption, our results should be interpreted as habitat use (Mackenzie 2005).

RESULTS

Acoustic Detections

During summer 2018 and 2019, we surveyed for 500 detector nights and recorded 61,928 echolocation passes. After

Table 1. *A priori* models for probability of detection (p) of myotis bats, tri-colored bats, and northern yellow bats during summer and winter 2018 and 2019 in Bluffton, South Carolina, USA.

Model	Model structure
Temperature	p(average nightly temperature)
Rain	p(total nightly rainfall)
Full weather	p(average nightly temperature + total nightly rainfall)
Clutter	p(midstory stem density + overstory basal area)
Date	p(date + date^2)
Year	p(study yr)
Null	Intercept only
Global	All above

Table 2. *A priori* models for myotis bats, tri-colored bat, and northern yellow bat nocturnal occupancy (ψ) for summer and winter at study sites in Bluffton, South Carolina, USA, 2018–2019.

Model	Model structure
Myotis bats	
Interior forest	ψ (canopy closure + canopy closure^2)
Land cover type	ψ (land cover type)
Site clutter	ψ (basal area + midstory stem density)
Landscape commuting	ψ (distance to edge + distance to road)
Landscape resources	ψ (distance to water + distance to pine stand + distance to hardwood stand + proportion of forest in 200-m buffer)
Anthropogenic disturbance	ψ (distance to residential cover + distance to road + study area)
Null	Intercept only
Global	All above
Tri-colored bats	
Edge and interior forests	Ψ (canopy closure + canopy closure^2 + distance to edge)
Land cover type	Ψ (land cover type)
Site clutter	Ψ (basal area + midstory stem density)
Landscape commuting	Ψ (distance to edge + proportion of forest in 200-m buffer + distance to road)
Landscape resources	Ψ (distance to water + distance to hardwood stands + distance to edge + proportion of forest in 200-m buffer)
Anthropogenic disturbance	Ψ (distance to road + distance to edge + distance to residential area + study area)
Null	Intercept only
Subglobal	All above except land cover type
Northern yellow bats	
Land cover type	Ψ (land cover type)
Site clutter	Ψ (basal area + midstory)
Landscape resources	Ψ (proportion of forest in 250-m buffer + distance to water + distance to salt marsh)
Landscape commuting	Ψ (proportion of forest in 250-m buffer + distance to road + distance to salt marsh)
Human disturbance	Ψ (distance to road + distance to residential area)
Study area	Ψ (study area)
Null	Intercept only
Subglobal	All above except land cover type

filtering out poor-quality passes, we identified 25,248 passes to 8 species or species groups. Of the identified passes, 32% (8,038) were tri-colored bats, 26% (6,595) were eastern red bats or Seminole bats, 15% (4,009) were evening bats, 12% (2,969) were big brown bats or silver haired bats, 11% (2,652) were Brazilian free-tailed bats, 3% (825) were northern yellow bats, <1% (116) were myotis bats, and <1% (44) were hoary bats.

During winter 2018 and 2019, we surveyed for 885 detector nights and recorded 52,651 bat passes. After removing poor-quality passes, we identified 18,356 passes to 8 species or species groups. Of the identified passes, 25% (4,627) were Brazilian free-tailed bats, 22% (3,995) were tri-colored bats, 18% (3,327) were red bats or Seminole bats, 18% (3,206) were big brown bats or silver haired bats, 8% (1,448) were evening bats, 4% (788) were hoary bats, 4% (729) were northern yellow bats, and 1% (236) were myotis bats.

Myotis Bat Models

We detected myotis bats at 42 sites (34%) during summer. We did not find evidence of overdispersion in our data ($\hat{c} = 0.73$, $P = 0.76$). Six models were in the detection

Table 3. Confidence sets for occupancy models of myotis bats, tri-colored bats, and northern yellow bats in summer and winter in Bluffton, South Carolina, USA, 2018–2019. We ranked models by second order Akaike's Information Criterion (AIC$_c$) or quasi-AIC$_c$ (QAIC$_c$) and the confidence sets include models with ΔAIC$_c$ or ΔQAIC$_c$ < 4; K = the number of parameters in the model.

Models	K	QAIC$_c$ or AIC$_c$	ΔQAIC$_c$ or ΔAIC$_c$	Model likelihood	QAIC$_c$ or AIC$_c$ weight
Myotis bats					
Summer					
Landscape resources	7	364.20	0.00	1.00	0.93
Winter					
Landscape resources	9	556.99	0.00	1.00	0.92
Tri-colored bats					
Summer[a]					
Null	4	151.74	0.00	1.00	0.76
Winter					
Land cover type	12	854.18	0.00	1.00	0.98
Northern yellow bats					
Summer[a]					
Land cover type	7	277.23	0.00	1.00	0.83
Global	14	280.53	3.30	0.19	0.16
Winter					
Land cover type	9	535.91	0.00	1.00	0.63
Landscape resources	8	537.06	1.15	0.56	0.35

[a] We used QAIC$_c$ in this analysis because of evidence of overdispersion.

probability confidence set (rain model, null model, temperature model, year model, full weather model, and clutter model; Appendix A), but midstory stem density was the only important covariate (Appendix B), so we retained it in the occupancy models. The landscape model was the only model in the confidence set for occupancy and had a weight of 0.93 (Table 3). Important covariates in this model were distance to fresh water, distance to pine stands, and distance to hardwood stands (Table 4). Occupancy decreased with increasing distance to hardwood-dominated stands (Fig. 1A), distance to water (Fig. 1B), and distance to pine stands (Fig. 1C).

