**Occurrence and Habitat Use of Bats in
Central Alabama Forests**

by

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Abstract

Limited information is available on the relationship between characteristics of landscape and seasonal use of habitat for forest-dwelling bats in central Alabama. This study was designed to clarify these relationships and to provide information for managers charged with restoring or maintaining native habitat. Bats were surveyed in randomly selected plots on lands administered by the U.S. Fish and Wildlife Service. Standard sampling techniques were used, primarily bat detectors and mist nets. Land use, type of land-cover, and vegetative and physical features of each plot were sampled and recorded. Occupancy analysis was used to examine use of habitat and distribution of species. The following taxa were detected and identified: *Tadarida brasiliensis*, *Eptesicus fuscus*, *Lasiurus borealis*, *L. cinereus*, *L. seminolus*, *Nycticeius humeralis*, *Perimyotis subflavus*, *Myotis grisescens*, and various unidentified species of *Myotis*. Temperature was the best indicator for detection for all groups and species. Species with echolocation frequency ≤29 kilohertz (kHz) selected open habitats, specifically rivers, streams, and fields. Bats with echolocation frequencies 30-39 kHz selected open habitats and showed a strong affinity for certain types of forested habitats. The group used pine stands and hardwood stands, but did not select for mixed forest stands. Use by species with echolocation frequencies ≥40 kHz was greater in open habitats as opposed to closed forests. Individual species showed varied probability of use to key types of habitat, type of forest, structure of forest, and slope.

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INTRODUCTION

Bats play a significant role in the health of ecosystems, simply by the number of insects they are able to consume in a given night (Harvey et al. 1999, Taylor 2007). Some species consume more than one-half their weight in insects each night (Harvey et al. 1999). Most species of bats in North America are insectivores, providing a natural system for control of nocturnal insects (Thompson 2006). One important benefit is a reduction in use of pesticides by the agricultural industry, which results in cleaner water and air (Taylor 2007). Significant additions have been made to our knowledge about bats. However, there is a paucity of basic information about certain groups, especially bats that inhabit forests.

The ecosystem characterized by longleaf pines (*Pinus palustris*) formerly dominated the landscape of the southeastern United States, but only about 1.2 million ha (3%) remains (Frost 1993, Van Lear et al. 2005). The distribution of habitat characterized by mountain longleaf pine is even more restricted, and is the focus of restoration and management on Cahaba River National Wildlife Refuge (NWR), Bibb County, and Mountain Longleaf NWR, Calhoun County, Alabama. Historically, when Native Americans inhabited what is now Alabama, the area was forested and maintained by natural cycles of fire that preserved a fire-dependent ecosystem (Van Lear et al. 2005). More recently, the natural landscape has undergone changes with introduction of invasive species, urbanization, and suppression of wildfires (Ford et al. 2006). This led to increased fragmentation of habitats, contamination of water, and alteration of natural systems.

Maintaining forested habitats is important for the conservation of bats (Broders et al. 2006, Miles et al. 2006), and managing natural resources is frequently necessary to preserve biological diversity. One important characteristic of healthy forests is structural complexity (Ellison et al. 2005, Miller 2003, Taylor 2007). Structural complexity can be attained by managing for uneven-aged stands with multiple native species and by retaining snags and damaged trees (Lacki et al. 2007, Perry and Thill 2008). Numerous characteristics may influence use of forests by bats, from specific trees to landscape-level attributes and from climate fluctuations to abundance of insects (Ford et al. 2006).

Much is known about habits of the endangered gray myotis (*Myotis grisescens*; United States Fish and Wildlife Service 1976a) and Indiana myotis (*M. soladis*; United States Fish and Wildlife Service 1976b). In northern Alabama, monitoring of these species has been ongoing for about 2 decades; especially, in areas with karst features (limestone regions with numerous sinkholes, underground streams, and caves; Clark et al. 1988, M.K. Hudson, pers. comm., Tuttle 1976). In addition, monitoring has occurred throughout the remainder of Alabama (M.K. Hudson, pers. comm.). Additional studies have focused on specific habitats, other species, or both (Durden et al. 1992, Hirt 2008, Kilgore 2008). Most research and monitoring has taken place on national forests, military bases, national parks, national wildlife refuges, and state managed areas (Gardner 2008, Samuel 2008), which represents about 4% of land in Alabama (Protected Areas Database of the United States, http://gapanalysis.nbii.gov).

Research indicates that some species of bats select specific characteristics of forests that may be used as day roosts, maternity roosts, foraging habitat, or all of these. A study of structure and fragmentation of forests in Missouri revealed preferences for various habitats among species of bats (Yates and Muzika 2006). Many species of bats roost beneath bark, in clusters of leaves,

or in natural cavities in live or dead trees (Kalcounis et al. 1999, Miles et al. 2006). Bats also select trees that have easy access, such as trees along edges, in open stands, and along tops of ridges (Taylor 2007). Ford et al. (2005) reported that northern long-eared bats (*M. septentrionalis*) roosted in trees and snags, and were dependent on prey present beneath the canopy. A study conducted in the southern part of the Appalachian Mountains with limited timber management determined that tri-colored bats (*Perimyotis subflavus*) and eastern red bats (*Lasiurus borealis*) preferred specific attributes of forests, and males of both species were detected roosting in foliage of various species of trees (O'Keefe et al. 2009). In that study, eastern red bats seem to prefer proximity to linear openings (roads) in selecting roost sites, with probability of use increasing nearer to the opening.

Characteristics of forested areas used as maternity roosts by bats vary among species. Foster and Kurta (1999) discovered that Indiana myotis were dependent on large snags for maternity roosts and seemed to prefer specific attributes when selecting roosting sites. In Missouri, Indiana myotis preferred loose bark on snags with minimal canopy cover (Timpone et al. 2010). In Mississippi and Georgia, evening bats (*Nycticeius humeralis*) favored fork-tops of loblolly pine trees (*Pinus taeda*; Taylor 2007) and were most likely to be encountered in open-canopy pine and hardwood forests (Ford et al. 2006, Miles et al. 2006). Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) and southeastern myotis (*M. austroriparius*) used hardwoods with cavities for maternity roosts (Taylor 2007). Additionally, southeastern myotis were more likely to be in hardwoods than in pines (Ford et al. 2006). Stevenson (2008) ascertained specific characteristics favored by Rafinesque's big-eared bats and southeastern myotis in roost trees at Noxubee NWR, Noxubee, Oktibbeha, and Winston Counties, in east-central Mississippi. Both species demonstrated a preference for large cavity trees with large vertical cavities. In addition,

both species preferred certain species of trees, although the study questioned whether the preference was for the species of trees or for the microhabitat that individual trees provided.

In addition to having a variety of roosting requirements, different species use different areas for foraging. Some fly along edges of forests, others over open water, some forage within forests, and some beneath, in, or above the canopy of trees (Menzel et al. 2005b, Patriquin and Barclay 2003, Rogers et al. 2006). Some researchers hypothesize that morphological differences and frequency of echolocation calls can be used to predict habitat preferences among species of bats (Ford et al. 2005, Kalcounis et al. 1999). Bats use these calls to forage, navigate, and communicate (Vaughan et al. 1997). Bats of smaller size, and therefore greater mobility, are more adapted for cluttered environments and have higher echolocation frequencies ($\geq$40 kilohertz; kHz; Adams et al. 2009, Broders et al. 2004, Hein et al. 2009a, Jacobs et al. 2007, Sleep and Brigham 2003). Medium-to-larger-sized bats are less maneuverable and, therefore, tend to be restricted to open spaces (Brooks and Ford 2005, Ford et al. 2005, Jacobs et al. 2007, Vaughan 1966), and their calls are generally long, low frequencies in the 15 to 35 kHz range (Hein et al. 2009a, Wund 2005). Further, calls of an individual species may change depending on habitat (Broders et al. 2004, Wund 2005).

Some researchers theorize that availability and abundance of prey determines use of a given habitat (Ford et al. 2005). A study in Canada examined the effect of clear-cuts and cut-blocks (small areas of clear-cut that created more edge habitat) and detected no difference among larger species of bats, but smaller species used edges of both types of cuts and would not forage in open areas (Hogberg et al. 2002). Therefore, they concluded, by cutting smaller plots, more edge was created and used by forest-dwelling species.

Bat activity and use of habitats varies seasonally and with temperature within seasons. An increase in activity in the latter part of summer is correlated with the appearance of volant young (Yates and Muzika 2006). Some studies have shown an increase in activity with increases in summer temperatures (Hein et al. 2009a, Yates and Muzika 2006). Barkalow (1948) reported Seminole bats (*L. seminolus*) migrating southward during the winter and remaining active in the coastal Alabama area. In the same study, eastern red bats and evening bats were observed during warmer winter days near Auburn, Alabama. Also, eastern red bat was observed active in temperatures as low as 13°C (Lewis 1940). Hoary bat (*L. cinereus*) has been shown to be tolerant of temperatures down to 0°C in the southwestern United States (Jones 1965).

A recent study conducted in the Ouachita Mountains, Garland and Perry Counties, Arkansas, focused on roosting behavior of silver-haired bats in winter (*Lasionycteris noctivagans*; Perry et al. 2010b). In warmer temperatures, the species roosted beneath bark or in cavities of mature trees on the south-facing aspect. When the temperature was less than 6°C, the bats moved to rocky outcrops or underground (base of trees or holes). Additional research has been conducted evaluating winter feeding behavior in species of bats found in North America and Europe (Geluso 2007, Kanuch et al. 2005, Lausen and Barclay 2006, Whitaker et al. 1997).

Multiple methods exist for surveying habitat use, abundance, and diversity of bats, including harp traps, mist nets, and ultrasonic acoustic monitors (also known as bat detectors). Mist nets and harp traps are frequently used to capture bats for information on identity, use of habitats, and an estimate of size of populations (Flaquer et al. 2007). Radio transmitters attached to individual bats can be used to locate roosts, providing specific information regarding habitat selection (Miller et al. 2003, Morris et al. 2011). However, capturing bats is stressful on the bats, labor intensive, and time consuming (Flaquer et al. 2007, Gorresen et al. 2008). Some studies

have questioned the ability of bat detectors to capture calls from all species of bats in a given location, while other studies have detected little difference in discovery of species between detectors and mist nets (Flaquer et al. 2007, Miller et al. 2003). Morris et al. (2011) evaluated the appropriateness of using radio-telemetry and detectors in habitat studies. They concluded detector studies should be limited to stand-level selection, while radio-telemetry could be used to determine more specific habitat selection. At present, bat detectors are the least stressful method available for assessing presence and diversity of bats in forested habitats (Broders et al. 2004, Fenton et al. 2001, Parsons et al. 2000, and Preatoni et al. 2005).

The objective of my study was to estimate the use of forest habitats by bats and to evaluate differences in distributions as they relate to characteristics of forests. This study compared multiple species of bats use of mountain longleaf, hardwood, and mixed pine-hardwood forests in central Alabama.

I developed my study based on *a priori* hierarchical hypotheses, first evaluating the potential detection influences on presence of bats, and then using those results to evaluate habitat use. Initially, I developed several hypotheses related to factors that could affect bat detection rates. First, I hypothesized that detection would not vary among surveys (*p.*). Then, I hypothesized that temperature would affect detection more in winter and less in spring and summer. My theory was that in spring and summer changes in temperature would have minimal effect given the relatively warm and stable weather patterns. In winter, an increase in temperature should result in an increase in activity. Hence, I developed multiple models for temperature to account for possible seasonal differences (Table 1).

I also hypothesized that bats would continue to be active in winter. In general, all species of bats tend to hibernate during very cold winter periods. However, certain species of bats have

been observed during winter on warmer evenings (Barkalow 1948, Geluso 2007, Jones 1965, Lausen and Barclay 2006, Lewis 1940, Perry et al. 2010b, Whitaker et al. 1997). Mild winters associated with the southeast, should result in bat activity during the winter months.

