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Habitat Associations of Overwintering Bats in Managed Pine Forest Landscapes

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Abstract: *Research Highlights:* Seasonal variation in environmental conditions coinciding with reproductive and energetic demands might result in seasonal differences in species-specific habitat use. We studied a winter assemblage of insectivorous bats and found that species acted as habitat generalists during winter compared to expectations based on the summer active season. *Background and Objectives:* In temperate regions, seasonal fluctuations in resource availability might restructure local bat assemblages. Initially perceived to only hibernate or migrate to avoid adverse winter conditions, temperate insectivorous bats appear to also employ intermediate overwintering strategies, as a growing body of literature suggests that winter activity is quite prevalent and even common in some lower latitude areas. However, to date, most studies have exclusively assessed habitat associations during summer. Because habitat use during summer is strongly influenced by reproduction, we hypothesized that habitat associations might differ during the non-reproductive winter period. We used acoustic monitoring to assess the habitat associations of bats across a managed pine landscape in the southeastern United States. *Materials and Methods:* During the winters of 2018 and 2019, we deployed acoustic detectors at 72 unique locations to monitor bat activity and characterized vegetation conditions at two scales (microhabitat and landscape). We used linear mixed models to characterize species-specific activity patterns associated with different vegetation conditions. *Results:* We found little evidence of different activity patterns during winter. The activity of three species (hoary bat: *Lasiurus cinereus*; southeastern myotis: *Myotis austroriparius*; and tricolored bat: *Perimyotis subflavus*) was not related to vegetation variables and only modest relationships were evident for four other species/groups (big brown bat: *Eptesicus fuscus*; eastern red bat: *L. borealis*; Seminole bat: *L. seminolus*; evening bat: *Nycticeius humeralis*; and Brazilian free-tailed bat: *Tadarida brasiliensis*). *Conclusions:* During winter, the bats in our study were active across the landscape in various cover types, suggesting that they do not exhibit the same habitat associations as in summer. Therefore, seasonal differences in distributions and habitat associations of bat populations need to be considered so that effective management strategies can be devised that help conserve bats year round.

Keywords: bat; activity; winter; southeast; acoustic detectors; forests; Louisiana; Texas; forest management

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1. Introduction

Considerations of how species adapt to varying ecological conditions can provide important insights into understanding the structure of local communities [1]. Seasonal changes in resource availability can cause concomitant season-specific differences in community structure [2,3]. Many temperate species avoid the challenges of winter by either hibernating or migrating and effectively removing themselves from winter-active communities [2,4], while others remain present and active year round but are subjected to changing environmental conditions [2]. However, the degree to which species remove themselves from the winter-active community varies, resulting in a gradient of responses.

In seasonal environments, intrinsic demands (e.g., reproduction during summer when resources are abundant) regularly coincide with seasonal resource availability. Consequently, there are opportunities or necessities for species to be more selective in their foraging strategies, roosting requirements, and therefore habitat use. During winter, intrinsic demands might be diminished alongside reduced resource availability, which might allow or require species to adopt more generalist strategies. Some species adopt specialized foraging strategies during winter (e.g., waterfowl reducing niche overlap; [5]), but restricted food webs in winter with limited bottom-up production typically favor generalists [2] with broader diets and habitat preferences than specialists [6]. Species might select particular cover types during summer, but those that remain active in winter (to varying degrees) might be less selective as they adopt more generalist strategies during this season.

Temperate insectivorous bats are a particularly relevant taxonomic group for addressing gradients of seasonal specialization. These mammals are particularly susceptible to winter conditions, as low temperatures lead to both the low availability of flying insect prey and high thermoregulatory costs [7,8]. As mobile heterotherms, temperate North American bats possess the unique ability to either hibernate or migrate to regions with milder temperatures [9–11], and thus alter their active state seasonally [2]. However, in North America, there is growing evidence from anecdotal records (summarized by [12]) and acoustic monitoring surveys [13–26] that bats remain active, to varying degrees, throughout winter, especially on warmer nights and at lower latitudes [17,20,24–27]. Even among migratory species, there is evidence that some individuals overwinter at temperate latitudes, alternating between periods of hibernation and activity (eastern red bats: *Lasiurus borealis*, [28,29]; hoary bats: *L. cinereus*, [30]; silver-haired bats: *Lasionycteris noctivagans*, [31]; Brazilian free-trailed bats: *Tadarida brasiliensis*, [32]). With the ability to enter torpor, bats can fluctuate between active and inactive states as temperatures vary, with generally greater winter activity at southern latitudes in response to milder winter conditions [33]. Thus, the idea that bats in temperate regions hibernate or migrate to avoid winter conditions might be oversimplified, especially at lower latitudes. It appears that bats might be more labile in their overwintering strategies, using torpor during unfavorable conditions and becoming active to exploit the limited resources that are available. It is important to consider habitat associations of winter-active bats, particularly in regions where winter activity might be common.

While the body of literature for winter activity in bats is growing, there are limitations in our ability to make inferences about habitat associations during this time of year. At high latitudes, winter bat activity is quite low with few active species [13,18]. Small sample sizes make the identification of winter habitat relationships difficult and limit the ability to infer differences in habitat associations, consequently restricting niche partitioning among species. Studies at lower latitudes have documented considerably higher winter activity and greater species richness, but have often been conducted at hibernacula [20], at coarse scales [17,24], or with a limited assemblage of bats [26]; therefore, they have not been designed to make inferences about the activity patterns of an entire assemblage of bats at a landscape scale. As a result, no study to date has comprehensively identified habitat associations across species in a winter active bat assemblage in temperate regions of North America.