We detected myotis bats at 46 sites (38%) during winter. We did not find evidence for overdispersion in our data ($ĉ = 1.32$, $P = 0.06$), so we used AIC_c to rank detection and occupancy models. Five detection models were in the

confidence set (temperature model, null model, full weather model, date model, and clutter model; Appendix A). Important covariates in this model were temperature and date, so these were retained in the occupancy model (Appendix B). The landscape resources model was the only model in the confidence set for occupancy and had a weight of 0.92 (Table 3). Important covariates were distance to water, distance to pine stand, and distance to hardwood stand (Table 4). Occupancy decreased with increasing distance to hardwood stand (Fig. 1D), distance to fresh water (Fig. 1E), and distance to pine stand (Fig. 1F).

Tri-Colored Bat Models

We detected tri-colored bats at 106 sites (85%) during summer. The data were overdispersed ($ĉ = 3.17$, $P = 0.001$),

Table 4. Estimates, standard errors (SE), and 85% confidence intervals (CI) for covariates in top models for myotis bat, tri-colored bat, and northern yellow bat occupancy in summer and winter 2018 and 2019 in Bluffton, South Carolina, USA. Important covariates have 85% confidence intervals that do not overlap zero. All beta estimates are based on standardized covariates.

| Covariate	Estimate	SE	Lower CI	Upper CI
Myotis bats				
Summer				
Intercept	−0.35	0.33	−0.83	0.13
Distance to water	−0.44	0.28	−0.84	−0.03
Distance to pine stand	−0.53	0.36	−1.05	0.00
Proportion of forest	0.39	0.30	−0.05	0.83
Distance to hardwood stand	−0.62	0.34	−1.11	−0.13
Winter				
Intercept	−0.65	0.31	−1.09	−0.20
Distance to water	−1.02	0.34	−1.50	−0.53
Distance to pine stand	−1.04	0.44	−1.66	−0.41
Proportion of forest	0.19	0.30	−0.23	0.61
Distance to hardwood stand	−0.58	0.34	−1.07	−0.09
Tri-colored bats				
Summer				
Intercept	1.74	0.14	1.53	1.95
Winter				
Intercept	2.55	0.94	1.19	3.91
Land cover type: field	−1.58	1.12	−3.18	0.03
Land cover type: pond	7.52	48.10	−61.74	76.78
Land cover type: salt marsh	−2.88	1.04	−4.38	−1.37
Land cover type: upland forest	−1.82	1.04	−3.32	−0.32
Northern yellow bats				
Summer				
Intercept	−1.63	0.85	−2.85	−0.40
Land cover type: field	3.76	1.50	1.60	5.91
Land cover type: pond	3.80	1.52	1.61	6.00
Land cover type: salt marsh	3.19	1.37	1.22	5.17
Land cover type: upland forest	0.00	1.14	−1.64	1.65
Basal area	0.06	0.75	−1.01	1.14
Midstory stem density	0.35	0.41	−0.24	0.94