I also hypothesized that detection would increase with Julian date ($p_{\text{julian date}}$) because species would be resuming activity after hibernation (Table 1). Julian date should not affect non hibernating species. My final detection hypothesis was that detection would decrease with increasing relative humidity ($p_{\text{relative humidity}}$), because of the high humidity in the southeast. I also considered incorporating precipitation into a detection model, but because the entire activity each night was compressed into a single observation it would not have been accurate unless it rained all night. My occupancy hypotheses were developed using common habitat models combined to reflect the environmental conditions found on the sites. Groups and species of bats were evaluated based on key types of habitats, type of forests, structure of forests, and distribution of slopes (Table 2). Previous studies have shown preferences of small species for interiors of forests (i.e., they depend on cluttered interior forests and use various types of trees) versus medium and large species that are mainly found in open, uncluttered habitats (Adams et al. 2009, Hein et al. 2009a, Loeb and O'Keefe 2006). Therefore, I thought small species would be indifferent to characteristics of microhabitats, such as canopy cover, mid-story cover, and height of canopy (Appendix B) and larger species would be observed less frequently as the complexity of forest structure increased. I hypothesized that smaller species would be associated with the interior of forests and observed more frequently in mid-slope forests ($\Psi_{\text{forest+mid slope}}$). Larger species would be more likely to use open uncluttered habitats and ridge tops ($\Psi_{\text{forest+ridge}}$) more than the interior of forests. In addition, roads (Ψ_{road}) were added as a model because they serve as travel corridors (Hein et al. 2009a, O'Keefe et al. 2009). I expected all groups and species to

use roads as travel corridors and some as feeding areas (Adams et al. 2009, Hein et al. 2008, Hein et al. 2009a, Morris et al. 2010).

My next set of hypotheses were evaluating specific habitat characteristic and the potential influence those may have on species of bats. Hence, my hypothesis was that use would increase in proximity to aquatic resources (Ψ_{river}, Ψ_{stream}), given the importance of water and prey associated with aquatic resources (Loeb and O'Keefe 2006, Menzel et al 2005a, O'Keefe et al. 2009, Perry et al. 2008). Additionally I hypothesized that diverse habitats would be used more frequently compared to mono-cultural forests (Ψ_{mono}). This is especially applicable at Cahaba River NWR where stands of loblolly pines were planted prior to establishment of the refuge. Bats use mono-cultural stands (Hein et al. 2009b, Morris et al. 2010), but diverse habitats are probably preferred. My final hypothesis was that bats would respond positively to management activities related to maintaining and restoring stands of mountain longleaf pines (Table 2).

Table 1. Detection rate hypotheses and model names used in the analysis of bat surveys conducted at Cahaba River National Wildlife Refuge, Bibb County, and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama 2009-2010.

Hypothesis	Model
Detection does not vary among surveys	$p_.$
Temperature affects detection, effect of temperature differs by season (temperature by season interaction)	p_{wss}
Temperature affects detection and the effect is similar each season (additive model of temperature and season)	p_{all}
Temperature affects detection and the effect is different in winter, but similar in spring and summer.	$p_{w/ss}$
Temperature affects detection	p_{temp}
Temperature affects decrease as temperature increases (quadratic)	p_{temp2}
Time of year affects detection	$p_{julian\ date}$
Relative humidity affects detection	$p_{relative\ humidity}$

Table 2. Hypotheses and associated models for occupancy (Ψ) rates for species of bats at Cahaba River National Wildlife Refuge, Bibb County, and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama 2009-2010. Multiple models represent each category specific to the various habitat components characterized by the sampled plots.

Categories	Models
Habitat affects rates of occupancy	Ψ_{forest}, $\Psi_{forest+stream}$, $\Psi_{field,}$ Ψ_{river}
Forested habitats in combination with forested habitats affects rates of occupancy	$\Psi_{forest+hardwood}$, $\Psi_{forest+pine}$, $\Psi_{forest+mixed}$
Stream habitats in combination with forested habitats affects rates of occupancy	$\Psi_{stream+hardwood}$, $\Psi_{stream+pine}$, $\Psi_{stream+mixed}$
River habitats in combination with forested habitats affects rates of occupancy	$\Psi_{river+hardwood}$, $\Psi_{river+\ mid\text{-}cover\ percentage}$, $\Psi_{river+\ canopy\ cover\ percentage}$
Field habitats in combination with forested habitats affects rates of occupancy	$\Psi_{field+YMLP}$
Forest habitats in combination with structure of forests affects rates of occupancy	$\Psi_{forest+average\ canopy\ height}$, $\Psi_{forest+basal\ area}$, $\Psi_{forest+canopy\ cover\ percentage}$, $\Psi_{forest+mid\text{-}cover\ percentage}$, $\Psi_{forest+presence\ of\ snags}$ $\Psi_{forest+xeric}$, $\Psi_{forest+ridge}$, $\Psi_{forest+mid\ slope}$
Forests affects rates of occupancy	Ψ_{pine}, $\Psi_{hardwood}$, Ψ_{mixed}
Pine forests in combination with structure of forests affects rates of occupancy	$\Psi_{pine+\ mid\text{-}cover\ percentage}$, $\Psi_{pine+\ average\ canopy\ height}$, $\Psi_{pine+\ presence\ of\ snags}$, $\Psi_{pine+\ basal\ area}$, $\Psi_{pine+\ canopy\ cover\ percentage}$
Hardwood forests in combination with structure of forests affects rates of occupancy	$\Psi_{hardwood+\ average\ canopy\ height}$ $\Psi_{hardwood+\ basal\ area}$, $\Psi_{hardwood+\ canopy\ cover\ percentage}$, $\Psi_{hardwood+\ mid\text{-}cover\ percentage}$, $\Psi_{hardwood+\ presence\ of\ snags}$,
Mixed forests in combination with structure of forests affects rates of occupancy	$\Psi_{mixed+\ average\ canopy\ height}$ $\Psi_{mixed+\ basal\ area}$, $\Psi_{mixed+\ canopy\ cover\ percentage}$, $\Psi_{mixed+\ mid\text{-}cover\ percentage}$, $\Psi_{mixed+\ presence\ of\ snags}$,
Structure of forests affects rates of occupancy	$\Psi_{mid\text{-}cover\ percentage}$, $\Psi_{canopy\ cover\ percentage}$, $\Psi_{average\ canopy\ height}$, $\Psi_{basal\ area}$, $\Psi_{presence\ of\ snags}$
Specific habitat affects rates of occupancy	$\Psi_{road,}$ $\Psi_{forest+road}$
Aquatic resources affects rates of occupancy	Ψ_{river}, Ψ_{stream}
Mono-cultural stands affect rates of occupancy	Ψ_{mono}
Management actions affect rates of occupancy	$\Psi_{mountain\ longleaf\ pine\ stand}$, $\Psi_{YMLP,}$ $\Psi_{fire,}$ $\Psi_{pine+fire,}$ $\Psi_{forest+fire}$

MATERIALS AND METHODS

The study was conducted on two national wildlife refuges in the ridge-and-valley ecological region of central Alabama (Griffith et al. 2001). Cahaba River NWR, Bibb County, Alabama, is between the cities of Tuscaloosa and Birmingham. In the late 1800s, the refuge was home to coal-mining operations and timber harvesting. Mountain Longleaf NWR, Calhoun County, is situated between Birmingham, Alabama, and Atlanta, Georgia. The land served as Fort McClellan, a training ground for the United States Army for >80 years prior to establishment of the refuge.

Cahaba River NWR consists of 1,460 ha of upland ridges and slopes, with elevations of 67-171 m. Average annual precipitation at Birmingham, Alabama, is 136 cm (National Oceanic and Atmospheric Administration-National Climate Data Center, http://www.ncdc.noaa.gov; NOAA). The refuge surrounds a portion of the Cahaba River and protects habitat for 11 threatened and endangered species. Multiple tributaries and streams drain into the Cahaba River. In addition to protecting aquatic resources, management of the refuge is focused largely on restoring mountain longleaf pine through prescribed burns, reforestation, and control of hardwoods.

Mesic communities on the refuge largely consisted of mountain longleaf pines, shortleaf pines (*P. echinata*), loblolly pines, Virginia pines (*P. virginiana*), chestnut oaks (*Quercus prinus*), blackjack oaks (*Q. marilandica*), white oaks (*Q. alba*), southern red oaks (*Q. falcata*),

sourwoods (*Oxydendrum arboreum*), black gums (*Nyssa sylvatica*), flowering dogwoods (*Cornus florida*), southern sugar maples (*Acer barbatum*), red maples (*A. rubrum*), and mountain laurels (*Kalmia latifolia*). Portions of the refuge dominated by plantations consisted mostly of even-aged loblolly pines planted prior to establishment of the refuge. Bottomland hardwoods and river bottoms were dominated by American beechs (*Fagus grandifolia*), mountain laurels, sweetgums (*Liquidambar styraciflua*), yellow poplar-tulip trees (*Liriodendron tulipifera*), and giant cane (*Arundinaria gigantea*).

Mountain Longleaf NWR encompasses 3,649 ha, with elevations of 247-629 m. The refuge is within the Choccolocco Mountain area. Average annual precipitation is 126 cm (NOAA-National Climate Data Center, http://www.ncdc.noaa.gov). Management on the refuge had focused largely on maintaining and enhancing mountain longleaf pine through prescribed burns and control of hardwoods, while continuing coordination with the U.S. Army on removal of unexploded ordnance and cleanup of environmental contamination. The steep terrain and annual rain fall create runoff of surface water and feed numerous springs, some of which form seepage wetlands.

The upland forest communities were dominated by mountain longleaf, shortleaf, loblolly, and Virginia pines, while the hardwood component included chestnut oaks, white oaks, southern red oaks, post oaks(*Q. stellata*), black oaks (*Q. velutina*), and pignut hickories (*Carya glabra*). Some of the common understory trees were black cherries (*Prunus serotina*), Alabama black cherries (*P. alabamensis*), hornbeams (*Carpinus caroliniana*), red maples (*A. rubrum*), flowering dogwoods, black gums, and persimmons (*Diospyros virginiana)*. The shrub layer is typically blueberry (*Vaccinium pallidum*), azalea (*Rhododendron canescens*), and hydrangea (*Hydrangea*

arborescens, H. quercifolia). Lower-elevation areas along waterways are predominantly

hardwoods including oaks, hickories, yellow poplars, and basswoods (*Tilia Americana*).

To determine locations of sampling points, ArcGIS 9.2 (Environmental Systems

Research Institute, Redlands, California) and Hawth's Tools (Beyer 2004) were used to

randomly generate points. The individual points were a minimum of 250 m apart and based on

habitat types (Kleiner et al. 2007). For Cahaba River NWR, 15 points were generated, of which

12 were used in my study. Three points were eliminated because of proximity to roads,

boundaries, and limited access. Points generated for Mountain Longleaf NWR were reduced

from 30 to 26, because proximity to cleanup activities associated with unexploded ordnance

resulted in unpredictable access. In total, 38 points were used in my study. Gorresen et al.

(2008) recommended using >15 sites when using bat detectors. Greater accuracy of detection

was obtained with 15 different sites rather than 15 visits to the same site (Gorresen et al. 2008).

Each sampling point was located using a Garmin 76S GPS unit (Global Positioning

System; Garmin International, Inc., Olathe, Kansas). A tree with a diameter at breast height

(DBH) of ≥45 cm and free from low-hanging branches and leaves was selected. At each

sampling point, one AnaBat SD1 Compact Flash Bat Detector (Titley Electronics, Lawnton,

Queensland, Australia) was placed in a retrofitted pelican case attached to a 12-volt battery. A 5

cm, 45°, PVC, elbow joint with drain holes was placed on the side of each case to allow the

microphone of the bat detector to be protected from the elements, while maintaining the ability to

capture sounds. The equipment was attached to the tree 1.5 m above the ground.

