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# The influence of forest management practices on seasonal bat species occurrence and activity at the Kisatchie National Forest in Louisiana, USA

Jane M. Kunberger [*], Ashley M. Long

*Agricultural Center and School of Renewable Natural Resources, Louisiana State University, 227 Renewable Natural Resources Building, Baton Rouge, LA 70803, USA*

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A B S T R A C T

In the southeastern United States, where forests are the primary land cover type, understanding how forest stand characteristics and forest management practices influence bat distributions is critical for bat conservation and management. We deployed passive acoustic monitors to record bat calls at sites representing six forest types at the Kisatchie National Forest in central Louisiana during two winter (January–February 2020 and December 2020–February 2021) and two summer (June–August 2020 and 2021) periods. We also collected environmental data at the landscape and local scales to help explain patterns in bat species occurrence. We detected big brown bats (*Eptesicus fuscus*), eastern red/Seminole bats (*Lasiurus borealis*/*L. seminolus*), *Myotis* species, tricolored bats (*Perimyotis subflavus*), Mexican free-tailed bats (*Tadarida brasiliensis*), and hoary bats (*Aeorestes cinereus*) during both periods, and additionally detected evening bats (*Nycticeius humeralis*) during the summer. We observed seasonal differences in habitat use, and found that three bat species were more active during the summer in pine forests with group selection harvest, pine forests managed for red-cockaded woodpeckers (*Leuconotopicus borealis*), and pine forests that were clearcut within five years of our study when compared to unmanaged pine forests, thinned pine forests, and bottomland hardwood forests. Contrary to other studies, we found that the predicted probability of occupancy decreased with increasing proximity to riparian areas for four bat species, which could reflect the complex understory vegetation conditions that we observed along the riparian corridors in our study area. Our research identified forest characteristics and management practices that promote bat species diversity and activity in central Louisiana and demonstrated that pine forests with open understories and small openings in the canopy provide important foraging habitat for bats that occur in our study area and possibly other regions in the southeast.

## 1. Introduction

Of >1,400 bat species worldwide, 47 occur in the United States, each with unique adaptations to a variety of roosting and foraging conditions (Kalko et al. 2008, Altringham 2011). Such biodiversity is the foundation for ecosystem processes and associated ecosystem services (i.e., human benefits derived from natural processes; Mace et al. 2012), which, for bats, includes nutrient relocation (Jones et al. 2009, Kunz et al. 2011), pollination and seed dispersal (Kunz et al. 2011), and opportunities for ecotourism (Kunz et al. 2011). Insectivorous bats also consume insect pests (McCracken et al. 2012, Maas et al. 2013, Russo et al. 2018), an ecological service that helps reduce zoonotic disease transmission to humans and livestock (Schneeberger and Voigt 2016) and contributes $3.7–54.0 billion per year toward protection of economically important agricultural crops (Boyles et al. 2011).

Nearly-one third of bat species in the United States are experiencing population declines associated with habitat loss and degradation (Hammerson et al. 2017), disease (e.g., white-nose syndrome caused by the fungus *Pseudogymnoascus destructans*; Blehert et al. 2009), and collisions with human infrastructure (e.g., wind turbines; Hammerson et al. 2017). Loss of forested habitat has been particularly problematic, as all bats that occur in the United States use forests during some portion of their life cycle (e.g., roosting, foraging; Altringham 2011). Given these declines, several bat species that use forested landscapes are now listed as Threatened (e.g., northern long-eared bat [*Myotis septentrionalis*]) or Endangered (e.g., Indiana bat [*M. sodalis*]), or are currently under review for listing protections by the United States Fish and Wildlife Service (e.g., tricolored bat [*Perimyotis subflavus*]). As such, we require more information on the life histories and ecologies of bat species that occur across the United States to make informed conservation and

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[*] Corresponding author.
*E-mail address:* janemkunberger@gmail.com (J.M. Kunberger).

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management decisions in light of current and emerging threats.

We particularly lack information on bat-habitat relationships in Louisiana, USA, where forests are the dominant land cover (~6,029,816 ha or ~50% of the state) and timber production is the primary land use on >40% of forested land (Oswalt et al. 2014). Forest management practices in Louisiana and across ~100 million ha of forested land in other southeastern states (~85 million ha of which is used for timber production; Oswalt et al. 2014) are influenced by a variety of factors (e.g., tree species composition, geographic location, local economies; LaFayette et al. 2012), but typically include (1) clearcuts (i.e., all trees and vegetation cleared from a stand); (2) thinning (i.e., proportion of trees harvested from a stand to encourage growth of remaining trees); and (3) group selection harvest (i.e., small plots clearcut throughout the stand to open up room for a new crop while the rest of the stand is allowed to grow; LaFayette et al. 2012). Forest heterogeneity created by multi-aged stand management may promote bat species diversity and provide increased opportunities for foraging on aerial insects along edges (Grindal and Brigham 1999, Menzel et al. 2002, Tibbels and Kurta 2003). Conversely, managed forests may provide less roosting habitat because trees are harvested before they are old enough to generate cavities, peeling bark, and snags (Drake et al. 2020).

Forest management practices and the physiognomy of resulting stands are not the only factors that influence bat occurrence, abundance, and foraging activity. Landscape-level environmental factors such as distances to water sources (Krusic et al. 1996, Ford et al. 2005), urban centers (Kurta and Teramino 1992), and mature forests (Grindal and Brigham 1999), as well as the amount of edge and nearby forest composition (Bender et al. 2015), can influence bat occurrence. In addition, annual movement patterns can influence trends in bat occurrence, abundance, and foraging activities, as some tree-dwelling bat species are year-round residents of the southeastern United States (e.g., northern yellow bats [*Dasypterus intermedius*]) and others are migratory (e.g., hoary bats [*Aeorestes cinereus*]; Cryan 2003, Fraser et al. 2012). Further, the distribution, abundance, and diversity of food resources for insectivorous bats can vary widely in response to seasonal patterns in temperature and precipitation (Wolda 1988). To date, most information about bat-habitat relationships and foraging activity in forests of the southeast is derived from data collected during the summer months to align with increased activity of adults and newly volant young (i.e., June–August; Harvey et al. 2011). Information collected across multiple seasons could provide important information on the phenology of bat species in this region.

Our objective was to examine the influence of forest stand characteristics and forest management practices on seasonal bat species occurrence and activity in central Louisiana. Our forest types included loblolly pine (*Pinus taeda*) managed with thinning, group selection harvest, and clearcutting; unmanaged loblolly pine; bottomland hardwoods; and loblolly or longleaf pine (*P. palustris*) forests managed for red-cockaded woodpeckers (*Leuconotopicus borealis*). We also measured environmental characteristics at local and landscape scales to help explain and predict variation in bat occurrence across forest types. A unique aspect of our study was that we monitored sites in a national forest, which allowed us to identify bat-habitat relationships and examine bat activity on tracts managed using principles of ecological forestry (e.g., emphasis on native biodiversity, silvicultural practices that mimic natural disturbances), an increasingly common approach to achieve management objectives on forested lands in North America (D'Amato et al. 2017).