Proportion of forest	−0.82	0.73	−1.87	0.23
Distance to road	0.25	0.58	−0.58	1.08
Distance to water	−1.66	0.75	−2.74	−0.58
Distance to residential area	0.84	0.66	−0.12	1.79
Distance to salt marsh	−1.08	0.53	−1.85	−0.31
Winter				
Intercept	1.76	1.63	−0.59	4.10
Land cover type: field	−1.74	1.70	−4.18	0.71
Land cover type: pond	0.36	1.85	−2.31	3.02
Land cover type: salt marsh	−3.57	1.74	−6.08	−1.06
Land cover type: upland forest	−3.10	1.67	−5.50	−0.69
Intercept	−0.16	0.29	−0.58	0.25
Proportion of forest	0.45	0.28	0.04	0.86
Distance to water	−1.48	0.37	−2.01	−0.95
Distance to salt marsh	−0.45	0.26	−0.82	−0.08
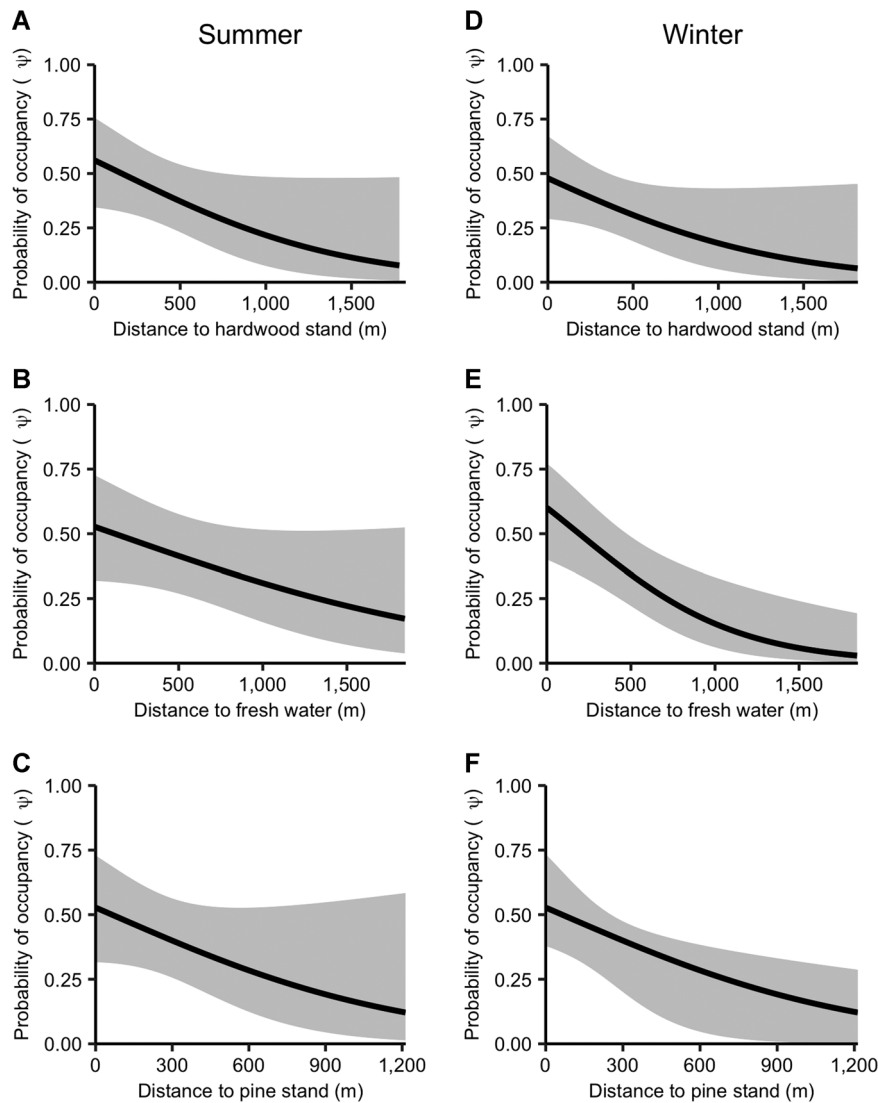
Figure 1. Probability of myotis bat site occupancy as a function of A) distance to nearest hardwood stand in summer, B) distance to fresh water in summer, and C) distance to nearest pine stand in summer, and as a function of D) distance to nearest hardwood stand in winter, E) distance to fresh water in winter, and F) distance to nearest pine stand in winter in Bluffton, South Carolina, USA, 2018 and 2019. Shaded areas represent 85% confidence intervals.

so we used $QAIC_c$ to rank detection and occupancy models. Six detection models (null model, temperature model, rain model, year model, full weather model, and date model) were in the confidence set (Appendix A), indicating high uncertainty. Temperature was important, so it was retained in the occupancy models (Appendix B). The null occupancy model was the only model in the confidence set (weight = 0.76), indicating that no covariates that we measured were good predictors of occupancy (Table 3).

We detected tri-colored bats at 78 sites (64%) during winter. We did not find evidence of overdispersion in our data ($\hat{c} = 1.18$, $P = 0.12$), so we used AIC_c to rank the detection and occupancy models. The global model and full weather model were the only models in the confidence set for detection (Appendix A). Temperature, rain, basal area, year, and date were all important detection covariates (Appendix B), so we retained them in the occupancy model. The land cover type model was the only model in the

confidence set for occupancy with a weight of 0.98 (Table 3); salt marsh and upland forest were important. Occupancy was lower in salt marsh and upland forest sites than in bottomland forest (Table 4; Fig. 2A). Occupancy estimates in field and pond sites were not different from occupancy in bottomland forest sites.