Detectors were programmed to turn on 0.5 hour before sunset and turn off 0.5 hour after

sunrise, and they were placed at each survey point for 5 nights during each of 3 seasons; winter,

spring, and summer. Most data were collected during 2009; some points were resurveyed during winter 2010 because batteries died during the original survey.

Echolocation calls have been shown to vary geographically within species (Murray et al. 2001) and in proximity to different habitat types (Schaub and Schnitzler 2007). Therefore, an echolocation-call library was used which was obtained from a regional Anabat training sponsored by Titley Electronics. Additionally, in order to enhance the call library, recordings of individual bats identified to species were made during the study. Calls were gathered in conjunction with mist net trapping activities and karst feature surveys.

Vegetative surveys were conducted within a 25 m-radius plot centered on each survey point. The protocol used was developed as part of a state-wide comprehensive monitoring program (A. Silvano, pers. comm). The site was categorized into one of four habitats based on observation: river, field, forest, or forest-stream. A river was a large body of water and classified as navigable; while a stream was typically a smaller body of water and not navigable. The habitat designated as forest-stream had a stream running through the forested site, while a forest site had no aquatic resources within the plot. In addition, any sites that were predominantly mountain longleaf pine or restoration sites with young pines were noted. Sites were separated further into types of forest: pine, hardwood, or mixed. A grid of sampling points 6.25 m apart and aligned in the cardinal directions was established for 49 points/ plot. At each point, a moosehorn densitometer (GRS Densitometer, Geographic Resource Solutions, Arcata, California) was used to determine cover of canopy, mid-story, reproductive shrubs, and herbaceous shrubs. Estimates of cover types were based on percentage of points where each respective type of cover was present. Average height of the canopy was calculated using the heights of three dominant trees in the plot. In each plot, the tallest trees of the most abundant

species were selected as the dominant trees and measured. The measurements were then averaged to determine the average height of the canopy. For each tree, total height, height to the first live branch, and proximity to center were recorded. Measurements were obtained using a measuring tape (15 or 30 m), compass, and a clinometer. Each tree was flagged 2 m above the ground and photographed, so that measurements could be validated. In addition, I recorded species, DBH, and distance to center of plot for each snag within the plot. A basal area angle gauge (Panama angle gauge, Panama Pump Company, Hattiesburg, Mississippi) was used to estimate basal area. For each tree indicated by the prism from the center of the plot, I noted species, DBH, and distance to center of the point.

Weather data for Cahaba River NWR were obtained 20 km southwest of the refuge from the Remote Automated Weather Station on Talladega National Forest, Oakmulgee District, Bibb County. Weather data for Mountain Longleaf NWR were from the on-site Remote Automated Weather Station. Analyses focused on temperature, percentage relative humidity, and precipitation. Hourly readings at weather stations were averaged per night.

Bat call data were analyzed using AnaLook 3.3q software (Titley Electronics, Lawnton, Queensland, Australia). Data were processed in stages: 1) each file that contained a minimum of three echolocation pulses was marked for further analysis; 2) files were placed in categories based on frequency of echolocation calls; 3) files were analyzed individually using a call library for identification; and 4) as a quality control measure, K. Livengood confirmed identifications on 30 representative files.

The acoustic data were subdivided into three groups based on frequency of echolocation calls (frequency class; FC) for the final analysis (Appendix A). Calls with frequencies ≤29 kHz were placed into FC20, which likely included *T. brasiliensis*, *Eptesicus fuscus*, and *L. cinereus*

and; all of which are large bodied bats (length of forearm, 43-53 mm; weight, 11-35 g; Adams et al. 2009, Kurta and Baker 1990, Shump and Shump 1982b, Wilkins 1989). Calls with frequencies of 30-39 kHz were placed into FC30, which likely included *L. borealis, L. seminolus*, and *N. humeralis*, which are medium-sized bats (length of forearm, 36-40 mm; weight, 5-16 g; Shump and Shump 1982a, Watkins 1972, Wilkins 1987). Calls with frequencies ≥40 kHz were placed into FC40, which likely included *P. subflavus, M. grisescens*, and *M. septentrionalis,* which are small bodied bats (length of forearm, 33-41 mm; weight, 4-12 g; Caceres and Barclay 2000, Decher and Choate 1995, Fujita and Kunz 1984). In addition, individual species were identified including *E. fuscus*, *T. brasiliensis*, and *P. subflavus*. Given the difficulty in separating certain species due to similar and overlapping frequencies of echolocation calls, *L. borealis* and *L. seminolus* were combined into one group (LABOSE) and all species of *Myotis* were combined into MYSPP. All groups and species were present if they were recorded at least once during the night at a site. Thus, each night was considered an independent sampling occasion.

I estimated relationships between probability of use by species and characteristics of habitats using multi-season (robust-design) occupancy analysis (Ψ - probability of use) and probability of colonization (γ) parameterization (MacKenzie et al. 2003). My study looked at bat activity during multiple seasons to determine variation between the seasons. Robust sampling design includes sampling when sites are assumed to be closed to changes in use interspersed with (open) periods when changes in use may occur (MacKenzie et al. 2003). In my study, each night was considered a trapping (detection) event. I assumed that within seasons bats consistently used the same sites each night; that is; sites were closed to changes in occupancy. I estimated changes in use between seasons (open periods); because there were resident and migrating

species and behavior could change among seasons. Thus, during open periods, sites that were

not used formerly could be colonized, and sites that were used the previous season could be

abandoned (local extinction).

For each frequency class and group of species, I estimated seasonal rates of occupancy

and colonization for each survey site, as well as the detection probability (p) on each sampling

occasion using Program MARK (version 6.1; White and Burnham 1999). I incorporated the

effects of site and sampling covariates using the logit link function. I used

AICc = -2 ln (L) + 2 K * (n / ($n - K - 1$)), to rank models, where L is the likelihood of the

model given the data, K is the number of estimated parameters, and n is the number of sites

surveyed. I selected best models from the candidate set based on $\Delta AICc_i \leq 2$, where

$\Delta AICc_i$ = $AICc_i$ – min ($AICc$) (Burnham and Anderson 2002). The model weights (w_i),

probability that each model was the best model in the candidate set, were calculated using the

equation: $w_i = e^{-0.5*\Delta AICc}{}_i$. Occupancy rates (Ψ) and 95% confidence limits (CL) were

constructed from the estimated effects sizes (β) and respective confidence limits using:

$\Psi = e^{X\beta} / (1 + e^{X\beta})$, where X is the matrix of covariate values and β is the vector or estimated

effect sizes estimated by MARK. Where indicated model-averaged estimates of Ψ and CL were

estimated using program MARK from using Ψ_i and w_i.

I performed occupancy analyses in a hierarchical fashion. First, I determined the best

models of bat detection by comparing models incorporating Julian date, temperature, and relative

humidity. Then, I paired the best models of detection with models of occupancy based on my *a

priori* hypotheses (Table 3). I developed hypotheses regarding occupancy (probability of use)

based on habitat types available on my study areas, and literature review. I evaluated the same

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set of models for each group and individual species. In the analyses presented here, I only

included groups and individual species with sufficient data (>30 observations).

Table 3. Covariates evaluated in comparing use of habitats by bats on Cahaba River National Wildlife Refuge, Bibb County, and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama, 2009-2010.

Type	Covariate	%[1]	Definition
Indicator	River	5.3	≤25 m of a flowing river[2]
	Forest	60.5	>75% forested ≤50 m of site
	Stream	13.2	≤25m of a flowing stream[3] surrounded by forest
	Field	2.6	>75% non-forested ≤50 m of site
	Mountain longleaf pine	18.4	>75% mature mountain longleaf pine ≤50 m of site
	YMLP[4]	5.3	>75% recently planted (<7 years old) mountain longleaf pine ≤50 m of site
	Pine	26.3	>75% pine forest ≤50 m of site
	Hardwood	13.2	>75% hardwood forest ≤50 m of site
	Mixed	60.5	>75% mixed pine-hardwood forest ≤50 m of site
	Monoculture	5.3	>50% loblolly pine forest ≤50 m of site
	Roads or trails	18.4	trails or road ≤25 m of site
	Prescribed fire	50.0	surrounding stand treated with prescribed fire >1 time during past 5 years
	Ridge	23.7	ridge top ≤25 m of site
	Mid-slope	52.6	Distribution of mid-slope
Continuous	Snag		density of snags/ha
	Basal area		basal area (m²/ha)
	Height of canopy		height of canopy (m)
	Canopy cover		percentage of canopy closure ≤25 m of site
	Mid-story Cover		percentage of mid-story closure ≤25 m

[1]Percentage of sites ($n = 38$)

[2]Large body of navigable water

[3]Small body of non-navigable water

[4]Young Mountain Longleaf Pine stand

RESULTS

I identified 36,449 bat calls that I recorded over 570 survey nights spanning 14 months.

Bats used all 38 sites and occupancy varied by species and season. I recorded 26,413 calls at

Cahaba River NWR and 10,036 calls at Mountain Longleaf NWR. Two-thirds of the calls I

recorded at Cahaba River NWR were from two sites adjacent to the Cahaba River ($n = 18,976$).

In contrast, at Mountain Longleaf NWR, I recorded the largest numbers of calls ($n = 3,457$), at a

road and a ridge top that were surrounded by an open, mature stand of mountain longleaf pines.

There were fourteen species of bats potentially found in my study areas, seven of which

are of special concern in the state (Appendix A). I identified calls by *T. brasiliensis*, *E. fuscus*, *L.*

borealis, *L. cinereus*, *L.seminolus*, *N. humeralis*, *P. subflavus*, and *Myotis grisescens* at both

refuges. In my analysis I combined calls of *L. borealis* and *L. seminolus* due to the similarity of

the sonograms of their calls. Both species were present on the study areas, but I could not

differentiate them on a large proportion of the recordings. For similar reasons I also combined

results for all species of *Myotis* (*M*. spp). The majority of *M.* spp echolocation calls appear as

vertical lines of varied ≥40 kHz frequencies, but echolocation calls by *M. grisescens* sometimes

appear with a reliable 45 kHz base with a distinct angle at 50 kHz.

Factors affecting detection

The best models for detectability of groups and species were based on season and temperature (Table 4). The model with an additive effect of season (p_{all}) received the greatest support ($\Delta = 0$, $w_i = 0.041\text{-}0.893$) for all three frequency groups (≤ 29, 30-39, and ≥ 40 kHz), *T. brasiliensis*, *L. borealis* or *L. seminolus*, *P. subflavus*, and *M*. spp (Table 4). However, I found strong support for differences in the effect of temperature on detection each season (interaction among seasons; p_{wss}) for *E. fuscus*, and all three frequency groups (≤ 29, 30-39, and ≥ 40 kHz; $\Delta = 0\text{-}0.478$, $w_i = 0.037\text{-}0.432$). There was also strong support for a quadratic effect of temperature on detection (p_{temp2}) for *T. brasiliensis* ($\Delta = 1.008$, $w_i = 0.224$). For the ≥ 40 kHz group, the best model estimated different rates of detection in winter versus spring and summer ($p_{w/ss}$; $\Delta = 0$, $w_i = 0.063$). Julian date and relative humidity were not important factors on rates of detection for any species or group.