We expected to detect different species between periods as species that roost in cavities move into human-built structures during the winter (i.e., December–February; Stevens et al. 2017). We expected to find species-specific occupancy relationships, but predicted that open space aerial foragers (i.e., big brown bats [*Eptesicus fuscus*], hoary bats, and Mexican free-tailed bats [*Tadarida brasiliensis*]; Denzinger and Schnitzler 2013) would have high activity in clearcuts during both periods because these species have more successful foraging bouts in open areas with less complex understory vegetation structure (Sherwin et al. 2000, Owen et al. 2004, Morris et al. 2010). We also expected that group selection harvest and red-cockaded woodpecker sites would promote high activity because these forest types provide vegetative conditions preferred by both large and small bat species (i.e., open and intermediate vegetation structure; Menzel et al. 2002, Morris et al. 2010, Titchenell et al. 2011), and because group selection harvests provide edges, which often equate to greater insect prey diversity and abundance for bats (Menzel et al. 2002, Morris et al. 2010).

## 2. Materials and methods

### 2.1. Study area

We conducted our research at the Catahoula and Winn Ranger Districts of the United States Department of Agriculture–Forest Service's Kisatchie National Forest in central Louisiana, USA. The 243,000 ha Kisatchie National Forest is located in the Level III South Central Plains ecoregion (Daigle et al. 2006) and, typical of the region, is composed primarily of loblolly and longleaf pine forests with hardwood tree species generally restricted to bottomlands and riparian areas. The climate of the Kisatchie National Forest is subtropical, with an average annual rainfall of 114 cm and daily temperatures ranging from around 5°C in January to around 35°C in July (National Weather Service 2021).

Portions of the Kisatchie National Forest are managed specifically for longleaf pine restoration, timber, and habitat for red-cockaded woodpeckers, wild turkey (*Meleagris gallopavo*), and northern bobwhite (*Colinus virginianus*; USDA Forest Service 1999). The methods used depend on harvest goals and site characteristics, but include clearcutting, group selection harvest, and thinning, among others. Site preparation typically includes drum chopping, burning, and herbicide, as needed. Stands are thinned when trees reach 10–20 years old to an average basal area of 16 $m^2$ $ha^{-1}$. Group selection harvests in the Kisatchie National Forest are generally 0.1–0.8 ha.

We collected data at 18 study sites (10–140 ha) representing six forest types. Our sites included three that were clearcut within five years from the start of our project (hereafter clearcut); three composed of thinned loblolly pine (hereafter thinned); three composed of loblolly pine with openings created by group selection harvests (hereafter group selection harvest; openings ranged from 0.1 to 0.3 ha); three composed of either loblolly or longleaf pine that were managed for red-cockaded woodpeckers (hereafter red-cockaded woodpecker); three that were composed of mature loblolly pine >40 years old and were not managed with thinning, burning, or herbicides for >5 years (hereafter unmanaged loblolly); and three composed of bottomland hardwood forests >40 years old that were characterized by intermittent flooding, and predominated by oaks (*Quercus* spp.), gums (*Nyssa* spp.), and bald cypress (*Taxodium distichum*; hereafter bottomland hardwood). We sampled 15 sites in 2020 and added two clearcut sites and one red-cockaded woodpecker site in 2021.

We collected data during the following sampling periods: January–February 2020 (winter 2020), June–August 2020 (summer 2020), December 2020–February 2021 (winter 2021), and June–August 2021 (summer 2021). Our sampling periods represent timing associated with torpor (i.e., November–April) and timing associated with increased foraging activity by adults and newly volant young (i.e., July–August) in bats throughout the southeastern United States (Harvey et al. 2011).

### 2.2. Acoustic monitoring

Within each study site, we deployed acoustic monitors to record bat echolocation calls at two points – one point in each half of the study site. We located each point >100 m from the edge (excluding group selection harvests, where we located points at the edge of a cut, and one loblolly red-cockaded woodpecker site, where we located points ~80 m from an edge due to area constraints; Owen et al. 2004, Morris et al. 2010) and

>200 m from other points (Hyzy et al. 2020). Our study design resulted in sampling 30 points during winter and summer 2020 and 36 points during winter and summer 2021. We monitored the same points during each sampling period.

We deployed full-spectrum Song Meter SM4BAT-FS monitors with external SMM-U2 microphones (hereafter monitors; Wildlife Acoustics, Inc., Maynard, Massachusetts, USA) at each point. During winter 2020, we deployed monitors for a total of 2 to 4 nights. In subsequent sampling periods, we deployed monitors for a total of 6 to 13 nights. The differences in sampling effort between years reflect delays and travel restrictions in year one of our study due to COVID-19. For each deployment, we secured the external microphone on top of a polyvinyl chloride (PVC) pole 2 m above the ground, with the microphone sitting flat on top of the pole to direct the microphone upwards (in accordance with Wildlife Acoustics, Inc., 2018). We placed our points in areas with minimal foliage to decrease the possibility of missed echolocation calls (Britzke et al. 2013). We programmed monitors to record from 30 min before sunset to 30 min after sunrise (Bender et al. 2015) with the default settings, which included triggering at a minimum detected frequency of 16 kHz for a minimum recording length of 1.5 ms and recording at a 256 kHz sample rate with a 12 dB gain.

### 2.3. Environmental characteristics

We measured environmental characteristics to determine which factors influenced bat species occurrence in our study area. At the landscape scale, we used ArcMap (v. 10.7; ESRI, Redlands, California, USA) to create buffer zones of 50, 100, 450, and 1,000 m (1 km) around each point. These buffer sizes reflect values used in other studies (Bender et al. 2015, Kirkpatrick et al. 2017, Andersen et al. 2022), with the 50 m and 100 m buffers representing local conditions that can influence bat occurrence and the 450 m and 1,000 m buffers representing the average distance that foraging bats move per night and landscape conditions that can influence bat occurrence.

We used ArcMap to measure the Euclidean distance (m) from each point to the nearest perennial water source (Bender et al. 2015, Hyzy et al. 2020) with the National Hydrography Dataset (USGS 2020b, c, 2021) and to measure the Euclidean distance (m) from each point to the nearest incorporated place (Shute et al. 2021) with the National Boundary Dataset (USGS 2020a). Within each buffer zone, we calculated the proportion of area attributed to each predominant tree species and the proportion of area attributed to stand age categories (i.e., stand ages 0 to 9 years, 10 to 19 years, 20 to 29 years, and >30 years; Bender et al. 2015) with U.S. Forest Service data for the Kisatchie National Forest (USDA Forest Service n.d.). With the proportion of predominant tree species and stand age data, we calculated forest and age diversity (Bender et al. 2015) using the Shannon Diversity Index (Shannon 1948). We also quantified structural heterogeneity within each buffer by calculating the variance in normalized difference vegetation index (NDVI; Weier and Herring 2000) with LANDSAT-8 imagery (LANDSAT-8 images courtesy of the U.S. Geological Survey) for each sampling period. Last, we used FRAGSTATS (V 4.2.1; McGarigal and Marks 1995) to calculate total distance of edge (Bender et al. 2015) and proportion of area attributed to wetlands and open water using 2016 National Land Cover Database (NLCD) data (NLCD data courtesy of the U.S. Geological Survey) for each buffer. Before we calculated these metrics, we manually edited the NLCD layer to include clearcuts that occurred after 2016.