Northern Yellow Bat Models
We detected northern yellow bats at 71 sites (57%) during summer. We found evidence of overdispersion in our data ($\hat{c} = 1.86$, $P = 0.03$), so we used $QAIC_c$ to rank detection and occupancy models. The null, temperature, rain, full weather, year, and date models were all within the confidence set (Appendix A), but no covariates were important (Appendix B), so we retained a null detection model for our occupancy models. The land cover type and global models were both in the confidence set for occupancy (Table 3). Land cover types field, pond, and salt marsh, and distance to
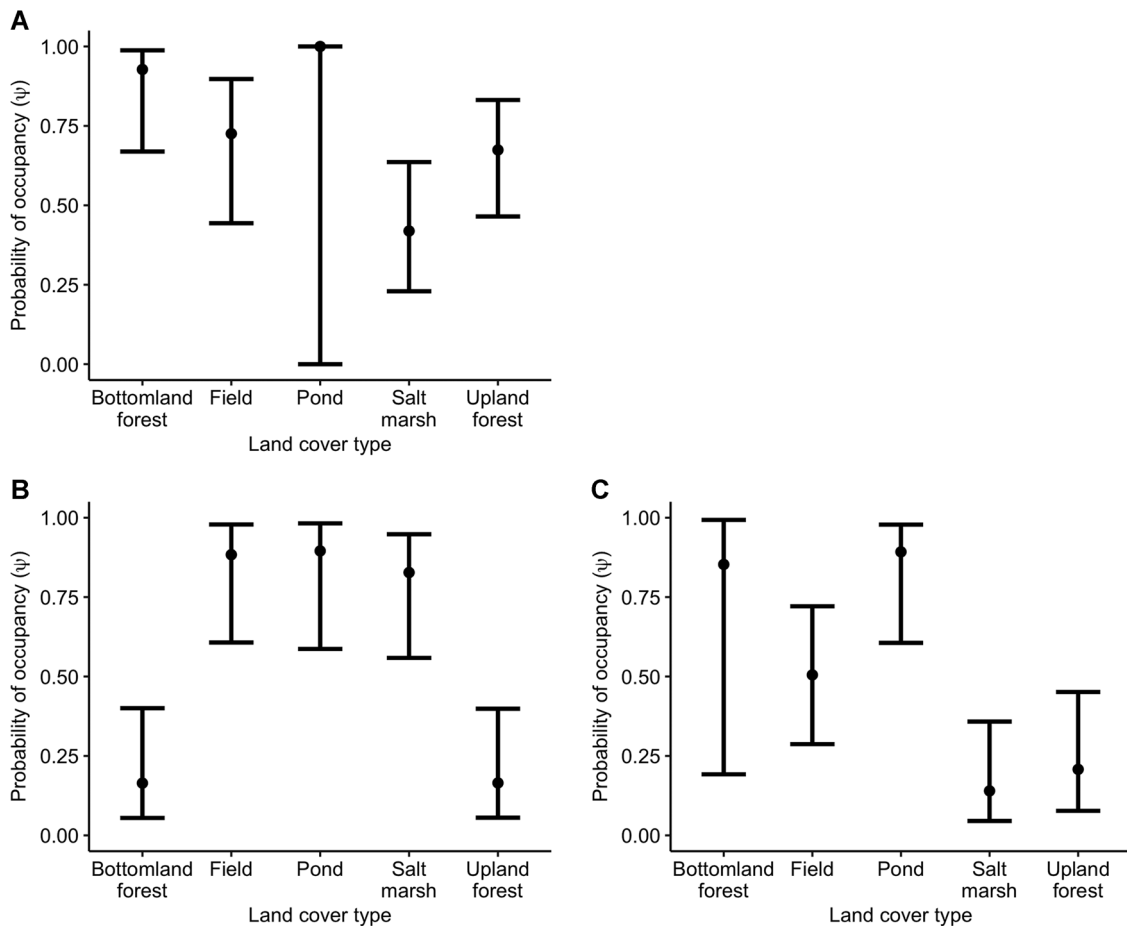
Figure 2. Probability of site occupancy as a function of land cover type (reference category: bottomland forest) for A) tri-colored bats in winter, B) northern yellow bats in summer, and C) northern yellow bats in winter in Bluffton, South Carolina, USA, 2018 and 2019. Error bars represent 85% confidence intervals.

water and distance to salt marsh were all important co-variates (Table 4). Occupancy was higher at field, pond, and salt marsh sites than at bottomland forest sites (Fig. 2B). Occupancy in upland forest sites was not different from occupancy in bottomland forest sites (Fig. 2B). Occupancy was also higher closer to water and closer to salt marsh (Fig. 3A, B).

We detected northern yellow bats at 48 sites (40%) during winter. We did not find evidence of overdispersion in our data ($\hat{c} = 1.14$, $P = 0.268$), so we used AIC_c to rank our models of detection and occupancy. The only model in our confidence set was the global model, with a weight of 0.97 (Appendix A). Important covariates were rain, basal area, and temperature, which we retained in our occupancy models (Appendix B). Two models were within the con-fidence set of occupancy models: land cover type with a weight of 0.63, and landscape resources with a weight of 0.35 (Table 3). Salt marsh and upland forests were im-portant as were proportion of forest within 250 m, distance to fresh water, and distance to salt marsh (Table 4). Occupancy was lower at salt marsh and upland forest sites compared to bottomland forest sites (Fig. 2C) and higher closer to fresh water and salt marsh (Fig. 3C, D).