The effects of temperature on detection rates during winter varied among groups and species (Figure 1). January and February were typically the coldest months on each study area (Table 5). However, though temperatures were cold during winter surveys on Cahaba River NWR; surveys on Mountain Longleaf NWR were conducted during an unusually warm February resulting in an 11.5 °C difference in observed temperatures. At Cahaba River NWR in January, temperatures ranged from -3.3 to 0°C when I conducted surveys. In February at Mountain Longleaf NWR, the range in temperatures was 12.2-14.4°C. I recorded 1,024 echolocation calls during the winter surveys: 75 at Cahaba River NWR and 949 at Mountain Longleaf NWR. The species I recorded were *T. brasiliensis*, *E. fuscus*, *L. borealis* or *L. seminolus*, *P. subflavus*, and various *M*. spp. I identified *L. cinereus* and *N. humeralis* only once at Mountain Longleaf NWR. The group with frequency ≥ 40 kHz was the most active and accounted for 69% of the total at Cahaba River NWR and 67% at Mountain Longleaf NWR.

Factors affecting habitat use

Across all the sites I surveyed, the model-averaged estimates of occupancy for the frequency ≤29 kHz group were 76.0% in winter (95% CL, 35.2-94.9%), 100% in spring, and 92.9% during summer (95% CL, 69.9-98.7%; Figure 2, Table 6). The best fit model for this group of bats was the refuge model (Ψ_{refuge}). Using this model, I estimated that 100% of sites at Cahaba River NWR were used in each season by frequency ≤29 kHz (Table 6). For Mountain Longleaf NWR, use varied from 69.8% (95% CL, 42.3-88.0%) of sites during winter to 100% of sites during spring, and 84.8% (95% CL, 26.8-98.8%) of sites in summer. The remainder of the best models included effects related to habitat types. Many of the best models estimated different occupancy rates in open habitats, specifically rivers (Ψ_{river}), streams (Ψ_{stream}), and fields (Ψ_{field}, Ψ_{YMLP}; Table 7). In particular, this group of bats use was affected by the presence of aquatic resources, specifically isolated river and stream models (Ψ_{river}, Ψ_{stream}; $\Delta = 0.478$, 0.531, $w_i = 0.049$, 0.048; Table 8). I also found support of ≤29 kHz group use of monoculture pine (Ψ_{mono}, $\Delta = 1.939$, $w_i = 0.024$; Table 8). In cross-species comparisons, bats had varied degrees of occupancy for mountain longleaf pines and prescribed burn habitats (Table 8). The group had support ($\Delta = 1.939$, $w_i = 0.024$; Table 8) with the restoration of young longleaf pines model.

Within the frequency ≤29 kHz group, *T. brasiliensis* was one of two species isolated for analysis. Model-averaged estimates of occupancy for this species suggest they were present at 0.5% (95% CL, 0-9.2%) of sites in winter, 99.9% (95% CL, 98.1-100.0%) in spring, and 68.2% (95% CL, 16.7-95.8%) in summer (Figure 3, Table 6). The best occupancy models for this species suggest that it occurred much more frequently along streams in hardwood forests than in other habitats ($\Psi_{\text{stream+hardwood}}$, $\Delta = 0$, $w_i = 0.367$). The best models included effects of hardwood

forest and streams and had a combined weight (Σw_i) of 0.811 (Table 7). Models incorporating

rivers, monoculture, and mountain longleaf pine were not supported ($\Delta > 18$; Table 8)

Also in this frequency group and based on model-averaged estimates, *E. fuscus* was

present at 62.3% of sites (95% CL, 33.1-84.6%) in winter, 89.3% of sites (95% CL, 74.6-96.0%)

in spring, and 51.0% of sites (95% CL, 26.7-74.9%) in summer (Figure 3, Table 6). The species

use of habitats was affected by the presence of the river as well as mid-cover and canopy cover

density ($\Psi_{river+midcover}$, $\Delta = 0$, $w_i = 0.432$). *E. fuscus* was much more likely to use sites near the

river, but use decreased as mid-cover increased (Figure 4). The next best model, also included

river and use decreased as canopy cover increased ($\Psi_{river+can-cover}$, $\Delta = 1.112$, $w_i = 0.248$; Figure

5). However, with this species, models incorporating streams ($\Delta \geq 11$), monoculture ($\Delta \geq 5$), and

mountain longleaf pine ($\Delta \geq 4$) were not supported (Table 8).

Based on model-averaged estimates of occupancy frequency group 30-39 kHz used 100%

(95% CL, 98.2-100%) of sites during winter, 100% (95% CL, 99.9-100%) of sites in spring, and

96.1% (95% CL, 70.7-99.6%) of sites in summer (Figure 2, Table 6). The best model for this

group was the refuge model (Ψ_{refuge}), suggesting that differences between refuges explained

more of the variation in use than habitat characteristics. I estimated that the group used 100% of

sites during winter, spring, and summer at Cahaba River NWR (Table 6), but at Mountain

Longleaf NWR use differed seasonally. In winter and spring use was 100%, and in summer I

estimated only 92.3% (95% CL, 92.3-92.3%) of sites were used. When I compared models

based on habitats, this group selected open habitats, and showed a strong affinity for some

forested habitats, specifically pines and hardwoods (Ψ_{MLP}, Ψ_{pine}, $\Psi_{river+hardwood}$, $\Psi_{stream+hardwood}$,

$\Delta = 0.233-1.953$, $w_i = 0.0.37-0.016$; Table 7). An important indicator of use for this group was

the presence of aquatic resources ($\Delta = 0.308-1.485$, $w_i = 0.035-0.020$; Table 8), pine

monocultures ($\Delta = 0.849$, $w_i = 0.027$), and open mature stands of mountain longleaf pines and young mountain longleaf stands (Ψ_{MLP}, Ψ_{YMLP}, $\Delta = 0.233$, 0.849, $w_i = 0.037$, 0.027; Table 8).

Within the 30-39 kHz group, *L. borealis* and *L. seminolus* model-averaged occupancy was 24.5% (95% CL, 16.1-35.4%) across all sites in winter, 55.4% (95% CL, 46.9-63.6%) in spring, and 47.0% (95% CL, 29.7-65.0%) in summer (Figure 3, Table 6). Occurrence of these species was best explained by the combination of forest habitat with canopy cover ($\Psi_{forest+can-cover}$; $\Delta = 0$, $w_i = 0.893$; Table 7). Canopy cover had a negative impact on use across all three seasons (Figure 5). The data did not support the remainder of the evaluated models ($\Delta > 6$; Table 7).

For frequency ≥ 40 kHz group, model-averaged use was 67.1% (95% CL, 29.5-90.8%) of sites during winter, 100% of sites during spring, and 98.2% (95% CL, 80.3-99.9%) of sites during summer (Figure 2, Table 6). This group of small bats use differed between refuges. I estimated that 89.8% (95% CL, 24.4-99.6%) of sites were used during winter, 100% of sites were used during spring, and 99.6% (95% CL, 53.0-99.9%) of sites were used during summer at Cahaba River NWR (Table 6). Mountain Longleaf NWR received 47.0% (95% CL, 28.8-66%), 100.0%, and 96.3% (95% CL, 58.6-99.8%) use in winter, spring and summer. The group was more likely to use open habitats as opposed to closed forested areas; 11 of the 14 top models ($\Delta \leq 2$), excluding the refuge model, suggested differential use of open habitats (Ψ_{river}, Ψ_{field}, Ψ_{YMLP}). This groups seasonal use of habitats was also related to factors associated with forest structure, specifically canopy cover ($\Psi_{river+can-cover}$, $\Delta = 0.374$, $w_i = 0.052$, Figure 5). Use declined as canopy cover increased, and the effect was greatest in winter. Also, this groups use was affected by the river ($\Delta = 0.374$-1.983, $w_i = 0.054$-0.023; Table 8). Lastly, in relation to

mountain longleaf pine management, I found support for models incorporating restored young

mountain longleaf pines ($\Delta = 1.475$, $w_i = 0.030$; Table 8).

In the $\geq$40 kHz group, *P. subflavus* occurred at 30.5% (95% CL, 0-100%) of sites in

winter, 90.9% (95% CL, 57.6-98.7%) of sites in spring, and 79.3% (95% CL, 40.7-95.5%) of

sites in summer based on model-averaged estimates (Figure 3, Table 6). The three best habitat

models ($\Delta \leq 2$) included effects of forest habitat, basal area, and canopy cover ($\Psi_{forest+ba}$, $\Psi_{can-cover}$, $\Psi_{forest+can-cover}$; w_i = 0.213, 0.105, 0.082; Table 7). Based on the best model for the species

($\Psi_{forest+ba}$; $\Delta = 0$), the probability of use in winter was low at 1.3% (95% CL, 0.2-8.2%), but

increased in spring (87.1%, 95% CL, 50.6-97.8%) and summer (70.9%, 95% CL, 27-94.2%).

Additionally, probability of use in winter (8.2%), spring (97.8%), and summer (94.2%) dropped

to near 0 as basal area increased (Figure 6). Similarly, use of sites declined as canopy cover

increased (Figure 5); however, the effect was less in spring compared to summer. I also found

weak support for an effect of aquatic resources on use by this species ($\Psi_{river+can-cover}$; $\Delta = 2.641$,

w_i = 0.057; Table 8).

Also, within the $\geq$40 kHz group, I found *M.* spp use based on model-averaged estimates

were 55.4% (95% CL, 7.0-95.5%) of sites in winter, 76.1% (95% CL, 50.5-90.8%) of sites in

spring, and 74.3% (95% CL, 46.9-90.4%) of sites in summer (Figure 3, Table 6). *M.* spp also

occurred more frequently near roads (Ψ_{road}, $\Delta = 0$, w_i = 0.327,). All other models ($\Delta \leq 2$) with

this group were associated with forested habitats, including hardwoods and mixed forests (Table

7). I estimated that *M.* spp used 100% of hardwood forest sites in every season with use related

to basal area ($\Psi_{hardwood+BA}$, $\Delta = 2.95$, w_i = 0.075). Basal area increase had no effect on

occupancy in winter (100%), but probability of use in spring increased from 55.0 to 99.9% and

in summer 49.4 to 99.9% (Figure 6). The probability of use of habitats in a hardwood forest with

snags was also 100% for all three seasons (Ψ hardwood+snag, $\Delta = 2.99$, $w_i = 0.073$). Further, density

of snags was correlated with an increase in occupancy across all three seasons, winter, spring,

and summer (Figure 7). Models incorporating aquatic resources, monoculture stands, and

mountain longleaf pine management were not supported for *M.* spp (Table 8).

Table 4. Best models ($\Delta \leq 2.0$) for detection of species of bats at Cahaba River National Wildlife Refuge, Bibb County, and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama, 2009-2010. Detection model results obtained prior to being paired with occupancy (Ψ). Some groups and species were detected in multiple models and are listed accordingly.

Model Group	AICc	Δ AICc	Model Weight	Likelihood	Number of parameters	Deviance
Detection does not vary among surveys ($p.$)						
Perimyotis subflavus	451.273	1.786	0.225	0.410	4	442.906
Temperature affects detection, effect of temperature differs by season (interaction among seasons; p_{wss})						
$\leq$29 kHz frequency group	605.131	0.080	0.490	0.961	8	587.760
30-39 kHz frequency group	526.803	0	0.562	1	7	511.747
$\geq$40 kHz frequency group	518.506	0.214	0.219	0.899	8	501.134
Eptesicus fuscus	511.256	0	0.865	1	10	489.120
Myotis spp.	531.861	0.068	0.182	0.967	11	507.273
Temperature affects detection and the effect is similar each season (additive effect of season; p_{all})						
$\leq$29 kHz frequency group	605.052	0	0.510	1	6	592.267
30-39 kHz frequency group	527.299	0.496	0.438	0.781	5	516.743
$\geq$40 kHz frequency group	518.783	0.491	0.191	0.783	6	505.997
Perimyotis subflavus	449.487	0	0.550	1	5	438.932
Myotis spp.	532.631	0.838	0.124	0.658	9	512.900
Temperature affects detection and the effect is different in winter, but similar in spring and summer ($p_{w/ss}$)						
$\geq$40 kHz frequency group	518.292	0	0.244	1	6	505.507
Temperature affects decrease as temperature increases (quadratic; p_{temp2})						
Tadarida brasiliensis	373.728	0	0.773	1	7	358.671
Lasiurus borealis and *L.seminolus*	330.762	0	0.632	1	8	313.391

Table 4. Best models ($\Delta \leq 2.0$) for detection of species of bats at Cahaba River National Wildlife Refuge, Bibb County, and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama, 2009-2010. Detection model results obtained prior to being paired with occupancy (Ψ). Some groups and species were detected in multiple models and are listed accordingly.