At the local scale, we measured vegetation characteristics at the point and at 25 and 50 m from the point in each cardinal direction. At each vegetation point, we used a wedge 10-factor prism to estimate basal area ($m^2$ $ha^{-1}$; Bender et al. 2015). In addition, we visually estimated percent ground cover (i.e., shrubs, herbaceous, or bare; Tibbels and Kurta 2003) to the nearest 10%, measured the diameter at breast height (DBH at 1.5 m) of trees >10 cm (Titchenell et al. 2011), and counted the number of saplings (trees <10 cm DBH) within a 5-m radius circle of the vegetation point. Last, we counted the number of snags (dead trees >10 cm DBH; Mattson et al. 1996, Klug et al. 2012, Lucas et al. 2015) and their decomposition state (Thomas et al. 1979) within a 12-m radius circle of the vegetation point (Kirkpatrick et al. 2017).

### 2.4. Echolocation call analysis

We used the echolocation analysis software SonoBat (V. 4.4.1; SonoBat, Arcata, California, USA) to analyze our bat call data, which automatically identifies bats to species using call characteristics such as minimum and maximum frequencies, duration, and slope (Fenton and Bell 1981). First, we used the SonoBat batch file scrubber with the settings for medium quality tolerance and >20 kHz call search to maximize detections of bat calls and minimize acoustic interference (e.g., insects). We ran the remaining files through the SonoBat Southeastern southeast classifier with the default values (acceptable call quality of 0.60 and decision threshold of 0.90) to automatically identify calls to species.

Because of their similar call structures, SonoBat does not distinguish between eastern red bats (*Lasiurus borealis*) and Seminole bats (*L. seminolus*) and refers to all identifications as eastern red bats. Therefore, we combined these species into the eastern red/Seminole bat group for our work (Titchenell et al. 2011). Similarly, of the two *Myotis* species known to occur in Louisiana, SonoBat only identifies southeastern bats (*M. austroriparius*) with the Southeastern southeast classifier. As such, we consider SonoBat's identifications of southeastern bats as a combination of southeastern and northern long-eared bats due to their similar call structures and refer to these identifications as the *Myotis* species group (Avila-Flores and Fenton 2005, Titchenell et al. 2011).

We used the maximum likelihood estimates from SonoBat output to determine detection or non-detection of a species at each point for each sampling period, considering a likelihood of presence value of ≥0.50 as a detection and <0.50 as a non-detection. We defined bat foraging activity as the number of feeding buzzes (i.e., echolocation sequences characterized by rapid calls with ~1 ms pauses, which represent a foraging attempt on an insect; Griffin et al. 1960) at points during individual nights. Due to the large number of files that we collected during the summer, we randomly subsampled 25% of scrubbed files from each point for manual feeding buzz identification during these periods and did not group feeding buzzes by species.

We acknowledge that our decision to utilize an automated classification process without manually verifying our species identifications may have influenced our results, in part because reference libraries are often comprised of recordings made while bats are in-hand or in open environments (Britzke et al. 2013, Nocera et al. 2019). However, manual verification can also result in misidentifications (Fritsch and Bruckner 2014, Rydell et al. 2017) and variation in counts per night across observers (Fritsch and Bruckner 2014). We minimized biases associated with automated classifiers to the extent possible by combining species with similar call structures that occurred within our study area, excluding species from our analyses with a small number of detections that were unlikely to occur within our study area (see Section 3), and conducting our research within a small geographic extent to avoid geographic variation in call structure (Murray et al. 2001). While no method is perfect, we believe that automated classification using the aforementioned constraints was appropriate given our objectives and allowed us to address challenges of reproducibility in bat call analyses (Nocera et al. 2019).

### 2.5. Statistical analyses

We used Program R (V. 4.1.1; R Core Team 2021) to summarize seasonal bat activity and our environmental data. We used occupancy models to investigate species-specific bat-habitat relationships in our study area (Burnham and Anderson 2002). We ran the summer and winter data separately because we assumed occupancy states changed between periods due to differences in foraging and roosting habitat, as well as possible migration of certain species (Cryan 2003, Stevens et al. 2017, Stevens et al. 2020). Before modeling our data, we examined correlations between all of the environmental characteristics that we measured, and we retained variables that had low to no correlation with another variable ($r < |0.50|$; Asuero et al. 2006). If two variables had a moderate to very high correlation ($r \geq |0.50|$; Asuero et al. 2006), we retained the most relevant environmental characteristic based on previous research. The variables we retained after this step included distance to water (m), distance to an incorporated area (m), variance in NDVI in a 50 m radius, variance in NDVI in a 1 km radius, total distance of edge in a 1 km radius (m), forest diversity in a 1 km radius (Shannon diversity value), proportion of forest aged >30 years in a 1 km radius, percent shrub cover, percent herbaceous cover, basal area ($m^2$ $ha^{-1}$), DBH (cm), and snag density (snags of decay categories 3–6 $ha^{-1}$). Our final candidate set for each species or species group included a null model, additive models representing combinations of one or two environmental variables and year, and a global model with all variables. We included year in all models to account for differences in sampling effort (i.e., the number of points and nights sampled) between years.

We scaled the uncorrelated variables, then used generalized linear modeling with binomial distributions and logit link functions to model occupancy. We calculated $\hat{c}$ values as residual deviance divided by the residual degrees of freedom for each global model in our candidate sets to look for evidence of overdispersion, which can result in misleading inferences and conclusions (MacKenzie and Bailey 2004). We used Akaike's information criteria corrected for small sample sizes ($AIC_c$) to rank each model; determined the relative support for each model using $\Delta AIC_c$ and model weights ($w_i$; Sugiura 1978, Anderson 2008). We considered models with $\Delta AIC_c < 2$ equally plausible, then identified the most parsimonious models as best fit (Burnham and Anderson 2002). We reported parameter estimates and their 95% confidence intervals for the best fit models to assess the magnitude and direction of effect of each variable on the predicted probability of occupancy (Burnham and Anderson 2002, Grueber et al. 2011) along with the results of our null models. If a 95% confidence interval included 0 for a parameter, we considered the parameter uninformative (Burnham and Anderson 2002, Grueber et al. 2011). We used the AICcmodavg package in R (V. 2.3–1; Mazerolle 2020) for model selection and the ggplot2 package in R (V. 3.3.5; Wickham 2016) to visualize our results. We summarized the results for species with sufficient detection/non-detection data to model occupancy and best fit models with at least one significant environmental parameter in Section 3.1.