Occupancy was also higher in areas with a higher proportion of forest within 250 m (Fig. 3E).

DISCUSSION

Our results provided support for our hypotheses that nocturnal habitat use by myotis bats, tri-colored bats, and northern yellow bats would vary based on morphology and ecology, and that some species would shift their habitat use between summer and winter. During summer, habitat use was related to characteristics that we would expect based on how bats of differing morphology interact with their environment. The large fast-flying northern yellow bat used open areas, the more maneuverable myotis bats were associated with forests, and the edge-space foraging tri-colored bat used both open and closed cover types across the landscape. When resource availability, forest structure, and temperature changed with season, we saw that northern yellow bats and tri-colored bats used interior forests. Our results demonstrate that changes in habitat use occurred between seasons and that failure to account for changes in habitat use throughout the year may limit our understanding of important habitat features (Weller et al. 2009).
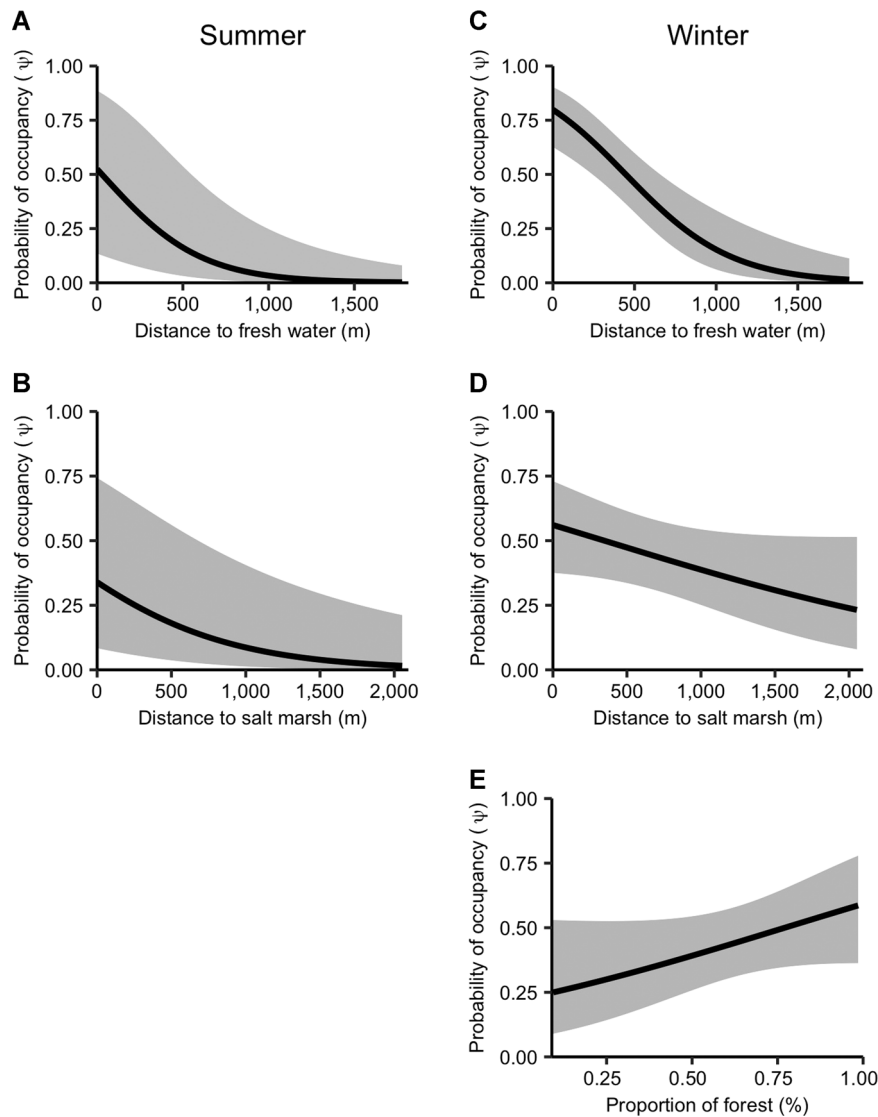
Figure 3. Probability of northern yellow bat site occupancy as a function of A) distance to fresh water in summer and B) distance to salt marsh in summer, C) distance to fresh water in winter, D) distance to salt marsh in winter, and E) proportion of forest in the surrounding 250 m in winter in Bluffton, South Carolina, USA, 2018 and 2019. Shaded areas represent 85% confidence intervals.