Model	Group	AICc	Δ AICc	Model Weight	Likelihood	Number of parameters	Deviance
	Myotis spp.	531.793	0	0.188	1	8	514.422
Temperature affects detection (p_{temp})							
	$\geq$40 kHz frequency group	518.663	0.371	0.203	0.831	4	510.296

Table 5. Temperatures (°C) observed in winter when bats were active at Cahaba River National Wildlife Refuge, Bibb County, and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama, 2009-2010.

Groups/Species	Cahaba River National Wildlife Refuge			Mountain Longleaf National Wildlife Refuge		
	Temperature[1]	Minimum[2]	Maximum[3]	Temperature	Minimum	Maximum
≤29 kHz frequency group	-2.51	-6.17	4.07	13.77	10.64	19.94
30-39 kHz frequency group	-2.83	-7.11	3.78	14.57	11.86	20.11
≥40 kHz frequency group	-1.12	-4.89	6.83	13.20	10.12	19.29
Tadarida brasiliensis	-0.28	-5.56	8.33	13.19	9.64	19.39
Eptesicus fuscus	-2.89	-6.43	3.49	12.92	9.19	19.19
Lasiurus borealis and *L.seminolus*	-2.08	-5.00	3.89	13.99	11.26	19.39
Myotis spp.	-1.18	-5.28	6.11	12.46	7.92	19.03
Average	-1.84	-5.78	5.22	13.44	10.09	19.48
Median	-2.08	-5.56	4.07	13.20	10.09	19.39

[1]actual temperature observed during bat activity in °C

[2]minimum temperature observed during the night in °C

[3]maximum temperature observed during the night in °C

Table 6. Model-averaged estimates of seasonal occupancy rates (Ψ), standard errors (SE) with lower and upper 95% confidence limits (CL) for bats detected at Cahaba River National Wildlife Refuge and Mountain Longleaf National Wildlife Refuge, Alabama, 2009-2010.

Group	Season	Ψ	SE	Lower 95% CI	Upper 95% CL
≤29 kHz frequency group					
	Winter	76	16.4	35.2	94.9
	Spring	100	0	100	100
	Summer	92.9	5.9	69.6	98.7
30-39 kHz frequency group					
	Winter	100	0.9	98.2	100
	Spring	100	0	100	100
	Summer	96.1	4.4	70.6	99.6
≥40 kHz frequency group					
	Winter	67.1	17.8	29.5	90.8
	Spring	100	0	100	100
	Summer	98.2	2.4	80.3	99.9
Tadarida brasiliensis					
	Winter	0.5	4.5	0	9.2
	Spring	99.9	0.9	98.1	100
	Summer	68.2	26.2	16.7	95.8
Eptesicus fuscus					
	Winter	62.3	14.4	33.2	84.6
	Spring	89.3	5.1	74.6	96
	Summer	51	13.4	26.7	74.9
Lasiurus borealis and *L.seminolus*					
	Winter	24.5	5	16.1	35.4
	Spring	55.4	4.3	46.9	63.6
	Summer	47	9.4	29.7	65
Perimyotis subflavus					
	Winter	30.5	1995.8	0	100
	Spring	90.9	8.4	57.6	98.7
	Summer	79.3	14.4	40.7	95.5
Myotis spp.					

Table 6. Model-averaged estimates of seasonal occupancy rates (Ψ), standard errors (SE) with lower and upper 95% confidence limits (CL) for bats detected at Cahaba River National Wildlife Refuge and Mountain Longleaf National Wildlife Refuge, Alabama, 2009-2010.

Group	Season	Ψ	SE	Lower 95% CI	Upper 95% CL
	Winter	55.4	35.5	6.9	95.4
	Spring	76.1	10.5	50.6	90.8
	Summer	74.3	11.5	47	90.4

Table 7. The top five models of occupancy (Ψ) for each group of bats detected at Cahaba River National Wildlife Refuge, Bibb County and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama, 2009-2010.

	AICc	Δ AICc	Model Weight	Likelihood	Number of parameters	Deviance
≤29 kHz frequency group						
Ψ refuge γ p all	602.430	0	0.063	1	6	589.644
Ψ river γ p wss	602.908	0.478	0.049	0.788	8	585.536
Ψ stream γ p all	602.960	0.531	0.048	0.767	7	587.903
Ψ river γ p all	602.990	0.560	0.047	0.756	6	590.205
Ψ refuge γ p wss	603.227	0.797	0.042	0.671	8	585.855
30-39 kHz frequency group						
Ψ refuge γ p all	525.732	0	0.041	1.000	5	515.177
Ψ MLP γ p wss	525.965	0.233	0.037	0.890	7	510.908
Ψ pine γ p all	526.040	0.308	0.035	0.857	5	515.484
Ψ stream+hardwood γ p all	526.040	0.308	0.035	0.857	5	515.484
Ψ river+hardwood γ p wss	526.096	0.364	0.034	0.834	7	511.039
≥40 kHz frequency group						
Ψ refuge γ p w/ss	514.523	0	0.063	0.999	7	499.466
Ψ refuge γ p all	514.684	0.161	0.058	0.923	7	499.627
Ψ field+MLP young γ p w/ss	514.782	0.260	0.055	0.878	6	501.997
Ψ refuge γ $p$wss	514.824	0.302	0.054	0.860	9	495.094
Ψ river+can-cover γ p w/ss	514.897	0.374	0.052	0.830	7	499.840
Tadarida brasiliensis						
Ψ stream+hardwood γ p all	350.094	0	0.369	1	6	337.309
Ψ stream+hardwood γ p temp2	351.102	1.008	0.224	0.604	4	342.735
Ψ hardwood γ p all	351.141	1.047	0.219	0.592	5	340.585
Ψ stream+hardwood γ p wss	352.122	2.028	0.134	0.363	7	337.065
Ψ hardwood γ p wss	355.469	5.376	0.025	0.068	7	340.413
Eptesicus fuscus						
Ψ river+mid-cover γ p wss	499.668	0	0.432	1	10	477.532

Table 7. The top five models of occupancy (Ψ) for each group of bats detected at Cahaba River National Wildlife Refuge, Bibb County and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama, 2009-2010.

	AICc	Δ AICc	Model Weight	Likelihood	Number of parameters	Deviance
Ψ river+can-cover γ p wss	500.779	1.112	0.248	0.574	10	478.643
Ψ river γ p wss	502.698	3.030	0.095	0.230	9	482.967
Ψ field+MLP young γ p wss	504.293	4.626	0.043	0.099	9	484.563
Ψ river+hardwood γ p wss	505.068	5.400	0.029	0.067	10	482.932
Lasiurus borealis and *L.seminolus*						
Ψ forest+can-cover γ p all	309.014	0	0.893	1	5	298.458
Ψ can-cover γ p temp2	315.882	6.869	0.029	0.032	8	298.511
Ψ forest+can-cover γ p temp2	316.183	7.169	0.025	0.028	9	296.452
Ψ pine+snag γ p all	316.819	7.806	0.018	0.020	4	308.453
Ψ river+can-cover γ p temp2	318.234	9.221	0.009	0.010	9	298.504
Perimyotis subflavus						
Ψ forest+BA γ p all	441.524	0	0.213	1	8	424.153
Ψ can-cover γ p all	442.927	1.403	0.105	0.496	8	425.556
Ψ forest+can-cover γ p.	443.438	1.914	0.082	0.384	7	428.382
Ψ forest+can-cover γ p all	443.749	2.225	0.070	0.329	9	424.019
Ψ can-cover γ p.	443.967	2.443	0.063	0.295	7	428.911
Myotis spp.						
Ψ road γ $p$all	523.809	0	0.328	1	8	506.437
Ψ hardwood+BA γ p wss	526.761	2.953	0.075	0.229	11	502.173
Ψ hardwood+snag γ p wss	526.798	2.999	0.073	0.224	11	502.210
Ψ mixed+snag γ p wss	526.967	3.159	0.068	0.206	11	502.379
Ψ forest+mid γ p all	527.752	3.943	0.046	0.139	9	508.021

Table 8. Selection statistics for models of bat occupancy (Ψ) grouped by resource type (aquatic, mono-cultural stands, and mountain longleaf pine) available at Cahaba River National Wildlife Refuge, Bibb County, and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama, 2009-2010.

Resource type Group	Model	AICc	Δ AICc	Model Weight	Likelihood	Number of parameters	Deviance
Aquatic Resources							
≤29 kHz frequency group	$\Psi_{river} \gamma p_{wss}$	602.908	0.478	0.049	0.788	8	585.536
	$\Psi_{stream} \gamma p_{all}$	602.960	0.531	0.048	0.767	7	587.903
30-39 kHz frequency group	$\Psi_{stream+hardwood} \gamma p_{all}$	526.040	0.308	0.035	0.857	5	515.484
	$\Psi_{river+hardwood} \gamma p_{wss}$	526.096	0.364	0.034	0.834	7	511.039
	$\Psi_{stream} \gamma p_{wss}$	526.223	0.491	0.032	0.782	7	511.166
	$\Psi_{river} \gamma p_{wss}$	526.581	0.849	0.025	0.654	7	511.525
≥40 kHz frequency group	$\Psi_{river+can\text{-}cover} \gamma p_{w/ss}$	514.897	0.374	0.052	0.830	7	499.84
	$\Psi_{river} \gamma p_{w/ss}$	515.997	1.475	0.030	0.478	6	503.212
	$\Psi_{stream} \gamma p_{w/ss}$	517.950	3.428	0.011	0.180	7	502.894
Tadarida brasiliensis	$\Psi_{river+can\text{-}cover} \gamma p_{temp2}$	369.905	19.811	<0.001	<0.001	9	350.174
	$\Psi_{river} \gamma p_{all}$	377.427	27.334	0	0	9	357.696

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Table 8. Selection statistics for models of bat occupancy (Ψ) grouped by resource type (aquatic, mono-cultural stands, and mountain longleaf pine) available at Cahaba River National Wildlife Refuge, Bibb County, and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama, 2009-2010.

Resource type Group	Model	AICc	Δ AICc	Model Weight	Likelihood	Number of parameters	Deviance
	$\Psi_{stream}\,\gamma\,p_{all}$	378.152	28.058	0	0	9	358.421
	$\Psi_{stream+hardwood}\,\gamma\,p_{all}$	350.094	0	0.369	1	6	337.309
Eptesicus fuscus	$\Psi_{river+mid\text{-}cover}\,\gamma\,p_{wss}$	499.668	0	0.432	1	10	477.532
	$\Psi_{river}\,\gamma\,p_{wss}$	502.698	3.030	0.095	0.220	9	482.967
	$\Psi_{stream}\,\gamma\,p_{wss}$	510.878	11.210	0.002	0.004	11	486.290
Lasiurus borealis and *L.seminolus*	$\Psi_{stream+hardwood}\,\gamma\,p_{all}$	323.359	14.346	0.001	0.001	4	314.992
	$\Psi_{stream}\,\gamma\,p_{wss}$	334.974	25.961	0	0	12	307.885
	$\Psi_{river}\,\gamma\,p_{wss}$	335.236	26.223	0	0	12	308.147
Perimyotis subflavus	$\Psi_{river+can\text{-}cover}\,\gamma\,p_{.}$	444.165	2.641	0.057	0.267	7	429.109
	$\Psi_{stream}\,\gamma\,p_{all}$	451.025	9.500	0.002	0.009	7	435.968
	$\Psi_{river}\,\gamma\,p_{wss}$	488.247	46.723	0	0	3	482.029
Myotis spp.	$\Psi_{stream+mixed}\,\gamma\,p_{wss}$	530.081	6.273	0.014	0.044	11	505.493

Table 8. Selection statistics for models of bat occupancy (Ψ) grouped by resource type (aquatic, mono-cultural stands, and mountain longleaf pine) available at Cahaba River National Wildlife Refuge, Bibb County, and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama, 2009-2010.