We created species-specific proportional odds models (McCullagh 1980) with logit link functions for each period using the MASS package in R (V. 7.3–54; Venables and Ripley 2002). Our response variable was nightly activity, which we categorized as "low" (1–5 call files), "moderate" (6–15 call files), or "high" (>15 call files) based on natural breaks in our data. We exponentiated the model coefficients to quantify odds ratios for high nightly activity across all combinations of forest types. We calculated the standard errors and 95% confidence intervals for each odds ratio and considered 95% confidence intervals that did not include 1 informative (McCullagh 1980). We followed the same procedure to create proportional odds models with our foraging activity data (all species combined). We chose this approach because we assumed that high odds of high activity at one forest type compared to another (odds ratio >1) indicated better conditions for foraging and navigation in the former if the species was present in both forest types. The odds ratios also allowed for simple interpretation and visualization of the magnitudes of difference in activity between the pairs of forest types.

## 3. Results

We collected data on 93 nights during winter 2020; 183 nights during summer 2020; 248 nights during winter 2021; and 233 nights during summer 2021. SonoBat identified 643 files to species during winter 2020; 17,216 files to species during summer 2020; 979 files to species during winter 2021; and 24,957 files to species during summer 2021. We detected the eastern red/Seminole bat group, the *Myotis* species group, tricolored bats, big brown bats, hoary bats, and Mexican free-tailed bats during both summer and winter, and additionally detected evening bats (*Nycticeius humeralis*) during summer. We had insufficient non-detection data for Mexican free-tailed bats and eastern red/Seminole bats during summer and insufficient detection data for Mexican free-tailed bats during winter so we excluded these combinations from our occupancy analyses. We only detected Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) at one thinned point during winter 2020 and excluded this species from our analyses. We detected silver-haired bats (*Lasionycteris noctivagans*) at two points during the winter and six points during the summer; however, due to the few confirmed observations of silver-haired bats in Louisiana (Stevens et al. 2020) and our low sample size for this species, we also excluded this species from our analyses. We further summarized seasonal bat activity in Figures A.1 and A.2 and summarized our environmental data in Table A.1.

### 3.1. Occupancy

During winter, the best fit model for eastern red/Seminole bat occupancy included forest diversity + year (Table 1); the predicted probability of eastern red/Seminole bat occupancy decreased with increasing forest diversity and was slightly higher in 2021 compared to winter 2020 with overlapping 95% CIs at low and high values of forest diversity (Figs. 1 and 2; Table A.2). As described in our methods, we included year in all of our models to account for differences in sampling effort, but the aforementioned response for eastern red/Seminole bats was the only relationship that varied by year. As such, we visualized the results for each year in our figures, but here forward only discuss relationships between occupancy and significant environmental variables for the best fit models.

During summer, the best fit model for tricolored bat occupancy was basal area + year (Table 1). Tricolored bat occupancy decreased ~25% with every 4 $m^2$ $ha^{-1}$ increase in basal area when basal area was above 20 $m^2$ $ha^{-1}$; however, the confidence interval for this relationship was wide at values >20 $m^2$ $ha^{-1}$ (Figs. 1 and 3; Table A.2). During winter, the best fit models for big brown bat occupancy included percent shrub cover + year and total distance of edge + year (Table 1). The predicted probability of big brown bat occupancy decreased ~10% with every 5% increase in percent shrub cover under 20%, but the confidence interval for this relationship was wide at values >20% (Figs. 1 and 2; Table A.2). Additionally, the predicted probability of big brown bat occupancy increased ~15% with every 5,000 m increase in the total distance of edge within the 1 km radius buffer (Figs. 1 and 2; Table A.2). During summer, the best fit model for big brown bat occupancy was forest diversity + year (Table 1); the predicted probability of big brown bat occupancy decreased with increasing forest diversity (Figs. 1 and 3; Table A.2).

During winter, the best fit model for the *Myotis* species group was proportion of forest aged >30 years + year (Table 1). The predicted probability of *Myotis* species occupancy decreased ~10% with every 5% increase in the proportion of forest aged >30 years (Figs. 1 and 2; Table A.2). During winter, the best fit model for hoary bats was DBH + year (Table 1). The predicted probability of hoary bat occupancy increased ~10% with every 10 cm increase in DBH during the winter (Figs. 1 and 2, Table A.2); however, the confidence interval for this relationship was wide at values >30 cm DBH (Fig. 1). During summer, the best fit models for evening bats included distance to water + year and proportion of forest >30 years + year (Table 1). The predicted probability of evening bat occupancy increased ~25% with each 500 m increase in distance to water, whereas the predicted probability of evening bat occupancy decreased ~15% with each 5% increase in the proportion of forest aged >30 years (Figs. 1 and 3; Table A.2).

**Table 1**

Plausible occupancy models ($\Delta AIC_c$ <2) with results from each null model for species and species groups during the winter (January–February 2020 and December 2020–February 2021) and summer (June–August 2020 and 2021) for our study examining the influence of forest management practices on seasonal bat species occurrence and activity in central Louisiana. We used generalized linear models with a binomial distribution and included year as a parameter in each model.