Although myotis bat habitat use was not associated with any site characteristics that we measured, the landscape surrounding sites was important in determining habitat use during both summer and winter. Distance to hardwood stands, distance to pine stands, and distance to fresh water were important during both seasons. Greater probability of use in sites close to forested stands reflects myotis bat habitat use elsewhere, where they use sites with high proportions of surrounding forest (Patriquin and Barclay 2003, Ford et al. 2006, Morris et al. 2010, Starbuck et al. 2015). Hardwood stands at our study areas included bottomland hardwood and maritime forests, which provide complex structure from which myotis bat species can glean insects (Ford et al. 2006). Additionally, a variety of forest types provide important roost trees for these myotis bat species. Southeastern myotis are closely tied to bottomland forests for roosting, using basal cavities in trees such as water tupelo, black tupelo (*N. sylvatica*), and sweetgum; Clement

and Castleberry 2013, Fleming et al. 2013), which dominated bottomland forests in our study area. Northern long-eared bats use a diversity of hardwood and pine trees across their range for roosting (Silvis et al. 2016) and limited data from our study area suggest individuals use pine-dominated and bottomland forests for roosting (Shute 2020). Associations with pine and bottomland forests for foraging may indicate that myotis bats in our study, like other species, use foraging habitat close to roost sites to reduce energy used for commuting (Veilleux et al. 2004, Broders et al. 2006). Grouping northern long-eared bat and southeastern myotis calls might have limited our ability to detect potential species-specific differences in habitat use. For example, northern long-eared bats in Kentucky, USA, forage closer to pine stands than hardwood stands in summer (Lacki et al. 2009), whereas southeastern myotis in South Carolina use pine stands less than hardwood stands (Ford et al. 2006). Thus, the importance of proximity to pine

stands may reflect northern long-eared bat habitat use more than southeastern myotis habitat use and the opposite for hardwood stands. Nevertheless, the foraging strategy of both species allows individuals to take advantage of structurally complex forests where they can glean insects. This behavior is especially important in facilitating foraging during cool periods (Burles et al. 2009, Shively et al. 2018) and would explain why these species may not need to shift their foraging and habitat use strategies during winter.

Tri-colored bat habitat use in summer was distributed across most of the landscape, counter to what we predicted. Some studies have reported that tri-colored bats are associated with edges, high canopy closure, and low vegetation density during summer (Ford et al. 2006, Loeb and O'Keefe 2006, Morris et al. 2010). In our study, predicted tri-colored bat occupancy was 85% in summer, which is likely why we had difficulty explaining variation in occupancy among sites. Tri-colored bats displayed generalist behavior during summer in our study area, similar to tri-colored bats in the study by Menzel et al. (2002) who reported that habitat use by this species did not differ among open canopy, closed canopy, harvested, and unharvested forests. We might have seen differences in use among land cover types if we had used relative activity as a measure of use instead of occupancy. Because occupancy models treat sites with different levels of activity (e.g., different numbers of passes per night) the same, it was not possible to determine how levels of use varied with habitat.

In contrast to summer, tri-colored bat habitat use in winter was higher in bottomland forests, ponds, and fields than in salt marsh and upland forest, potentially reflecting changes in resource availability and environmental conditions between seasons. Although insect abundance does not affect bat activity during summer in coastal South Carolina (Moore and Best 2018), it is possible that during the winter when temperatures are lower, bats either remain torpid or constrain habitat use to areas where insects are present. When temperatures decrease, insects are not able to sustain flight for prolonged periods of time (Rowley and Graham 1968) and bottomland forests provide structure for insects to rest on. Additionally, bottomland forests provide water sources and higher temperatures than open areas, and consequently, potentially higher abundance of insects (Janzen and Schoener 1968, Li et al. 2015). Fields and ponds received similar use to bottomland forests and likely also provided occasional food resources for tri-colored bats during winter. Specifically, freshwater ponds and forest edges may be places to forage and drink even when resources may be limited on the landscape (Verboom and Huitema 1997, Morris et al. 2010, Stahlschmidt et al. 2012).

The association of northern yellow bats with open land cover types in the summer supported our prediction that forests are likely too cluttered for efficient foraging by this relatively large species (Norberg and Rayner 1987, Morris et al. 2010). In contrast, northern yellow bats used bottomland forests in the winter. Bottomland forests were mostly dominated by deciduous hardwoods like tupelo and

sweetgum, and upland forests were mostly dominated by evergreen species including live oak and pines. As a result, canopy closure decreased by about 30% in bottomland forests during winter but only decreased by about 11% in upland forests. The winter reduction in clutter in bottomland forests may open flight space for this and other species, making these sites easier to maneuver in and forage (Brigham et al. 1997, Loeb and O'Keefe 2006, Suarez-Rubio et al. 2018). Additionally, during winter nights, forests retain more heat than open areas (Li et al. 2015) and are more protected from wind, potentially causing flying insects to be more abundant. Thus, forests may provide more food for hawking bat species like the northern yellow bat throughout the winter. Further, higher temperatures in interior forests during winter may ease thermoregulatory constraints associated with the decrease in body temperature during foraging (Reichard et al. 2010, Klüg-Baerwald et al. 2016).