Resource type / Group	Model	AICc	Δ AICc	Model Weight	Likelihood	Number of parameters	Deviance
	$\Psi_{\text{stream}}\,\gamma\,p_{\text{wss}}$	531.422	7.613	0.007	0.022	11	506.834
	$\Psi_{\text{river}}\,\gamma\,p_{\text{wss}}$	531.571	7.762	0.007	0.021	11	506.983
Mono-cultural forest							
≤29 kHz frequency group	$\Psi_{\text{mono}}\,\gamma\,p_{\text{all}}$	604.368	1.939	0.024	0.379	6	591.583
30-39 kHz frequency group	$\Psi_{\text{mono}}\,\gamma\,p_{\text{wss}}$	526.581	0.849	0.027	0.654	7	511.525
≥40 kHz frequency group	$\Psi_{\text{mono}}\,\gamma\,p_{\text{w/ss}}$	520.557	6.034	0.003	0.049	7	505.500
Tadarida brasiliensis	$\Psi_{\text{mono}}\,\gamma\,p_{\text{all}}$	374.797	24.703	0	0	8	357.425
Eptesicus fuscus	$\Psi_{\text{mono}}\,\gamma\,p_{\text{wss}}$	505.265	5.598	0.026	0.061	9	485.535
Lasiurus borealis and *L.seminolus*	$\Psi_{\text{mono}}\,\gamma\,p_{\text{wss}}$	327.116	18.102	<0.001	<0.001	11	302.528
Perimyotis subflavus	$\Psi_{\text{mono}}\,\gamma\,p_{\text{wss}}$	511.031	69.507	0	0	9	491.300
Myotis spp.	$\Psi_{\text{mono}}\,\gamma\,p_{\text{all}}$	530.883	7.074	0.010	0.029	9	511.152

Table 8. Selection statistics for models of bat occupancy (Ψ) grouped by resource type (aquatic, mono-cultural stands, and mountain longleaf pine) available at Cahaba River National Wildlife Refuge, Bibb County, and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama, 2009-2010.

Resource type Group	Model	AICc	Δ AICc	Model Weight	Likelihood	Number of parameters	Deviance
Young mountain longleaf pine (*Pinus palustris*)							
≤29 kHz frequency group	$\Psi_{\text{MLP young}} \gamma p_{\text{all}}$	604.368	1.939	0.024	0.379	6	591.583
30-39 kHz frequency group	$\Psi_{\text{MLP young}} \gamma p_{\text{wss}}$	526.581	0.849	0.027	0.654	7	511.525
≥40 kHz frequency group	$\Psi_{\text{MLP young}} \gamma p_{\text{w/ss}}$	515.997	1.475	0.030	0.478	6	503.212
Tadarida brasiliensis	$\Psi_{\text{MLP young}} p_{\text{all}}$	379.004	28.910	0	0	9	359.273
Eptesicus fuscus	$\Psi_{\text{MLP young}} \gamma p_{\text{wss}}$	507.012	7.344	0.011	0.025	9	487.281
Lasiurus borealis and *L.seminolus*	$\Psi_{\text{MLP young}} \gamma p_{\text{wss}}$	327.971	18.958	<0.001	<0.001	11	303.383
Perimyotis subflavus	$\Psi_{\text{MLP young}} \gamma p_{\text{wss}}$	488.247	46.723	0	0	3	482.029
Myotis spp.	$\Psi_{\text{MLP young}} \gamma p_{\text{wss}}$	534.205	10.397	0.002	0.006	12	507.116
Mountain Longleaf Pine (*P. palustris*)							
≤29 kHz frequency group	$\Psi_{\text{MLP}} \gamma p_{\text{wss}}$	607.173	4.744	0.006	0.093	9	587.442
30-39 kHz frequency group	$\Psi_{\text{MLP}} \gamma p_{\text{wss}}$	525.965	0.233	0.037	0.890	7	510.908

Table 8. Selection statistics for models of bat occupancy (Ψ) grouped by resource type (aquatic, mono-cultural stands, and mountain longleaf pine) available at Cahaba River National Wildlife Refuge, Bibb County, and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama, 2009-2010.

Resource type Group	Model	AICc	Δ AICc	Model Weight	Likelihood	Number of parameters	Deviance
≥40 kHz frequency group	$\Psi_{MLP} \gamma p_{wss}$	520.018	5.496	0.004	0.064	9	500.288
Tadarida brasiliensis	$\Psi_{MLP} \gamma p_{wss}$	382.089	31.996	0	0	11	357.501
Eptesicus fuscus	$\Psi_{MLP} \gamma p_{wss}$	508.226	8.559	0.006	0.014	10	486.09
Lasiurus borealis and *L.seminolus*	$\Psi_{MLP} \gamma p_{wss}$	332.228	23.215	<0.001	0	12	305.139
Perimyotis subflavus	$\Psi_{MLP} \gamma p_{.}$	506.652	65.128	0	0	9	486.922
Myotis spp.	$\Psi_{MLP} \gamma p_{wss}$	534.142	10.333	0.002	0.006	12	507.053
Prescribed Fire							
≤29 kHz frequency group	$\Psi_{fire} \gamma p_{all}$	605.488	3.058	0.014	0.217	7	590.431
30-39 kHz frequency group	$\Psi_{fire} \gamma p_{all}$	529.528	3.796	0.006	0.150	6	516.743
≥40 kHz frequency group	$\Psi_{fire} \gamma p_{all}$	520.232	5.709	0.004	0.058	7	505.175
Tadarida brasiliensis	$\Psi_{fire} \gamma p_{all}$	378.927	28.834	0	0	9	359.196
Eptesicus fuscus	$\Psi_{fire} \gamma p_{all}$	521.196	21.528	<0.001	0	8	503.824

Table 8. Selection statistics for models of bat occupancy (Ψ) grouped by resource type (aquatic, mono-cultural stands, and mountain longleaf pine) available at Cahaba River National Wildlife Refuge, Bibb County, and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama, 2009-2010.

Resource type Group	Model	AICc	Δ AICc	Model Weight	Likelihood	Number of parameters	Deviance
Lasiurus borealis and *L.seminolus*	$\Psi_{\text{fire}}\, \gamma\, p_{\text{all}}$	338.138	29.124	0	0	10	316.002
Perimyotis subflavus	$\Psi_{\text{fire}}\, \gamma\, p_{\text{all}}$	461.129	19.605	<0.001	0	9	441.398
Myotis spp.	$\Psi_{\text{fire}}\, \gamma\, p_{\text{all}}$	534.091	10.283	0.002	0.006	10	511.955

Figure 1. The relationship between detection probability and temperature for groups and species of bats during winter at Cahaba River National Wildlife Refuge, Bibb County, and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama, 2009-2010. Frequency groups include ≤29 kHz, 30-39 kHz, and ≥40 kHz. Species of bats include *Tadarida brasiliensis* (TABR), *Eptesicus fuscus* (EPFU), *Lasiurus borealis* and *L. seminolus* (LABOSE), *Perimyotis subflavus* (PESU), and various unidentified *Myotis* (*Myotis* spp.).
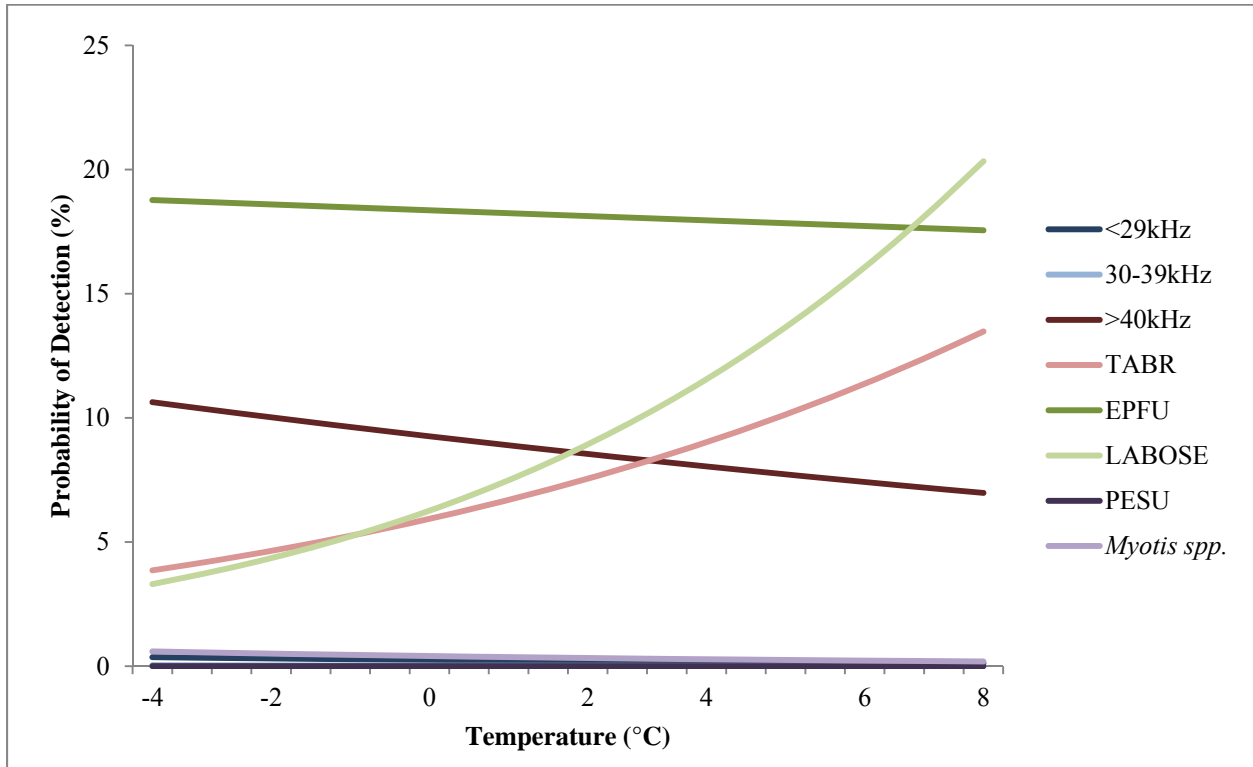
Figure 2. Model-averaged estimates (♦), 95% confidence limits (line), and standard errors (box) of occupancy (probability of use) by frequency groups of bats detected on acoustical surveys conducted during winter, spring, and summer at Cahaba River National Wildlife Refuge, Bibb County, and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama, 2009-2010.