Habitat associations are especially important to consider in managed landscapes. Many bat species are dependent on forests for essential activities including foraging, roosting, and reproduction [34]. The harvest of older forest age classes or the conversion to non-forest land uses might be the most influential factors for many bat species. While the loss of forests to other land uses or the harvest of older age classes might negatively affect some bat species [35–37], the subsequent fragmentation of contiguous older forest age classes increases bat activity for edge and open-air specialists that use linear features such as roads and forest edges for navigation and foraging [38–42]. Additionally, the presence of younger forest age classes that lack the clutter associated with closed-canopy forests might facilitate feeding opportunities [43–47]. Therefore, forest management practices, including forest harvest, can contribute to maintaining bat populations in managed forest landscapes, which contain a diversity of forest types and ages [48,49].

To date, studies of habitat use or activity patterns in managed forest landscapes have been mostly conducted during summer [38,39,50–53], when female bats select roosts and areas to meet the demands of producing and rearing offspring [54–56]. Conversely, little is known about winter habitat associations outside of cave systems [12], and studies in managed forests have been concentrated to areas near the Atlantic Coast [17,24–26]. During winter, bats are not subject to the energetic challenges of reproduction and, therefore, different patterns of habitat association might result from seasonal influences on foraging and roosting ecology. To better understand this knowledge gap, we used acoustic detectors to examine the habitat associations of bats during winter in a managed forest landscape. Although activity levels cannot be used to quantify habitat use [50], they do provide an indication of general associations of bats across cover types, including foraging activity and during different environmental conditions (e.g., temperature changes). We predicted that bats would be ubiquitous across the landscape during winter and not show strong habitat associations. Species associated with particular cover types during winter would suggest some level of winter specialization, but a lack of differential activity might suggest bats employ a generalist strategy during winter.

2. Methods

2.1. Study Area and Site Selection

Our study region was located at the western edge of the historical distribution of longleaf pine (*Pinus palustris*) forests. Uneven-aged longleaf pine forests historically dominated much of the southeastern United States [57], but these forests have declined by >95% as a result of urbanization and agriculture [58,59]. Much of the forest in the region now consists of intensively managed pine (*Pinus* spp.) forests mixed with other forest types and land uses [60,61]. We concentrated our survey efforts on three managed pine forest landscapes in the South Central Plain ecoregion [62] of central Louisiana (Bienville, Jackson, and Winn Parishes) and eastern Texas (Newton County; Figure 1). Forest stands in our study landscapes were largely comprised of planted loblolly pine of various ages, from newly established stands to stands thinned and ready for final harvest at approximately 25–35 years of age. Hardwood forests were dominated by oak (*Quercus* spp.), sweet gum (*Liquidambar styraciflua*), American beech (*Fagus grandifolia*), and bald cypress (*Taxodium distichum*), the latter of which typically occurred in emergent wetlands. Jackson-Bienville, LA, was the northernmost study region consisting of the most contiguous forests and oldest stands. Winn, LA, was highly fragmented but possessed contiguous forest of older trees primarily along waterways. Newton, TX, occurred south of the Toledo Bend Reservoir and was comprised primarily of younger conifer stands with dense understory.

2.2. Acoustic Detector Deployment and Monitoring

We examined four stand age classes grouped into 20-year intervals. We selected 6 locations within each stand age class for 72 detector sites (6 replicates of 4 age classes within each of Jackson-Bienville, Winn, and Newton). We used 12 acoustic detectors (SM4BAT-FS with SMM-U1 microphone; Wildlife Acoustics, Inc., Maynard, MD, USA) deployed weekly from 30 December to 11 March in the winters of 2017/2018 and 2018/2019. We mounted microphones 3 m above ground [63] in areas with limited understory because echolocation call structure is altered when bats fly in cluttered environments, causing difficulty when trying to identify calls to species [64]. Detectors recorded bat passes from

30 min before sunset to 30 min after sunrise and we selected additional parameters of the detectors to reduce the influence of background noise and increase the likelihood of detection: gain—12 dB; 16k high filter—off; sample rate—256 kHz; minimum duration—1.5 ms; maximum duration—none; minimum trigger frequency—16 kHz; trigger level—12 dB; trigger window—3 s; and maximum length—15 s. During each round of recording, we deployed detectors at each site for a minimum of 7 days and moved them to the next site as weather permitted. Due to low activity in the first round of 2018, we redeployed detectors at those locations in the third round, thus sampling the first 12 sites twice, while only surveying the second round once. To account for seasonal variability, we reversed the rounds and sites deployed during the first and third efforts in 2019 with the second round of deployments from 2018. This resulted in a minimum of 21 days of recording at each detector location over the two years. To obtain sunset temperature (°C) at each site, we suspended an iButton (model: DS1921G iButtonLink, LLC., Whitewater, WI, USA) from the base mounting flange of each acoustic detector. iButtons recorded the temperature every 10 min, allowing us to use the temperature at the time of recording that was nearest to sunset to determine site-specific sunset temperature for that day.