Northern yellow bats were more likely to use salt marsh sites and sites closer to salt marsh in the summer, providing support that this was an important land cover type for the species. During winter, use of salt marsh sites was low even though use was high at sites close to the salt marsh. Shifts in insects away from the more open salt marsh where there are cooler temperatures, little resting space, and no protection from the elements (Verboom and Huitema 1997, Li et al. 2015) may explain low use of this land cover type in winter. But northern yellow bats may continue to use sites close to salt marsh during winter because individual home and roosting ranges remain in the same general area throughout the year. Further, the decline in probability of use of salt marshes between summer and winter (83% to 14%; Fig. 2B, C) was greater than the decline in use of fields (89% to 50%; Fig. 2B, C) between summer and winter. Differences in changes in seasonal habitat use of these 2 open land cover types may have been due to relative changes in insect abundance that were specific to fields and salt marshes. In winter, insect abundance may have been higher in fields than the salt marsh because fields in our study area were typically surrounded by more hard edge and edges are positively related to insect density because they provide more protection for insects than open areas (Verboom and Huitema 1997).

Our data suggest that sources of fresh water were important for multiple species during summer and winter. Ponds are important for many bats, especially in human-dominated areas (Henderson and Broders 2008, Fabianek et al. 2011, Ancillotto et al. 2019, Parker et al. 2019) and human-constructed ponds provided most of the permanent freshwater sources for bats in our study areas. Permanent water sources are particularly important in the Coastal Plain and on coastal islands where naturally occurring freshwater sources can be scarce and ephemeral. The presence of ponds as permanent water sources allows bats to easily access fresh water throughout the year and potentially exploit water features with an abundance of insect prey.

There are several likely reasons why we did not observe support for our prediction that residential development

would influence habitat use for our study species. First, disturbance and fragmentation associated with low-density housing development in our study areas may have increased complementation (i.e., access to multiple habitats and resources needed at various times of day; Dunning et al. 1992). Complementation can increase bat activity by providing access to both roosting and foraging sites (Ethier and Fahrig 2011), and intermediate disturbance due to low-level development may increase access to a diversity of resources (Gehrt and Chelsvig 2004, Rhodes and Catterall 2008, Threlfall et al. 2011). At a broader spatial scale, for example across the Atlantic Coastal Plain, habitat use may be influenced by urbanization because of more variable degrees of habitat loss and human disturbance (Caryl et al. 2016). Further, some of these species may have already shifted their habitat use or abandoned patches as a result of disturbance or removal of habitat and replacement by low-density residential development.

Although some researchers reported that bats shift roost habitat use and other mammals display shifts in den site use between summer and winter (Mormann and Robbins 2007, Hein et al. 2008, Goldberg et al. 2020) and there has been some focus comparing seasonal differences in bat activity (Grider et al. 2016), little attention has been paid to nocturnal foraging habitat use of bats during winter (Loeb 2020). In this study, we demonstrated that there are some differences in habitat use between summer and winter for specific species. Our study does not, however, assess potential within-season shifts in habitat use, which others have demonstrated (Vasko et al. 2020). It is possible that, especially in winter when conditions are highly variable and bats and their prey experience more thermoregulatory stress, habitat use may vary within season based on environmental conditions. A lack of understanding of how bats and other animals interact with their environment throughout the year may obscure the full scope of habitat associations and needs.

Across landscapes and ecosystems, bats face loss of habitat features because of continued land use change. Anthopogenic disturbance (e.g., clearing of forests for urban and suburban development, increased agricultural production, clear cutting) remove and alter forested landscapes that bats rely on during their lives. The loss, fragmentation, and degradation of these landscapes and forests has the potential to threaten bat populaitons, some of which may already face other conservaiton threats. As a result, understanding important habitat features and year-round habitat assocations that can support healthy bat populations is important to long-term conservation.

MANAGEMENT IMPLICATIONS

Our data suggest that maintaining a diversity of land cover types and features that are important to bat species during different times of the year is important for their conservation. Specifically, bottomland hardwood forests appear to benefit multiple species throughout the year in coastal South Carolina and management activities that retain these forests may be especially important. In addition, heterogeneity of the landscape provides habitat for interior forest species and open areas like fields and the salt marsh benefit the larger and edge-associated species; however, even larger and edge-associated species may still rely on forests during particular parts of the year. Salt marsh in this region is under threat because of construction associated with boating and development activity. As a result of this threat, the conservation of salt marsh is important to ensure the habitat needs of northern yellow bats are met. Additionally, continued construction of small ponds would likely benefit these species by providing access to fresh water and potentially higher insect abundances. Although suburban development in our study did not appear to influence habitat use, more intense development may affect the ability of some bat species to remain on the landscape when forest loss becomes great. This is especially true if forests of importance for roosting and foraging are removed in development. Finally, an understanding of how habitat use changes over seasons is important for making accurate management decisions.