| Period | Common name Scientific name | Model | K | $AIC_c$ | $\Delta AIC_c$ | $AIC_c$ Wt. | LL |
|---|---|---|---|---|---|---|---|
| Winter | Eastern red/Seminole | Forest diversity (1 km)[1] | 3 | 75.86 | 0.00 | 0.26 | −34.74 |
| | *Lasiurus borealis/L. seminolus* | Null | 1 | 86.08 | 10.22 | 0 | −42.01 |
| | Tricolored | Total distance of edge (1 km) | 3 | 67.47 | 0.00 | 0.17 | −30.54 |
| | *Perimyotis subflavus* | DBH | 3 | 69.12 | 1.65 | 0.08 | −31.37 |
| | | Distance to an incorporated area | 3 | 69.30 | 1.82 | 0.07 | −31.45 |
| | | Percent shrub cover | 3 | 69.32 | 1.84 | 0.07 | −31.46 |
| | | Null | 1 | 70.27 | 2.80 | 0.04 | −34.11 |
| | Big brown | Percent shrub cover[1] | 3 | 39.17 | 0.00 | 0.26 | −16.39 |
| | *Eptesicus fuscus* | Forest type | 7 | 39.29 | 0.12 | 0.25 | −11.68 |
| | | Total distance of edge (1 km)[1] | 3 | 40.85 | 1.69 | 0.11 | −17.23 |
| | | Basal area + percent shrub cover | 4 | 41.13 | 1.97 | 0.10 | −16.24 |
| | | Null | 1 | 46.70 | 7.54 | 0.01 | −22.32 |
| | *Myotis* species | Proportion forest > 30 years (1 km)[1] | 3 | 66.06 | 0.00 | 0.46 | −29.83 |
| | | Snag density + DBH | 4 | 68.05 | 1.99 | 0.17 | −29.70 |
| | | Null | 1 | 72.81 | 6.75 | 0.02 | −35.37 |
| | Hoary | DBH[1] | 3 | 48.06 | 0.00 | 0.34 | −20.84 |
| | *Aeorestes cinereus* | Variance in NDVI (1 km) + DBH | 4 | 49.50 | 1.43 | 0.17 | −20.42 |
| | | Null | 1 | 50.81 | 2.75 | 0.09 | −24.38 |
| Summer | Tricolored | Basal area[1] | 3 | 21.50 | 0.00 | 0.65 | −7.56 |
| | *Perimyotis subflavus* | Basal area + percent shrub cover | 4 | 22.82 | 1.32 | 0.34 | −7.08 |
| | | Null | 1 | 37.48 | 15.97 | 0 | −17.71 |
| | Big brown | Forest diversity (1 km)[1] | 3 | 68.24 | 0.00 | 0.42 | −30.93 |
| | *Eptesicus fuscus* | Null | 1 | 72.81 | 4.57 | 0.04 | −35.37 |
| | *Myotis* species | Basal area | 3 | 72.10 | 0.00 | 0.17 | −32.86 |
| | | Null | 1 | 72.81 | 0.71 | 0.12 | −35.37 |
| | | Forest diversity (1 km) | 3 | 73.57 | 1.47 | 0.08 | −33.59 |
| | | Total distance of edge (1 km) | 3 | 73.86 | 1.76 | 0.07 | −33.74 |
| | | Snag density | 3 | 74.00 | 1.90 | 0.06 | −33.80 |
| | Evening | Distance to water[1] | 3 | 84.48 | 0.00 | 0.49 | −39.05 |
| | *Nycticeius humeralis* | Snag density + distance to water | 4 | 85.75 | 1.27 | 0.26 | −38.55 |
| | | Proportion forest > 30 years (1 km)[1] | 3 | 86.15 | 1.67 | 0.21 | −39.88 |
| | | Null | 1 | 93.50 | 9.02 | 0.01 | −45.72 |
| | Hoary | Variance in NDVI (1 km) | 3 | 42.92 | 0.00 | 0.16 | −18.27 |
| | *Aeorestes cinereus* | Total distance of edge (1 km) | 3 | 42.98 | 0.06 | 0.15 | −18.30 |
| | | Variance in NDVI (50 m) | 3 | 44.42 | 1.50 | 0.07 | −19.02 |
| | | Percent herbaceous | 3 | 44.55 | 1.73 | 0.07 | −19.14 |
| | | Variance in NDVI (1 km) + DBH | 4 | 44.69 | 1.77 | 0.07 | −18.02 |
| | | Null | 1 | 46.70 | 3.78 | 0.02 | −22.32 |

[1] Best fit models (i.e., the most parsimonious models with 95% confidence intervals for at least one parameter that did not include 0).

### *3.2. Activity*

During winter, eastern red/Seminole bats had 6 times the odds of high activity in group selection harvest and red-cockaded woodpecker sites compared to bottomland hardwood sites and 90% lower odds of high activity in thinned sites compared to group selection harvest and red-cockaded woodpecker sites (Fig. 4; Table A.3). We were unable to examine proportional odds models for other species or species groups in winter because most nightly activity was categorized as “low” (Table A.4). During summer, eastern red/Seminole bats, tricolored bats, and evening bats had 4–30 times the odds of high activity in group selection harvest and red-cockaded woodpecker sites compared to unmanaged loblolly and bottomland hardwood sites and 3–8 times the odds of high activity in clearcuts compared to bottomland hardwoods (Fig. 4; Table A.5). Further, eastern red/Seminole bats and tricolored bats had an average of 80% lower odds of high activity at thinned sites compared to clearcut, group selection harvest, and red-cockaded woodpecker sites and an average of 90% lower odds of high activity at unmanaged loblolly sites compared to clearcut sites (Fig. 4; Table A.5). Similarly, big brown bats had an average of 3 times the odds of high activity in red-cockaded woodpecker and clearcut sites compared to unmanaged loblolly and bottomland hardwood sites and 80% lower odds of high activity in thinned sites compared to red-cockaded woodpecker sites (Fig. 4; Table A.5). Last, Mexican free-tailed bats had 2–4 times the odds of high activity at unmanaged loblolly, clearcut, and group selection harvest sites compared to bottomland hardwood sites (Fig. 4; Table A.5). The odds ratio confidence intervals for hoary bats in summer included 1 and we were unable to examine proportional odds models for *Myotis* species in summer because most nightly activity was categorized as “low” (Table A.4).

Bat foraging activity was similar across all forest types during the winter (Fig. 5; Table A.6). During the summer, the odds of detecting high foraging activity in clearcut, group selection harvest, and red-cockaded woodpecker sites was 6–10 times the odds of bottomland hardwood sites and the odds of detecting high foraging activity in group selection harvest and red-cockaded woodpecker sites was an average of 36 times the odds of unmanaged loblolly sites (Fig. 5; Table A.6). Also, the odds of detecting high foraging activity in unmanaged loblolly and thinned sites was 98% and 93% lower than the odds of clearcut sites, respectively (Fig. 5; Table A.6). Last, the odds of detecting high foraging activity at thinned sites was 90% lower than the odds of group selection harvest and red-cockaded woodpecker sites (Fig. 5; Table A.6).

## 4. Discussion

We detected similar bat species at our study sites in summer and winter; found species-specific trends in occupancy; and observed considerable differences in activity across forest types for some bat