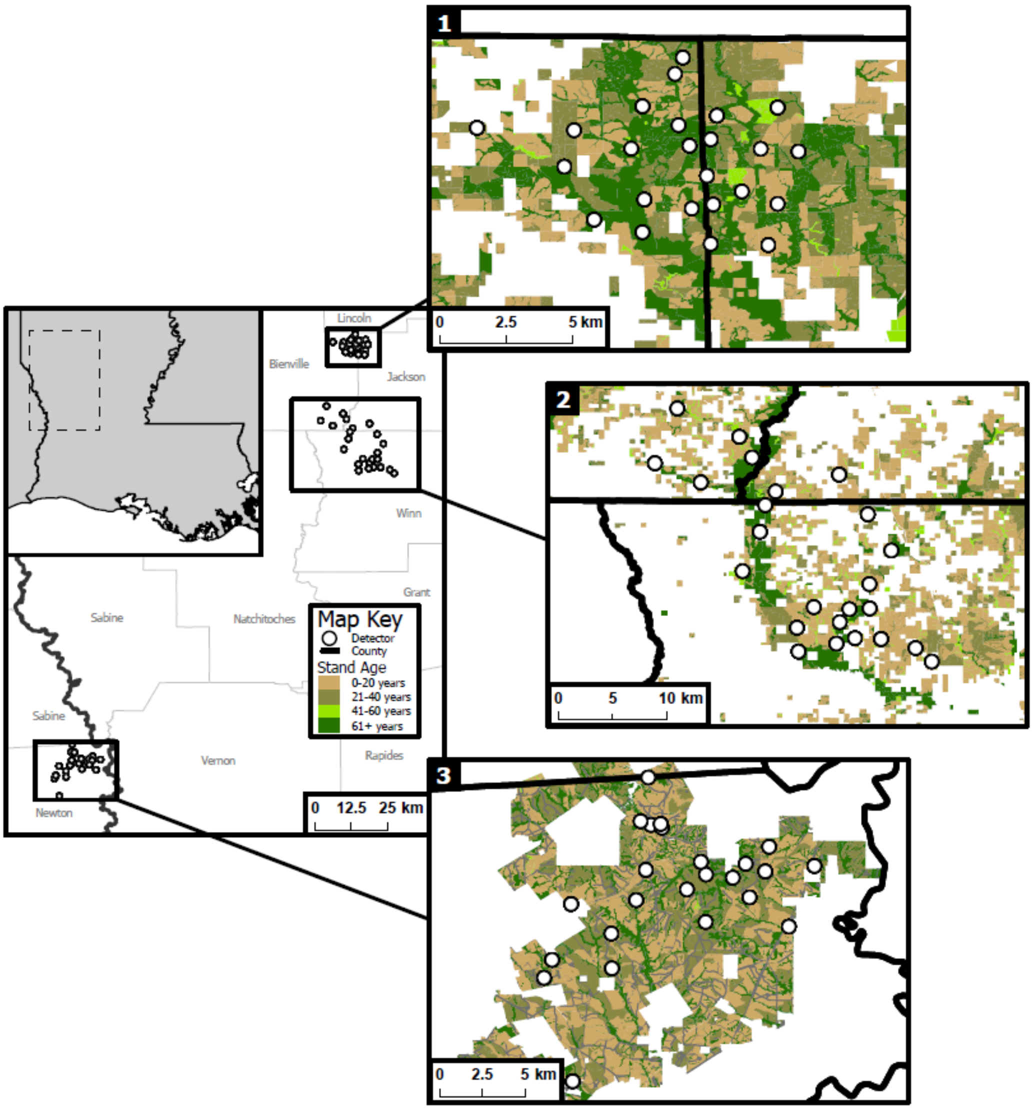

Figure 1. Twenty-four detector locations were placed in each of three main study sites: (**1**) Jackson-Bienville, LA, (**2**) Winn, LA, and (**3**) Newton, TX during the winters of 2018 and 2019.

2.3. Acoustic Analysis

Twelve bat species occur in the South Central Plain: Rafinesque's big-eared bat (*Corynorhinus rafinesquii)*, big brown bat (*Eptesicus fuscus*), eastern red bat *(Lasiurus borealis*), hoary bat (*L. cinereus*), northern yellow bat (*L. intermedius*), Seminole bat (*L. seminolus*), silver-haired bat (*Lasionycteris noctivagans*), southeastern myotis (*Myotis austroriparius*), northern long-eared bat (*M. septentrionalis*), evening bat (*Nycticieus humeralis*), tricolored bat (*Perimyotis subflavus*), and Brazilian free-tailed bat (*Tadarida brasiliensis*; [65–67]). Eastern red bats and Seminole bats cannot be differentiated by echolocation call, so we subsequently grouped them in our analyses. Northern long-eared bat calls were readily differentiated from southeastern myotis by having short durations and steep slopes. We analyzed echolocation passes using two automated identification programs: SonoBat v4.2.2 southeast region pack SE[C20170529]; (SonoBat, Arcata, CA, USA) and Kaleidoscope Pro v5.1.9i (Wildlife Acoustics Inc., Maynard, MD). We excluded recordings that were assigned conflicting identifications by the two programs. We manually vetted all remaining recordings with corresponding identifications and excluded obvious misidentifications (e.g., low frequency noise mistakenly identified as hoary bats).

2.4. Microhabitat Assessment

At each detector location, we measured the microhabitat variables that could influence species-specific activity patterns at a local scale. We used a 0.1 ha circular plot (17.8 m radius) centered on the detector [63,68,69]. We used a clinometer (Suunto Oy: Vantaa, Finland) to assess the overstory and understory (if applicable) height (m) within the stand and measured canopy cover using a GRS densitometer (Forestry Suppliers, Inc: Jackson, MS, USA). We visually estimated the sub-canopy clutter by standing at the base of the detector and approximating the amount of understory vegetation in each cardinal direction, averaging the percentage across all four directions. We measured the diameter at breast height (DBH; cm) of each tree, categorizing all trees with DBH > 5 cm [63] as either a hardwood or conifer, whether the tree was part of the overstory or understory, and if the tree was alive or dead. We used ArcMap (v10.5.1; ESRI, Redlands, CA, USA) to measure the distance from each detector to the nearest road [70,71] and water source [72]. We also obtained elevation data (m) by using the extract value feature to collect the raster values at each point [73].

2.5. Landscape Assessment

To estimate landscape characteristics, we collected raster imagery from the 2016 USGS National Land Cover Dataset (NLCD) that provided 16 different land cover classes at 30 m resolution [74]. Perennial ice and cultivated cropland did not occur in our study region; the remaining 14 land cover classes are listed in Table 1. Using ArcMap (v10.5.1), we clipped the NLCD dataset at 450 m and 1000 m buffers around each detector location. These distances have been estimated as home range sizes for foraging bats [52,75]. We analyzed these images in FRAGSTATS v4 [76] to obtain percent land cover for each of the 16 landcover types, edge (m), and habitat variable aggregation or dispersion (i.e., contagion). To obtain the forest core area and edge length in the vicinity of each detector location at the two buffer ranges, we reclassified the raster image to group the forest types (deciduous forest, evergreen forest, and mixed forest) into a single cover type.