Figure 3. Model-averaged estimates (♦) of occupancy (probability of use), 95% confidence limits (line), and standard errors (box) of bats detected on acoustical surveys conducted during winter, spring, and summer at Cahaba River National Wildlife Refuge, Bibb County, and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama, 2009-2010. Species of bats include *Tadarida brasiliensis* (TABR), *Eptesicus fuscus* (EPFU), *Lasiurus borealis* and *L. seminolus* (LABOSE), *Perimyotis subflavus* (PESU), and various unidentified *Myotis* species. (MYSPP).
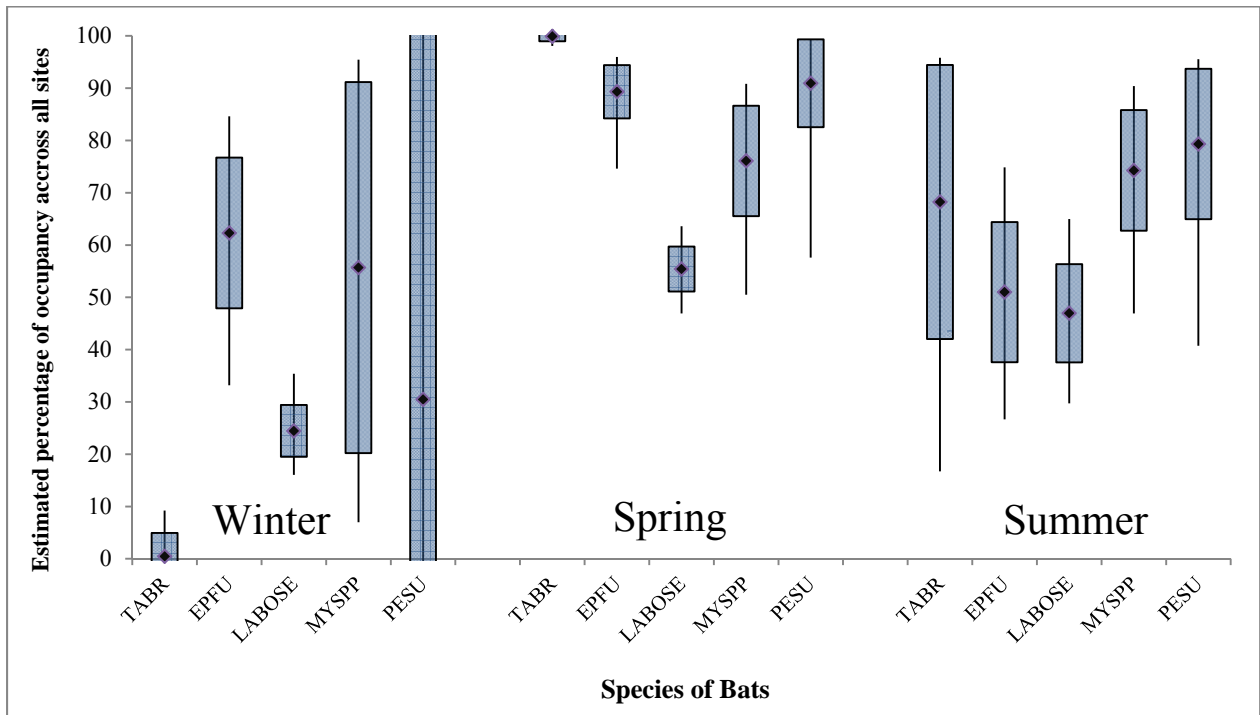
Figure 4. Relationship between percent mid-story cover in association with a river covariate and site use by *Eptesicus fuscus* species during winter, spring, and summer based on logit link function calculations at Cahaba River National Wildlife Refuge, Bibb County, and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama, 2009-2010.
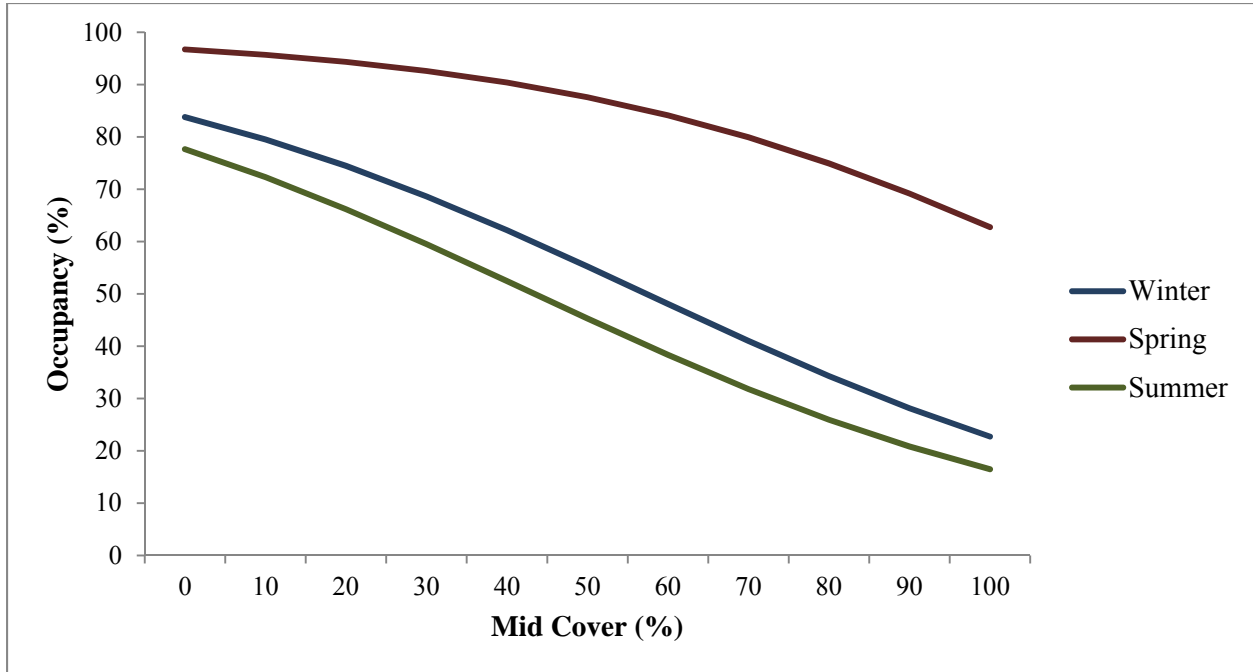
Figure 5. Relationship between occupancy (probability of use) and canopy cover (%) for small bats (frequency ≥40 kHz), *Eptesicus fuscus*, *Lasiurus borealis* and *L. seminolus*, and *Perimyotis subflavus* during winter, spring, and summer at Cahaba River National Wildlife Refuge, Bibb County, and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama, 2009-2010.
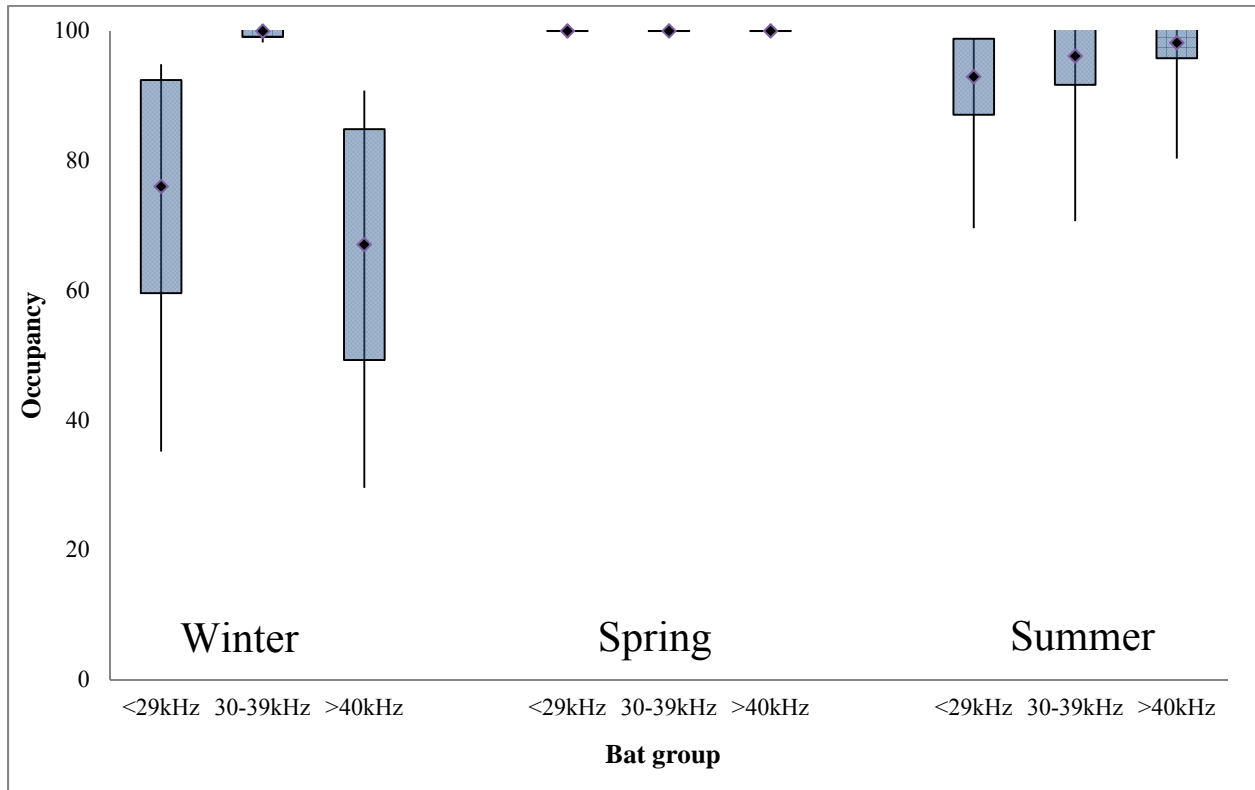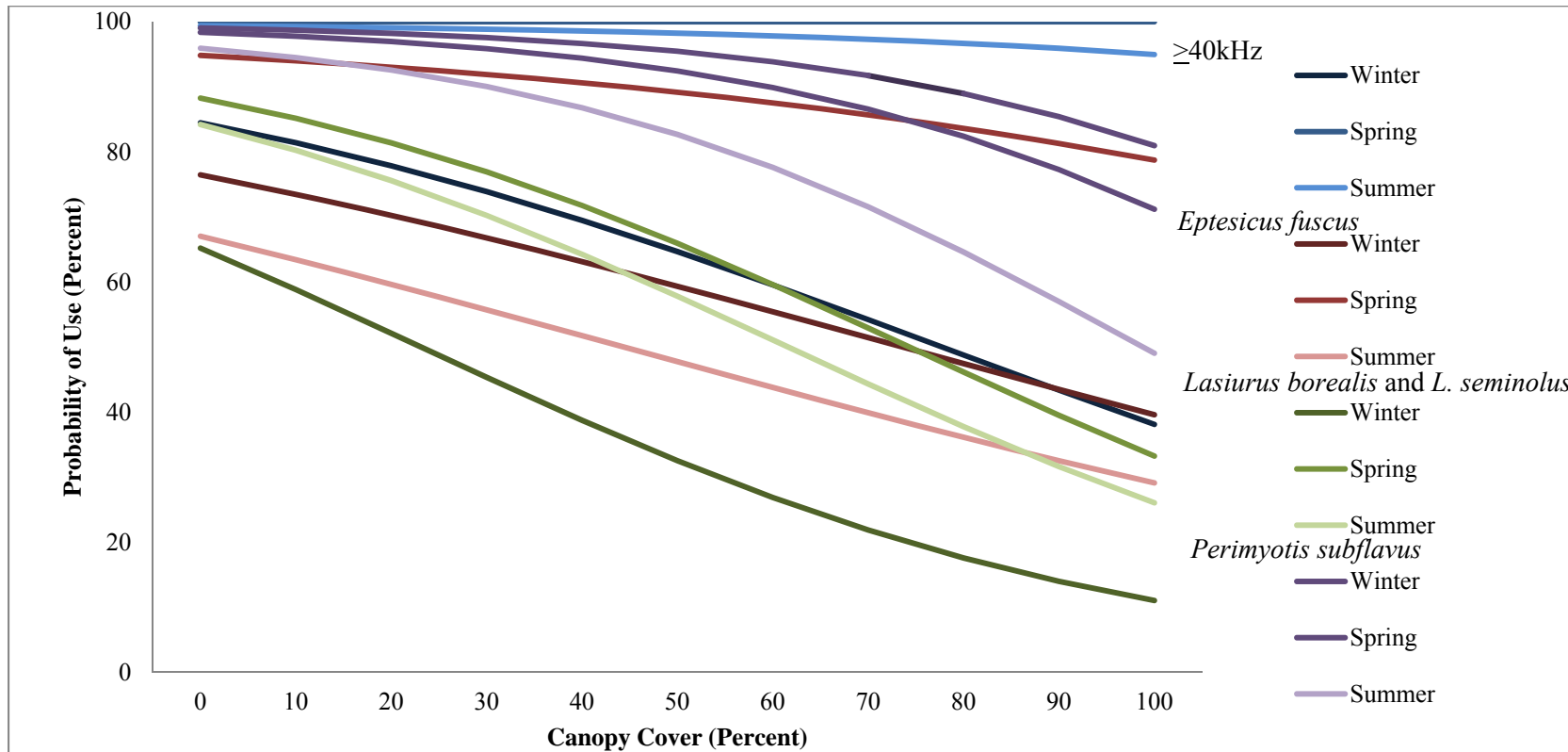
Figure 6. Estimated occupancy (probability of use) of forested basal area (m^2/ha) by *Myotis* species in hardwood forest type and *Perimyotis subflavus* species in forested area during winter, spring, and summer based on logit link function calculations at Cahaba River National Wildlife Refuge, Bibb County, and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama, 2009-2010.
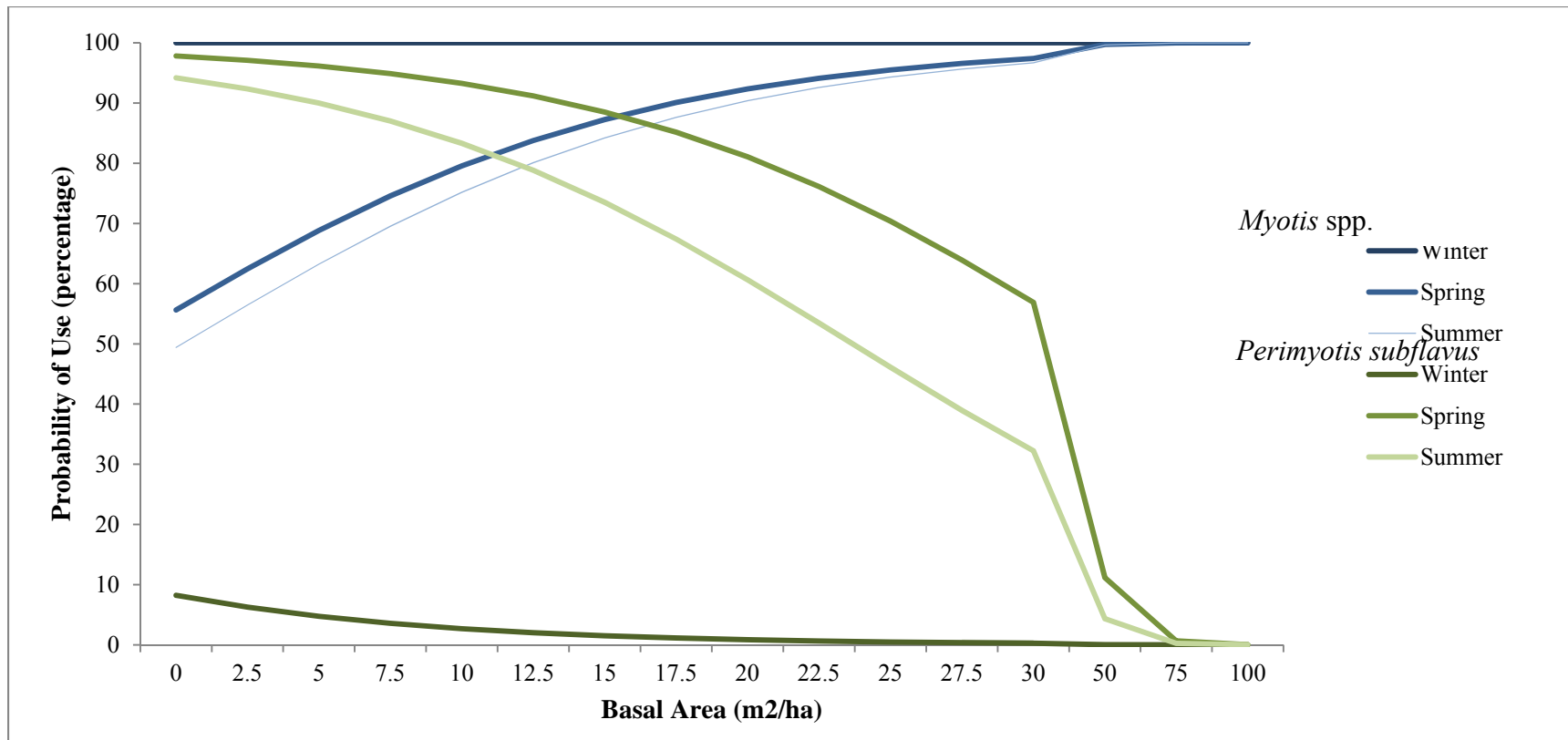
Figure 7. Relationship between hardwood stand snag density and use (Δ = 2.99) by *Myotis* species during winter, spring, and summer at Cahaba River National Wildlife Refuge, Bibb County, and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama, 2009-2010.
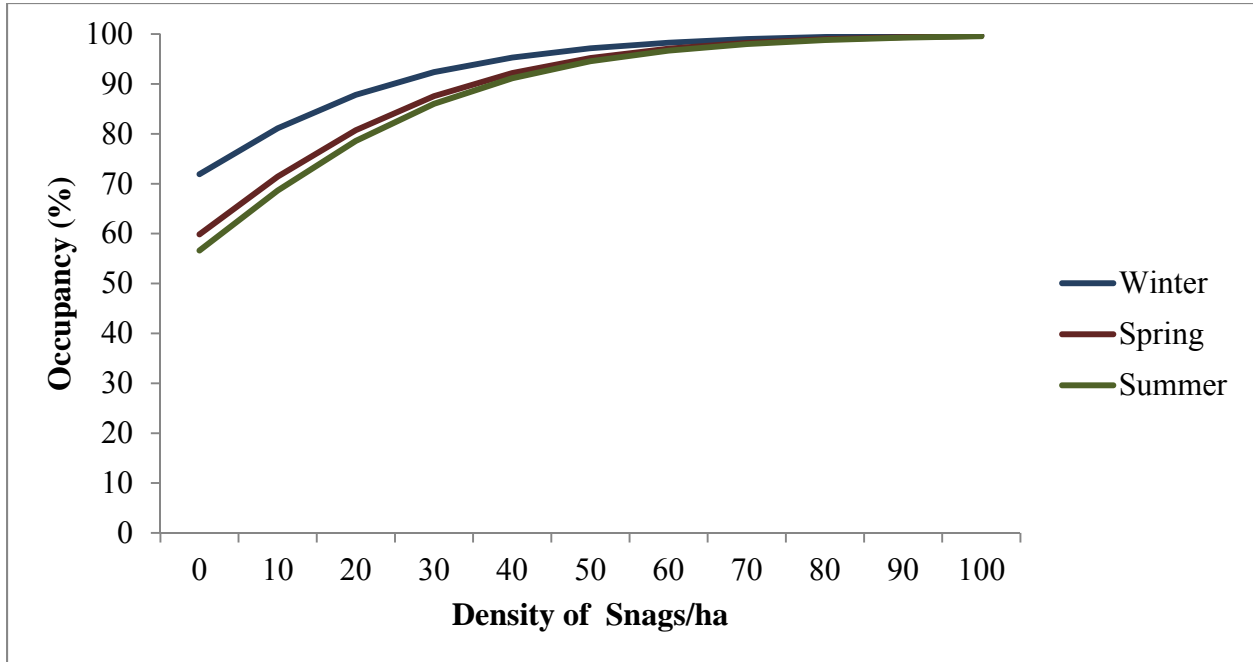
DISCUSSION