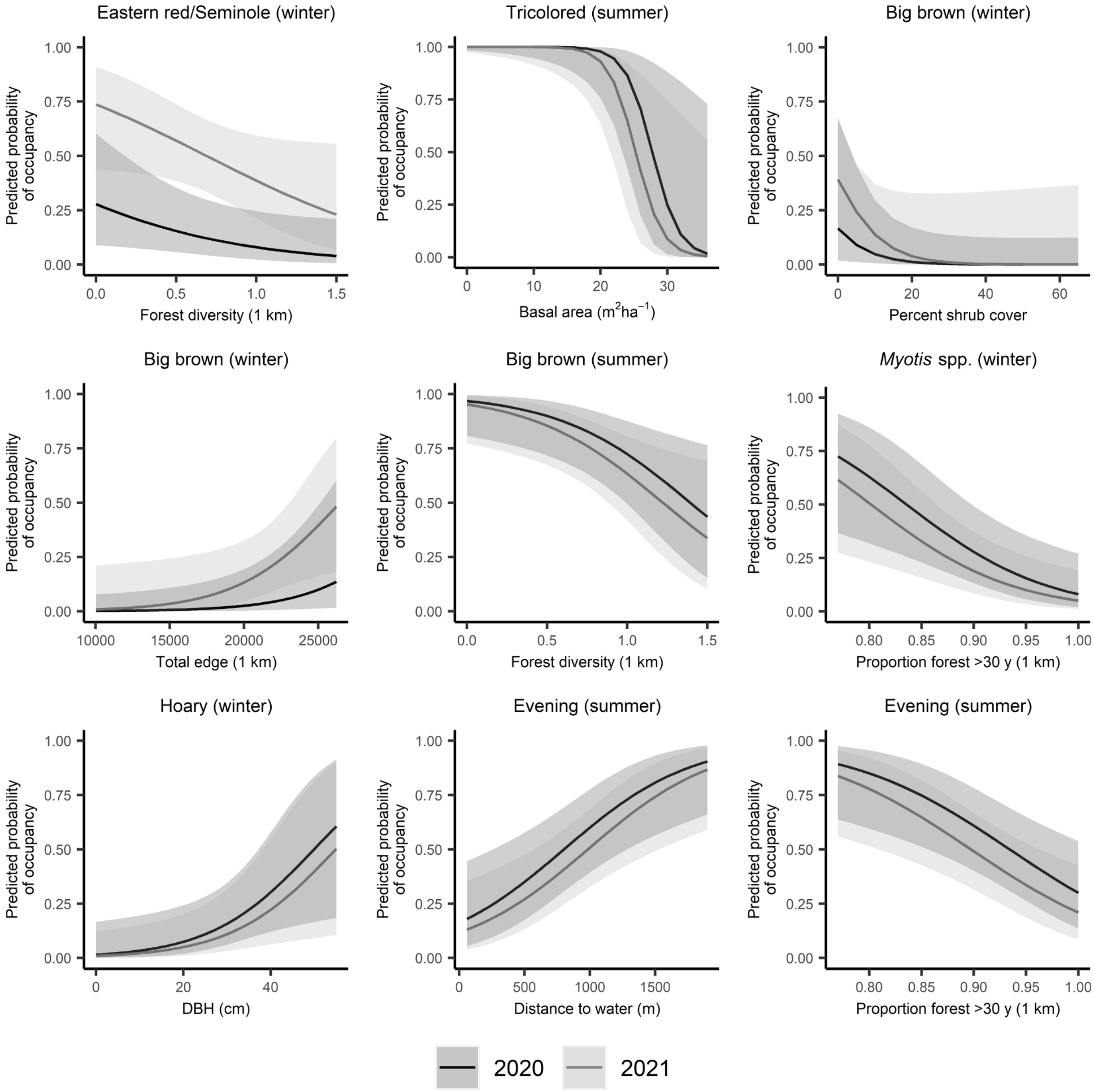

**Fig. 1.** Predicted probability of occupancy for a subset of bat species detected during our study examining the influence of forest management practices on bat species occurrence and activity in central Louisiana during the winter (January–February 2020 and December 2020–February 2021) and summer (June–August 2020 and 2021).

species. The only species we did not detect in both seasons was the evening bat. Stevens et al. (2020) previously captured evening bats in the Kisatchie National Forest in winter, but this species may not utilize the forest types we studied during this period. Winter occupancy for four of the bat species we detected during our study (eastern red/Seminole bats, big brown bats, *Myotis* species, and hoary bats) was associated with environmental variables like DBH and percent shrub cover. In contrast, Andersen et al. (2022) conducted research on three managed pine forest landscapes in Louisiana and Texas and did not observe strong evidence of winter habitat associations for any of the bat species they detected, including the four species we mentioned above. However, Andersen et al. (2022) monitored bats in relatively homogenous stands that represented four different age classes and we monitored bats across stands with different management regimes; thus, it is difficult to make direct comparisons between the two studies.

We found that different environmental variables influenced occupancy and activity in each season, which may reflect spatial and temporal variation in resource availability (Shute et al. 2021). It is also possible that differences in sampling effort between years influenced our results (i.e., more nights and the addition of two clearcut sites and one red-cockaded woodpecker site in year two of our study), particularly for species that are less common on the landscape (MacKenzie and Royle 2005) and species that primarily forage in areas with open vegetation structure (e.g., hoary bats; Sherwin et al. 2000, Owen et al. 2004, Morris et al. 2010). However, we included year in our occupancy models to account for differences in sampling effort and only observed annual variation in eastern red/Seminole bat occupancy, suggesting that sampling effort had little influence on the overall trends.

In contrast to previous research (e.g., Owen et al. 2004, Menzel et al. 2005, Stuemke et al. 2014), we found inverse relationships between eastern red/Seminole bat, big brown bat, *Myotis* species, and evening bat occupancy and environmental variables that described riparian areas at our study sites (i.e., forest diversity, proportion of forest >30 years, and distance to water), which were often located in bottomland hardwoods

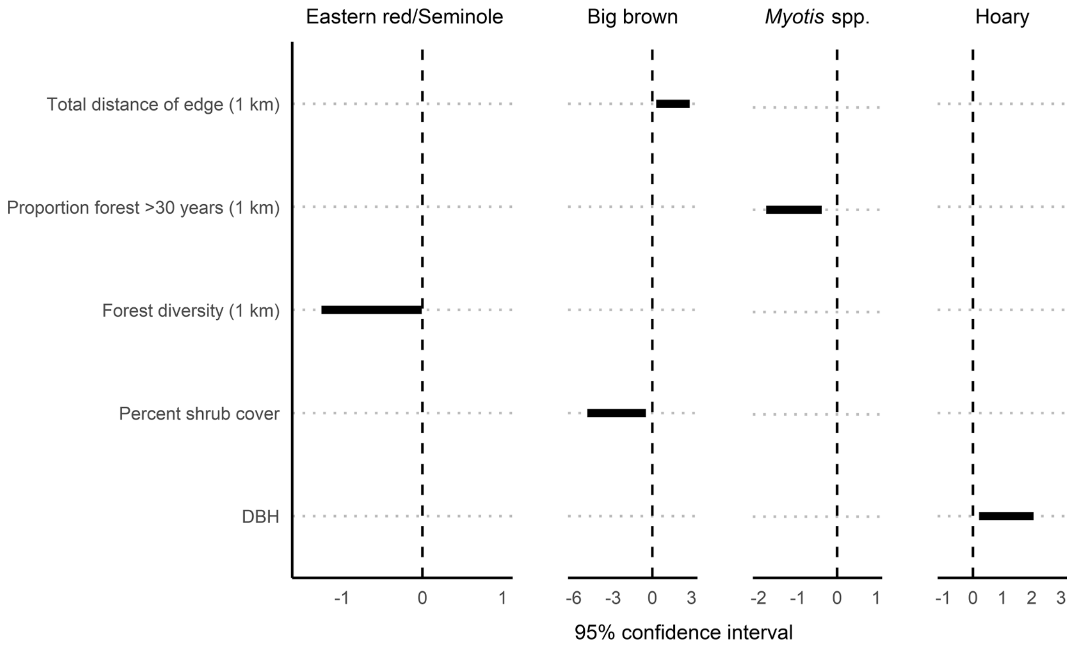

**Fig. 2.** Parameter estimates for environmental variables in the best fit occupancy models (models with $\Delta AIC_c < 2$ that were most parsimonious and had 95% confidence intervals for at least one parameter that did not include zero) during winter (January–February 2020 and December 2020–February 2021) for our study examining the influence of forest management practices on seasonal bat species occurrence and activity in central Louisiana.