2.6. Statistical Analysis

We completed all statistical analyses in R (v4.1.2; [77]) including packages *nlme* [78] and *multcomp* [79]. We used principal components analysis (PCA; [80]) to reduce the number of variables characterizing vegetation and landscape. We used the broken stick method as a stopping rule to eliminate the principal components (PCs) that did not account for sufficient variance in the original variable matrices [81]. We considered factor loadings ≥ 0.30 to identify habitat variables that characterized significant PCs [82].

Table 1. Principal components of microhabitat and landscape variables measured from 450 m (L450) and 1000 m (L1000) buffers. Only those PC's that exceeded expectations from the broken stick stopping rule are included. Variable loadings ≥ 0.3, highlighted in bold, are considered explanatory variables of each principal component.

Microhabitat	H-PC1	H-PC2	H-PC3	Landscape	L450-PC1	L450-PC2	L1000-PC1	L1000-PC2
Stand Age (Years)	**0.36**	−0.22	<0.01	Landcover Diversity	**−0.40**	−0.29	**−0.34**	**−0.30**
% Canopy Clutter	0.27	0.11	−0.18	Total Edge (m)	**−0.38**	−0.04	**−0.35**	−0.02
% Understory Clutter	−0.04	0.05	**0.43**	Total Forest Edge (m)	**−0.38**	0.21	**−0.40**	−0.04
# Trees	0.29	**0.42**	−0.12	Total Core Area (m^2)	**0.42**	−0.01	**0.38**	0.10
Mean DBH (cm)	−0.04	**−0.45**	**−0.33**	Total Contagion	0.28	0.09	**0.41**	0.08
Mean Tree Height (m)	0.11	**−0.38**	**−0.33**	% Open Water	0.09	−0.12	0.02	−0.17
# Conifers	−0.22	**0.39**	**−0.30**	% Developed, Open Space	−0.11	0.27	−0.12	0.08
# Hardwoods	**0.42**	0.01	0.15	% Developed, Low Intensity	−0.23	0.22	−0.18	0.07
# Overstory Trees	0.01	**0.47**	**−0.35**	% Developed, Moderate Intensity	−0.08	0.26	−0.18	**0.31**
# Understory Trees	**0.39**	0.05	0.22	% Developed, High Intensity	−0.16	0.06	−0.11	0.19
# Snags	**0.34**	0.02	−0.05	% Barren Land	−0.05	0.16	−0.10	0.24
% Snags	**0.31**	−0.02	−0.05	% Deciduous Forest	−0.13	−0.16	−0.02	−0.17
Distance to Water (m)	−0.28	−0.10	−0.08	% Coniferous Forest	0.09	**0.55**	0.02	**0.52**
Distance to Road (m)	−0.11	0.01	**0.43**	% Mixed Forest	−0.07	−0.02	−0.11	0.17
Elevation (m)	−0.12	0.13	0.26	% Shrub/Scrub	−0.27	−0.04	−0.25	−0.26
				% Hay/Pasture	NA	NA	0.02	−0.03
				% Herbaceous	−0.25	−0.03	−0.29	0.13
				% Woody Wetlands	0.12	**−0.50**	0.17	**−0.44**
				% Emergent Wetlands	−0.13	−0.22	−0.05	−0.25
Proportion of Variance	0.304	0.178	0.152		0.223	0.139	0.245	0.141

Number of.

We quantified bat activity (either overall or species-specific) as the number of passes recorded per night. To avoid bias in the interpretation of activity patterns (i.e., inferring absence when ambient temperature was cooler than that expected for active bats), we omitted nights where low temperatures likely inhibited bat activity (false negatives). Different bat species respond to low temperatures differently, and species in our study sites vary widely in the lower temperature threshold for activity. We calculated this lower temperature threshold for each species as the 10th percentile of the temperature distribution of a random subset of identified passes for a given species, as described in [83] (Table 2). Although some activity was recorded below these temperature cutoffs, these detections were likely atypical.

Table 2. Nights above the temperature threshold identified in [83] were retained for the analysis of habitat associations. Those below this threshold were discarded even if passes were recorded and identified to species.

Species	# of Detector Nights Present	Temperature Cutoff (°C)	# of Detector Nights Present Above Threshold	% Detected Nights Discarded
All Species	937	11.5	657	29.9%
Big brown bat	182	15.5	145	20.3%
Eastern red/Seminole bat	609	12	517	15.1%
Hoary bat	134	10	128	5.2%
Southeastern myotis	389	7	364	6.4%
Evening bat	102	9.5	96	5.9%
Tricolored bat	256	14.0	221	13.7%
Brazilian free-tailed bat	158	8.5	153	3.2%

Number of.

We used linear mixed models to test if microhabitat or landscape PCs were related to bat activity. We fit a model for overall bat activity and separate models for each species. Each model included microhabitat and landscape PCs as predictor variables, and temperature at sunset as a covariate. We included site as a random effect to account for multiple nights of sampling at each site. We assessed overall model significance with a likelihood ratio test to compare the model with a null model. Given that the overall model was supported, we report parameter estimates and *p*-values for each significant effect.

3. Results

During the winters of 2018 and 2019, we recorded for 1576 detector nights and documented 36,724 bat passes, of which 14,041 were classified to species (38.2%). There were few recordings of the northern yellow bat, silver-haired bat, Rafinesque's big-eared bat, and northern long-eared bat, and because recordings from each of these species represented <1% of all identified passes (n < 140 passes for each species), we excluded them from further analyses (Table 3). The most common identification was the eastern red/Seminole bat, representing 43.7% of identified passes. We recorded bats at all survey locations (n = 72; Table 3) and eastern red/Seminole bats were the only species/grouping at all locations. After removing nights below the respective temperature threshold for each species, we retained at least 70% of nights when activity was detected for a given species for analyses (Table 2).