ACKNOWLEDGMENTS

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

APPENDIX A: DETECTION MODEL SELECTION

Table A1. Confidence sets for detection analyses of myotis bats, tri-colored bats, and northern yellow bats in summer and winter 2018 and 2019 at 3 study areas in Bluffton, South Carolina, USA. We ranked models by second order Akaike's Information Criterion (AIC$_c$) or quasi-AIC$_c$ (QAIC$_c$) and the confidence sets include models with ΔAIC$_c$ or ΔQAIC$_c$ < 4; K = the number of parameters in the model.

Models	K	QAIC$_c$ or AIC$_c$	ΔQAIC$_c$ or ΔAIC$_c$	Model likelihood	QAIC$_c$ or AIC$_c$ weight
Myotis bats					
Summer					
Rain	16	380.92	0.00	1.00	0.36
Null	15	381.39	0.47	0.79	0.28
Temperature	16	383.54	2.61	0.27	0.10
Full weather	17	383.57	2.65	0.27	0.09
Year	16	384.02	3.10	0.21	0.08
Clutter	17	384.29	3.37	0.19	0.07
Winter					
Temperature	16	562.15	0.00	1.00	0.42
Full weather	17	563.22	1.06	0.59	0.25
Null	15	564.95	2.80	0.25	0.10
Date	17	565.67	3.51	0.17	0.07
Clutter	17	566.00	4.85	0.15	0.06
Tri-colored bat					
Summer[a]					
Null	15	176.22	0.00	1.00	0.32
Temperature	16	176.33	0.06	0.97	0.31
Rain	16	178.29	2.01	0.37	0.12
Year	16	178.84	2.56	0.28	0.09
Full weather	17	178.90	2.63	0.27	0.09
Date	17	179.98	3.71	0.16	0.05
Winter					
Global	17	868.44	0.00	1.00	0.68
Full weather	12	870.50	2.06	0.36	0.24
Northern yellow bat					
Summer[a]					
Null	14	280.53	0.00	1.00	0.38
Temperature	15	281.49	0.95	0.62	0.23
Year	15	282.72	2.18	0.34	0.13
Rain	15	282.99	2.46	0.29	0.11
Full weather	16	284.12	3.59	0.17	0.06
Date	16	284.44	3.91	0.14	0.05
Winter					
Global	16	550.99	0.00	1.00	0.97

[a] We used QAIC$_c$ in this analysis because of evidence of overdispersion.

APPENDIX B: DETECTION COVARIATE TABLE

Table B1. Estimates, standard errors, and 85% confidence intervals for covariates in top models for myotis bat, tri-colored bat, and northern yellow bat detection in summer and winter 2018 and 2019 in Bluffton, South Carolina, USA. Important covariates have 85% confidence intervals that do not overlap zero. All beta estimates are based on standardized covariates.

	Estimate	SE	Lower CI	Upper CI
Myotis				
Summer				
Intercept	−0.87	0.24	−1.22	−0.52
Rain	−0.47	0.36	−0.99	0.06
Temperature	0.07	0.17	−0.17	0.32
Basal area	−0.11	0.23	−0.45	0.22
Midstory	0.34	0.17	0.09	0.58
Year 2	0.01	0.37	−0.53	0.55
Winter				
Intercept	−1.02	0.15	−1.24	−0.81
Temperature	0.32	0.13	0.14	0.50
Rain	−0.14	0.13	−0.33	0.05
Date	0.56	0.28	0.16	0.95
Date^2	−0.09	0.05	−0.15	−0.02
Tri-colored bats				
Summer				
Intercept	1.76	0.27	1.37	2.14
Temperature	0.39	0.26	0.02	0.76
Rain	−0.12	0.20	−0.42	0.17
Date	0.24	0.29	−0.18	0.66
Date^2	0.23	0.28	−0.17	0.64
Year 2	−0.13	0.49	−0.83	0.57
Winter				
Intercept	−0.68	0.17	−0.93	−0.44
Temperature	1.01	0.11	0.85	1.17
Rain	−0.20	0.08	−0.31	−0.08
Basal area	−0.19	0.09	−0.33	−0.06
Midstory	0.10	0.08	−0.01	0.22
Date	0.73	0.26	0.36	1.10
Date^2	−0.13	0.04	−0.19	−0.07
Year 2	0.34	0.21	0.04	0.64
Northern yellow bats				
Summer				
Intercept	0.31	0.19	0.03	0.59
Temperature	0.23	0.18	−0.03	0.49
Rain	−0.05	0.22	−0.36	0.27
Date	−0.24	0.22	−0.55	0.07
Date^2	0.06	0.13	−0.12	0.24
Year 2	0.22	0.34	−0.28	0.71
Winter				
Intercept	−1.26	0.26	−1.64	−0.89
Rain	−0.35	0.15	−0.56	−0.14
Basal area	−0.81	0.19	−1.09	−0.53
Midstory	0.00	0.13	−0.18	0.18
Temperature	1.01	0.15	0.79	1.23
Date	0.04	0.33	−0.44	0.51
Date^2	−0.04	0.05	−0.11	0.04
Year 2	0.07	0.29	−0.35	0.49