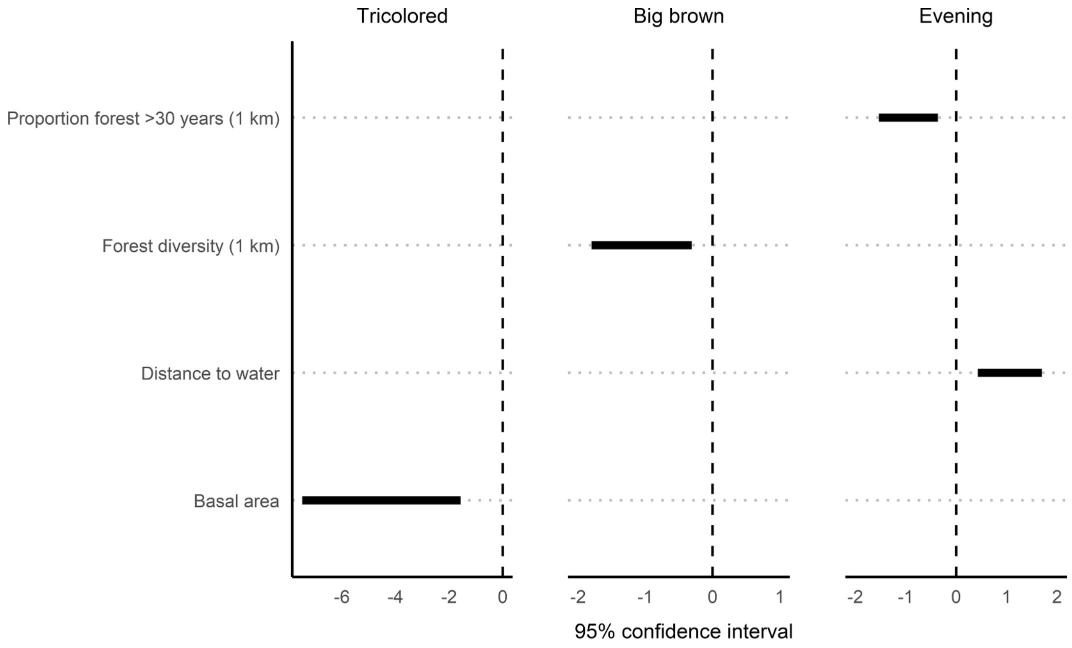

**Fig. 3.** Parameter estimates for environmental variables in the best fit occupancy models (models with $\Delta AIC_c < 2$ that were most parsimonious and had 95% confidence intervals for at least one parameter that did not include zero) during summer (June–August 2020 and 2021) for our study examining the influence of forest management practices on seasonal bat species occurrence and activity in central Louisiana.

that were more diverse, older than the surrounding pine landscape, and contained most perennial water sources in our study area (Table A.1). The understory vegetation in riparian areas that occurred in our study area was quite complex, so it is possible that the bat species we detected preferred to use the more open conditions and linear landscape features of adjacent pine forests for foraging and navigation. Management techniques that reduce understory vegetation and maintain large trees and snags in riparian areas could provide increased foraging opportunities while preserving cavity roosts for species like southeastern and Rafinesque's big-eared bats (Gooding and Langford 2004, Clement and Castleberry 2013).

In line with our expectations, we found high odds of high activity at group selection harvests for several species, including eastern red bats, Seminole bats, tricolored bats, and evening bats, which have echolocation and body characteristics that make them better adapted for foraging and navigating along edges (Denzinger and Schnitzler 2013). Group selection harvests provide edges that bats can use for foraging (Jantzen and Fenton 2013, Morris et al. 2010) and as conduits for navigation (Kalcounis-Rueppell et al. 2013) immediately following the cut and for several years thereafter. Though beyond the scope of our research,