Table 3. Number of passes recorded for each species across all detector locations during winter survey efforts in 2018 and 2019. Number of detector locations where each species was recorded and the percentage of sites (n = 72).

Species	Number of Passes	Number of Sites Detected	Percentage of Sites Detected	Mean Number of Bat Passes per Site per Night (±SE)
All Bats	36,724	72	100%	24.0 ± 3.6
Rafinesque's big-eared bat *	12	8	11.1%	0.008 ± 0.003
Big brown bat	2711	50	69.4%	1.8 ± 0.4
Eastern red/Seminole bat	6129	72	100%	3.85 ± 0.4
Hoary bat	608	34	47.2%	0.4 ± 0.1
Northern yellow bat *	119	6	8.3%	0.03 ± 0.02
Silver-haired bat *	52	15	20.8%	0.07 ± 0.03
Southeastern myotis	1900	64	88.9%	1.1 ± 0.1
Northern long-eared bat *	101	34	47.2%	0.07 ± 0.02
Evening bat	344	37	51.3%	0.22 ± 0.06
Tricolored bat	1725	56	77.8%	1.1 ± 0.2
Brazilian free-tailed bat	340	50	69.4%	0.2 ± 0.04

* Too few passes to assess habitat use.

3.1. Principal Components Analysis

Based on the broken-stick criterion, three microhabitat principal components (PCs), two 450 m buffer landscape PCs, and two 1000 m buffer landscape PCs accounted for significant variation in environmental characteristics (Table 1). Three sites accounted for all hay/pasture in the 450 m buffer landscape scale resulting in no variance among the retained sites; thus, we dropped these sites from further analyses (n = 3) and we removed the hay/pasture variable from the remaining sites. Microhabitat PC1 (H-PC1) was related to amount of older hardwood forests, H-PC2 was related to amount of open conifer forest, and H-PC3 was related to greater cluttered understory, fewer conifers, and being away from roads. These three PCs accounted for 63.4% of the overall microhabitat variation. Both the 450 m and 1000 m buffer scales identified the same significant variables in their respective PCs, resulting in collinearity (PC1: r = 0.75; PC2: r = 0.67). Therefore, we removed the 450 m landscape buffer from further analysis as it accounted for less landscape-scale variation (36.2%) than the 1000 m buffer (38.6%). Landscape PC1 at the 1000 m buffer (L1000-PC1) was related to more homogeneous landscapes with less edge and more core area. The second PC (L1000-PC2) was positively related to the amount of conifer forest in the area and negatively related to the area of woody wetland.

3.2. Habitat Association

After accounting for the expected variation in activity with ambient temperature (sunset temperature; Table 4), there was varying, but generally limited, evidence of habitat association during winter in Louisiana and Texas. Overall activity was positively related to L1000-PC2, indicating greater activity at sites with lower landcover diversity, more moderate intensity development, more conifer forest, and less woody wetlands ($F_{1,63} = 4.40$, $p = 0.04$). The same pattern was observed for species-specific activity related to L1000-PC2 in evening bats ($F_{1,63} = 6.98$, $p = 0.01$) and Brazilian free-tailed bats ($F_{1,63} = 7.02$, $p = 0.01$), but the opposite was true for big brown bats ($F_{1,63} = 8.80$, $p = 0.004$). The activity of evening bats was also negatively associated with L1000-PC1 ($F_{1,63} = 4.69$, $p = 0.03$), indicating greater activity at sites with greater landcover diversity, more edge, less core area, and less contagion. There was no evidence for a relationship between activity and microhabitat characteristics except for eastern red/Seminole bats ($F_{1,63} = 13.40$, $p = 0.0005$), and big brown bats ($F_{1,63} = 9.93$, $p = 0.003$) which were positively and negatively related to H-PC3, respectively. The activity of big brown bats was greater at sites with less clutter, larger trees, a greater number of conifers and overstory trees, and closer proximity to roads, while the opposite was true for eastern red/Seminole bats.

Table 4. Results from linear mixed models comparing number of bat passes for a given species with sunset temperature and each principal component of microhabitat and landscape variables. Nights with sunset temperature below the species-specific threshold were excluded, omitting nights when temperature was too low to expect active bats. Significance of predictor variables was only considered for species where the overall model was significant (Model Sig.). For significant terms, we report parameter coefficients and *p*-values.

Species	Model Sig.	Sunset Temp	H-PC1	H-PC2	H-PC3	L1000-PC1	L1000-PC2
All Species	$p < 0.0001$	0.25 ($p < 0.0001$)	n.s.	n.s.	n.s.	n.s.	8.60 ($p = 0.04$)
Big brown bat	$p < 0.0001$	0.06 ($p = 0.002$)	n.s.	n.s.	−1.45 ($p = 0.003$)	n.s.	−2.06 ($p = 0.004$)
Eastern red/Seminole bats	$p < 0.0001$	0.02 ($p = 0.008$)	n.s.	n.s.	1.25 ($p = 0.001$)	n.s.	n.s.
Hoary bat	$p = 0.04$	0.003 ($p = 0.001$)	n.s.	n.s.	n.s.	n.s.	n.s.
Southeastern myotis	$p = 0.18$						
Evening bat	$p < 0.001$	0.003 ($p = 0.0002$)	n.s.	n.s.	n.s.	−0.13 ($p = 0.03$)	0.18 ($p = 0.01$)
Tricolored bat	$p < 0.0001$	0.03 ($p < 0.0001$)	n.s.	n.s.	n.s.	n.s.	n.s.
Brazilian free-tailed bat	$p < 0.0001$	0.004 ($p < 0.0001$)	n.s.	n.s.	n.s.	n.s.	0.10 ($p = 0.01$)

4. Discussion

Bats were active across the region, being recorded at all detector locations (n = 72), and throughout the winter. Therefore, we were able to address winter habitat associations in a diverse assemblage of bats. With >14,000 identified detections from an assemblage of 11 bat species and an analysis of habitat associations at microhabitat and landscape scales, our dataset presents the most extensive analysis of winter bat activity to date and the westernmost survey of winter habitat associations in southeastern pine forests. Despite intentionally deploying detectors in a variety of stand age classes and cover types and incorporating vegetative characteristics measured at three different spatial scales into the analysis, overall bat activity was associated with conifer forest, the most abundant cover type in managed forest landscapes of the South Central Plain ecoregion and within our study areas.

Although limited overall bat activity was accounted for by vegetation characteristics, grouping all species into a single group might obscure patterns of activity as differences in morphology, physiology, and life history characteristics contribute to species-specific habitat use [84–86].

4.1. Species-Specific Habitat Use

Our results suggest that temperate insectivorous bats adopted a habitat generalist strategy during winter. Despite characterizing numerous habitat variables at three different scales (microhabitat, 450 m, and 1000 m), spatial activity patterns were only related to microhabitat for two species/groups, and activity was related to landscape for only three species (Table 4). Furthermore, although two species/groups exhibited different activity patterns based on microhabitat characteristics (eastern red/Seminole bat and big brown bat; Table 4), the principal component characterizing such differences only accounted for 15% of the variation in microhabitat (Table 1). Similarly, landscape-level habitat associations accounted for little variation in the dataset, suggesting only modest variation at larger scales that could affect activity patterns. This lack of habitat associations could be explained by the need for bats to search more broadly for prey, as insect abundance decreases with colder temperatures [87–89], and is consistent with other studies suggesting bats switch roosts more frequently and occupy larger home ranges during winter [29,90]. However, the results from this study differ from those documented in [26], where winter-active bats (tricolored bats and northern yellow bats) shifted habitat association towards ponds and bottomland forests. Our study region lacked elevational variation and the distance to water was never a significant variable at the microhabitat scale due to its prevalence on the landscape (Table 4).

We did not identify enough recordings to assess habitat association for four species in our study area: the northern yellow bat, silver-haired bat, Rafinesque's big-eared bat, and northern long-eared bat. Although these species were recorded in low numbers, three of the four (excluding northern yellow bats) were documented during winter during opportunistic mist netting and culvert surveys (B. R. Andersen, *pers. obs.*). The region does represent the northern distributional extent of northern yellow bats, and while this species has been shown to select for both bottomland hardwood and pine forests in winter [25,26], it appears to be more abundant in coastal areas [91]. Efforts should likely be concentrated on those areas to assess habitat use or association during winter. The notable absence of silver-haired bats was surprising, as these bats are believed to overwinter in the southeastern United States [10] and were commonly detected in winter surveys in North Carolina [24]. A lack of older pine stands (>50 years) in our study region, the preferred cover type for this species in winter [31], might have restricted their occurrence. Future studies should investigate whether overwintering silver-haired bats might be more abundant in older pine forests, including remnant older long-leaf pine forests of the southeastern Unites States. Low numbers of recordings for Rafinesque's big-eared bats could be a result of their low intensity echolocation calls, which decrease the likelihood of detection in acoustic surveys [92–95]. Winter habitat use of Rafinesque's big-eared bats remains poorly understood, but this species has regularly been documented using bridges and culverts as winter roosts in our study region [67,96], and changes in roost selection through the winter indicate that this species is active year round [97]. Future studies should use alternative methods to study their winter activity and habitat use. The winter activity of northern long-eared bats is poorly documented, although surveys have noted winter activity near cave entrances [20,98,99], along rock faces [19], and across the landscape [26]. Northern long-eared bats are not known to occur in eastern Texas [100], but recordings of this species were documented in Newton County, only 100 km southwest of known populations in the Kisatchie National Forest [67,101]. While we cannot confirm the presence of this species in Texas from acoustic recordings alone, the findings in this study should prompt more intensive mist netting and culvert survey efforts to provide the in-hand verification of this federally threatened species.

4.1.1. Big Brown Bat (*Eptesicus fuscus*)

We recorded big brown bats at 50 locations across the study region (69.4% of sites detected) and this was the only species in our study that exhibited habitat associations at both microhabitat and landscape scales. At the microhabitat scale, this species was affiliated with less understory clutter and smaller distances from roads (Table 4). These bats would be expected to use more open-cover types given their size [102–104], and typically roost in areas with less understory clutter [105–107]. These findings correlate with habitat use in summer where big brown bats have been shown to be flexible in their habitat selection [108]. While some studies have noted that they do not appear to be influenced by high clutter environments [52], as observed by their use of early-successional cover types [103], others have documented a negative relationship between big brown bat activity and understory clutter [51,109].

At the landscape scale, big brown bat activity was related negatively to amount of conifers and positively to landcover diversity. While this species is known to be active throughout winter across its range [13,16,22,25], they are commonly associated with buildings in winter [110–112]. Nonetheless, we did not observe a relationship between big brown bat activity and developed landscapes, similar to that observed in other studies [113].