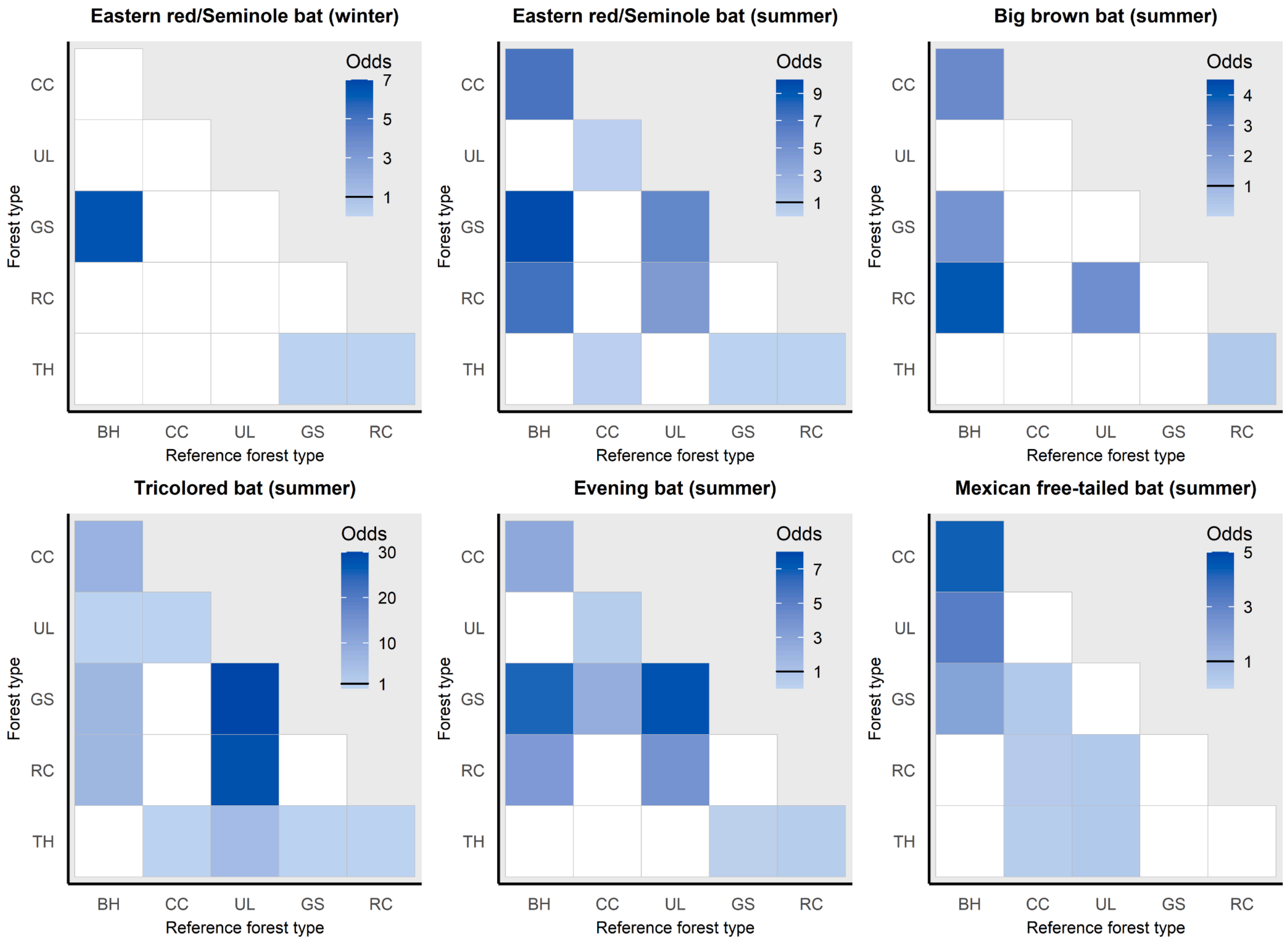

**Fig. 4.** Proportional odds modeling results for our study examining the influence of forest management practices on bat species occurrence and activity in central Louisiana during the winter (January–February 2020 and December 2020–February 2021) and summer (June–August 2020 and 2021). Forest types are bottomland hardwood (BH), clearcut (CC), unmanaged loblolly (UL), group selection harvest (GS), red-cockaded woodpecker habitat (RC), and thinned (TH). White boxes represent odds ratios with 95% confidence intervals that included 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

wildlife openings (i.e., <1 ha cuts to benefit game [Stewart et al. 2000, Massé and Côté 2012, Pollentier et al. 2017] and non-game [Campbell et al. 2012, Smetzer et al. 2014] species; Healy 1989) could elicit a similar and potentially prolonged positive response from edge space aerial foragers because land managers often limit growth of woody plants in wildlife openings for time intervals that exceed tree regeneration in group selection harvests.

We found high odds of high activity in red-cockaded woodpecker habitat for several bat species. One of the red-cockaded woodpecker sites in our study was predominated by longleaf pine and had an herbaceous understory, which was last burned during the 2020 growing season. Prescribed burns in this fire-dependent ecosystem can provide roosting opportunities for both cavity (Boyles and Aubrey 2006, Johnson et al. 2009) and foliage roosting bats (Jorge et al. 2021) and can decrease the density of trees and tall shrubs (Armitage and Ober 2012). The resulting open forest conditions often lead to increased bat activity for open space aerial foragers like big brown bats (Armitage and Ober 2012, Braun de Torrez et al. 2018). The other two red-cockaded woodpecker sites in our study area were composed of loblolly but also had an open forest structure; however, these sites were recently created and had no history of burning after they were converted to red-cockaded woodpecker habitat. Though the ground cover and snag composition of these sites differed from the burned longleaf red-cockaded woodpecker site, bats were also highly active at the loblolly red-cockaded woodpecker sites, which suggested that bat activity was driven by the open forest structure rather than ground cover or snag densities. This is unsurprising, as bat activity is often primarily influenced by the physical structure of a forest (Grindal and Brigham 1999, Ober and Hayes 2008).

We expected that open space aerial foragers (e.g., big brown bats) would be more active at clearcuts compared to other forest types because they provide a homogenous open environment, which aligned with our findings. Further, we found that edge space aerial foragers (e.g., eastern red/Seminole bats; Grindal and Brigham 1999, Caldwell et al. 2019) were more active at clearcuts compared to other forest types. The clearcuts in our study may have provided both foraging habitat for the less-maneuverable open space aerial foragers and the generalist edge space aerial foragers because our clearcuts were small (<50 ha) compared to a majority of our other study sites. More specifically, bat activity in open vegetation is often related to the distance to available edge (Jantzen and Fenton 2013). As such, the small size of clearcuts in our study may have decreased the distance to edge at any given point within the clearcut, which would explain why we found high activity for multiple foraging groups in this forest type. Larger clearcuts could have negative effects on activity of species that tend to occur away from homogenous openings (e.g., *Myotis* species), but there were no larger clearcuts with similar management histories or site conditions within our study area.

Lands managed by the U.S. Forest Service represent a critical asset

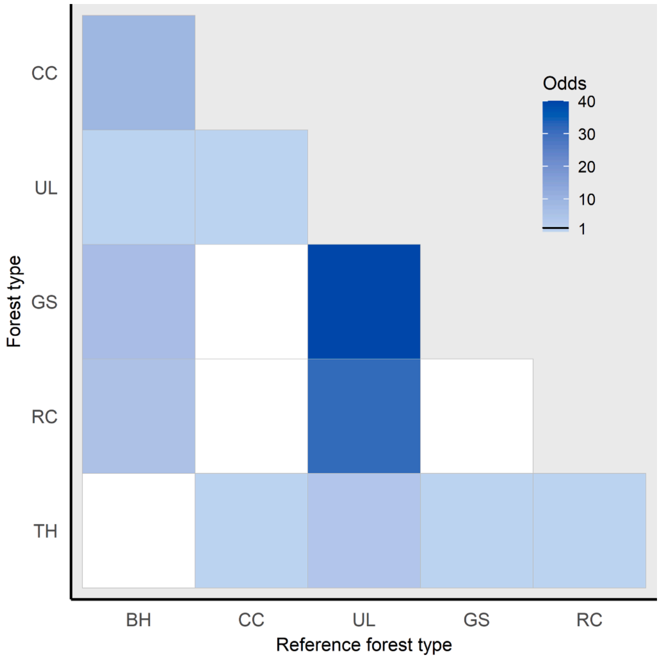

**Fig. 5.** Proportional odds modeling results for foraging activity during the summer, for our study examining the influence of forest management practices on bat species occurrence and activity in central Louisiana during the winter (January–February 2020 and December 2020–February 2021) and summer (June–August 2020 and 2021). Forest types are bottomland hardwood (BH), clearcut (CC), unmanaged loblolly (UL), group selection harvest (GS), red-cockaded woodpecker habitat (RC), and thinned (TH). White boxes represent odds ratios with 95% confidence intervals that included 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

for bat conservation in North America and have multiple-use goals and objectives that require changes to the structure and composition of the forests they contain. Understanding how bats respond to forest management practices used in national forests can help the agency develop guidelines and standards that help sustain bat diversity on their lands and beyond. Overall, our research reiterated the importance of studying bats throughout the year, as occupancy and activity were influenced by different forest types and environmental characteristics in summer and winter. Our results also demonstrated that bats benefit from techniques that increase edge (e.g., group selection harvest) and decrease understory vegetation structure (e.g., thinning in red-cockaded woodpecker stands) in managed forests. Future research should attempt to elucidate the mechanistic drivers of the patterns we observed and long-term studies are needed to monitor bat populations in Louisiana, particularly for species of conservation concern that have experienced range-wide population declines due to habitat loss and white nose syndrome.

## CRediT authorship contribution statement

**Jane M. Kunberger:** Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization, Funding acquisition, Project administration, Data curation. **Ashley M. Long:** Conceptualization, Methodology, Validation, Resources, Writing – review & editing, Supervision, Funding acquisition, Project administration.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data available upon request and approval of the US Forest Service

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120579.

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