4.1.2. Eastern Red/Seminole Bat (*Lasiurus borealis*/*seminolus*)

The eastern red/Seminole bat group was the most recorded group during winter and the most broadly distributed, occurring at all detector locations (n = 72; Table 3). Despite their prevalence, the only habitat associations identified for this group were with increased cluttered understories, smaller trees, fewer conifers, and more overstory trees away from roads. This observation differs from summer studies where eastern red bats selected less cluttered areas [51,103,104,109,114], and winter mist netting records where eastern red bats were often captured over roads [29]. Eastern red bats appear to be habitat generalists in summer [113,115,116] and exhibit flexibility by foraging in multiple cover types if suitable roosts are available [116]. These bats might implement similar strategies in winter. Seminole bats are known to roost away from edges (e.g., roads) in winter as a potential means to limit exposure to wind and cold temperatures [90]. However, considering that Seminole bats tend towards roosting in conifers during winter [90,117], explanations for this winter habitat association in Louisiana might be less apparent.

The inability to differentiate the echolocation calls of eastern red and Seminole bats potentially prevented us from identifying additional habitat associations for these species. These two species have different roosting preferences in other regions of the US. Eastern red bats predominantly select the foliage of hardwoods during summer [118–121] and winter [29,122], while Seminole bats predominantly use conifers [118,119,123–125] and may be pine obligates [123]. At this time, we are not confident in the ability to separate the very similar echolocation calls of these species. Until these species can be more reliably differentiated acoustically, the use of acoustic sampling to describe habitat associations will remain difficult considering the overlap in their respective winter ranges [10,126].

4.1.3. Hoary Bat (*Lasiurus cinereus*)

Hoary bat activity was low across our study area, being detected at the fewest number of sites among species included in habitat analyses (n = 34, Table 3). Low activity was consistent with other winter studies in the southeastern United States [24,26]. Overall, temperature was the only predictor of occurrence; this species exhibited no habitat associations. Hoary bats may forage above the forest canopy [104], and it is possible that our detectors failed to record echolocating bats. Ultimately, our understanding of the habitat requirements for this large-bodied migrant remain limited, especially in winter. In managed pine landscapes in summer, hoary bats have been shown to use older pine stands [114] and avoid recently clear-cut forests [127]. As a foliage-roosting species, hoary bats are dependent upon forests, roosting in the foliage of hardwoods and conifers during summer [128–131] and winter [117]. Because roost, occurrence, and activity records for this species are quite scarce in the southeastern United States, a lack of data prevents us from drawing many comparisons between our study and others across the broad range of hoary bats.

The overwintering behaviors of *L. cinereus* in the eastern half of its range remain largely unknown. This species has been documented to use long torpor bouts in winter [30,132], but has not been observed retreating to leaf litter as observed in eastern red and Seminole bats [29,90,122,124,133,134]. Acoustic surveys in the eastern United States suggest that hoary bats are disproportionately distributed along the Atlantic Coast during winter [17], but their occurrence along the Gulf Coast remains unknown. Despite being between 150 and 300 km from the coast, our study locations differed from [17] due to a lack of elevational variation. Thus, it is possible that hoary bats in this region can reside further inland. We found no winter habitat associations for hoary bats, emphasizing the need for the continued study of this declining species.

4.1.4. Southeastern Myotis (*Myotis austroriparius*)

Southeastern myotis were the second most broadly dispersed bats across our study region (88.9% of detector locations; Table 3). Summer surveys suggest that activity is most associated with the wetland systems, namely bottomland hardwoods and swamps, that are abundant across the southeastern United States [75,127,135]. This relationship was also found during winter, where southeastern myotis activity was greater around deciduous forests compared to pine forests [25]. Although these forest types were common in our study, we did not find a relationship between southeastern myotis activity and any habitat characteristics that might be associated with bottomland hardwoods. In other parts of their distribution, southeastern myotis do not form large winter colonies and males remain reproductive until spring (as evidenced by enlarged epididymis; [136]). Reproductive activity might explain the high levels of activity and lack of habitat associations. Additionally, populations in the South Central Plain ecoregion occur where cave systems are few or absent. Although other populations of southeastern myotis are known to use non-cave roosts during winter [137], populations in the South Central Plain often use man-made structures (e.g., culverts) as roosts during winter [67,96,138]. Variation in activity and subsequent habitat selection across the distribution of the southeastern myotis may be influenced by the availability of roost structures during winter.

4.1.5. Evening Bat (*Nycticeius humeralis*)

Evening bat activity was low across our study region and occurred at approximately half of the sites (51.3%; Table 3). Winter activity in the southeastern United States is not usual [12,139]. While this species is known to occur into southern Wisconsin during summer [140], it is believed to be migratory [141,142], with wintering populations occurring as far north as southern Missouri [139]. In our study, evening bat activity was greatest in areas where the surrounding landscape consisted of greater land cover diversity, greater forest complexity, more moderate intensity development, more coniferous forest, and less woody wetlands. This differs from winter acoustic surveys in Florida that found associations between evening bat activity and deciduous forests [25], and roosting ecology surveys in Missouri that identified oaks as the primary roost type selected in winter [139]. However, roost surveys during summer documented evening bats predominantly using live and dead pines [119,143]. Because evening bats select for roosts in cavities and under the bark of live trees and often roost solitarily [139], they might have been opportunistically roosting and foraging in the interiors of the conifer forests that were most prevalent in our study region.

4.1.6. Tricolored Bat (*Perimyotis subflavus*)

Tricolored bats were prevalent and quite active throughout winter in our study region (detected at 56 of 72 locations, 77.8%; Table 3), but were not associated with any particular habitats (Table 4). Their frequent use of manmade structures (e.g., culverts) as winter roosts in our study region [67,96,138,144–146] could contribute to this observed lack of association. It is possible that activity could have been concentrated around these structures, or around roadways more generally [144]. However, we did not incorporate distance to nearest structure into our analyses. Because tricolored bats select culverts based on microclimate [138,144,146], the various habitat metrics incorporated into this study (e.g., distance to road, distance to water) do not permit us to make inferences on the presence of suitable manmade roost structures. Little is known about roost use outside of these structures during winter. Tricolored bats have been found to use live hardwoods in bottomland forests on warmer nights [147]. While our model indicated that tri-colored bat activity was related to temperature (Table 4), we found no association between activity and hardwoods. This might indicate that the tricolored bats in our study behave differently than more easterly populations, or the lack of habitat association might be attributed to the relative lack of hardwood forest in this pine-dominated landscape.

4.1.7. Brazilian Free-Tailed Bat (*Tadarida brasiliensis*)

Brazilian free-tailed bats were infrequently recorded throughout our study system, and were detected at 50 sites (69.4%, Table 4). The association between Brazilian free-tailed bat activity and coniferous forest is consistent with findings of winter habitat use in Florida [25]. Due to their proclivity to overwinter in caves and other manmade structures in winter [32,148], it is unlikely that these bats were roosting in the forest.

4.2. Expanations for a Lack of Associations

Based on the few observed effects of microhabitat or landscape, and the low variance explained when effects were observed, our overall conclusion is that there is not strong evidence for winter habitat associations in our study region. Limited differences in spatial activity patterns by overwintering bats might stem from a shift in motivation between seasons. Reproductive events occur throughout most of the year, with pregnancy in spring, parturition, lactation, and spermatogenesis in summer, and copulation in fall, but few copulation events in winter (summarized in [12]). Without the constraints of reproduction (e.g., high energetic demand, proximity to high-quality foraging sites, reliance on high-quality roosts), bats may be more flexible regarding winter habitat associations. In the absence of high reproductive energetic demands or the need to select roost microclimates to promote the growth of offspring, bats in winter may use a broader selection of roost structures [29,90,117,122,124,149] and behave as habitat generalists.

Lack of relationships between bat activity and habitat characteristics could also be attributed to the relative homogeneity of our study landscapes. Although we intentionally selected comparatively diverse cover types, within-stand structure tends to be more homogeneous for managed pine forests than non-managed forests [75,150,151], and recently clear-cut stands also tend to lack structural diversity [152]. Historically, the South Central Plain was primarily comprised of uneven-aged longleaf pine savannas with spacious understories intermixed with other cover types [57], but large areas within this region now consist of even-aged loblolly–shortleaf pine stands mixed with other forest types (e.g., pine–hardwood, hardwood) and other land uses [153]. Relative to non-planted forest stands, the homogeneous within-stand structural conditions of planted pines, which were abundant in our study region, might explain the limited differences in activity patterns. Younger stands, a product of frequent or recent harvests, also likely provide fewer roosting sites for species that depend on large trees and snags with crevices or exfoliating bark for refuge [118,120,154–156], although roosts are invariably available in the landscape of streamside management zones and other portions of landscape not managed with shorter rotations. Because resource use may change with availability [157], additional studies that include a wider range of forest landscape conditions, including landscapes with uneven-aged, older longleaf pine stands, might yield different results.

Studies of winter habitat associations must first incorporate the effects of cooler winter temperature. We recorded zero passes on 40.5% of all detector nights, and these zeroes must be differentiated between absence of bats because of a potential habitat or landscape factor and the absence of bats simply because it was too cold for bats to be active that night. By using temperature thresholds, as identified in [83], we removed nights where we would not expect a species to be active, regardless of cover type (false negatives). Our temperature thresholds were higher than those identified in North Carolina [24] and lower than in Florida [25], suggesting that temperature thresholds vary at a regional scale. Importantly, while winter temperature thresholds exclude periods when it is too cold for bats to be active, activity above the threshold remains strongly related to temperature (Table 4, [16–18]).

While acoustic monitoring is an important method for studying the activity of winter-active bats, it is important to acknowledge limitations. Acoustic monitoring allows for the passive monitoring of bat activity, surveying multiple sites simultaneously, and limiting the person-hours devoted to surveying. However, acoustic monitoring can be challenging to interpret because some species are not readily distinguishable by recordings alone (e.g., eastern red and Seminole bats), and the ultrasonic characteristics of echolocation calls bias detections in favor of some species and against others [95,158]. Acoustic analysis software has a low agreement across programs [159,160], so an overreliance on any one program could skew species detection. We used two different acoustic analysis programs (SonoBat and Kaleidoscope) coupled with manual vetting to classify our recordings. Although this resulted in the omission of over 60% of the passes recorded in our study, we were more confident in the results of our analyses knowing that multiple methods had verified the species-level identification. We recommend that future studies using acoustic monitoring adopt similar approaches.

5. Conclusions

Our study provided a baseline of winter activity patterns in managed pine landscapes. Unlike in summer, when bats exhibit substantive and species-specific selection, possibly influenced by reproduction, we found little support for winter habitat associations. These results suggest that overwintering bats, especially in regions similar to the southeastern United States with comparatively mild winters, adopt more generalist strategies and are not disproportionately active relative to habitat characteristics measured at either landscape or microhabitat scales. However, our study was conducted on an intensively managed forest landscape with many stands having relatively homogenous within-stand structural conditions, and comparisons were not made to more structurally diverse forests (rare in our study region). Future study in a wider set of forest landscape conditions, including landscapes with substantial amounts of unmanaged or lightly managed forests, will contribute to a more comprehensive understanding of the effect of different forest types and age classes on overwintering bats. Although our study design did not permit comparisons of managed and unmanaged forests, all species expected to occur in the region were documented, reaffirming that managed lands support a diverse bat assemblage [48,49]. Therefore, it is important to consider habitat quality for overwintering bat populations. Current forest management practices emphasize summer habitat associations [124], but effective conservation efforts must consider a year-round perspective [161], accounting for seasonal differences in behavior, responses to weather, and subsequent habitat requirements [162]. Our results indicate that bats generally do not use cover types during winter in the same way as during summer, suggesting that seasonal variation warrants consideration. With mounting evidence that bats are active during winter, it is important to determine whether the generalist activity patterns identified in this study extend to other regions, different bat species, or other landscape conditions.

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