There are many limitations when using passive detection to survey bat

populations. Although it is possible to determine the presence of various bats using passive

detection, this method does not allow estimates of abundance, because it does not differentiate

between multiple individuals and a single individual recorded multiple times (Kalcounis et al.

1999). Another limitation is that identification of species is difficult, especially for bats in the

genus *Myotis* (Duchamp et al. 2006, Yates and Muzika 2006). Evaluation of recordings is time

consuming, and relatively few calls are of sufficient quality for identification (Loeb and O'Keefe

2006). Further, bats are highly mobile; thus, my estimates of occupancy can only be interpreted

as probability of use of sites, and not the probability of residency. For the purpose of this study,

I recorded presence and absence of bats based on high quality calls, and used occupancy models

to estimate use (MacKenzie et al. 2002).

I found differences in detectability and probability of use of sites among species and

frequency groups of bats. Use of occupancy models to compensate for imperfect detection

allowed me to obtain estimates of the relationship of various covariates to detectability when bats

were calling. Sources of variation in rates of detection result from differences among species

and individuals, placement of detectors, and environmental conditions. While each of these

contributes to differences in detection, not all of them can be estimated or identified when using

passive detectors to construct models of occupancy. I only estimated the effects of factors

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related to detection that were measureable as characteristics of calls, sampling occasions, or survey sites.

Within species, size, age, and sex of individuals contribute to variation in detectability (Murray et al. 2001, Perry et al. 2010a). Some species, such as *M. septentrionalis*, have a low-frequency call making them hard to detect (Ford et al. 2005). In addition, placement of detectors significantly affects quality and content of recording, especially when probability of detecting some species is low (Duchamp et al. 2006). Species niches vary within forested areas, especially while feeding, which further complicate detection. Some species forage within or below the canopy, while others forage above the canopy. Menzel et al. (2005b) suggested placing detectors 30 m above canopy to record species that use canopy as foraging habitat. They reported a 3-fold increase in detection of *N. humeralis* when using detectors above versus below canopy in a mature stand of pines. However, they reported similar rates of detection above and below canopy for other clutter-adapted species. Even so, they consistently detected *E. fuscus* and *L. cinereus* above canopy. I was unable to sample this microhabitat in my study. Therefore, I likely detected *N. humeralis* in my study less frequently than they did. Additionally, my detection for *E. fuscus* may not reflect above canopy-use of forested areas. The only other species that I did not detect, which may only occur above the canopy, was *L. noctivagans*.

Across the sites surveyed, I recorded the greatest number of detections at four locations in open environments. The number of detections I recorded at those sites was almost certainly the result of higher detection rates in habitats with less clutter. In these habitats, sounds are unobstructed by objects. Conversely, species occupying cluttered areas have much lower detection rates, and may not be detected at all.

I expected date, temperature, and relative humidity to have strong effects on detection. Temperature had the strongest relationship to detectability of bats, and the strength of that relationship was less in spring and summer than in winter. Surprisingly, date had no effect on detectability. Because I sampled over a wide range of dates, I expected a stronger relationship with date for some species. In a similar study conducted in South Carolina, temperature seemed to affect only *N. humeralis* (Hein et al. 2009a). Rates of detection of four other species, three of which were identified in my study (*L. borealis, L. seminolus, P. subflavus*), were more correlated to Julian date ($\Delta = 0$, $w_i = 0.270$-0.528). However, they conducted their study from June to August; thus, the range of temperatures was less than I observed. Relative humidity did not have an effect. It consistently ranked lowest among all models of detection. I believed that the high water content of humid air would affect detectability, but that was incorrect.

I predicted that activity would resume during warmer weather in winter in the southeast. Many species of bats hibernate in karst features or man-made structures during winter (Brooks and Ford 2006, Harvey et al. 1999, Wilson 1997). Species of *Lasiurus* hibernate at the base of trees in leaf litter (Taylor 2007). Perry et al. (2010b) assessed *L. noctivagans* activity and selection of roosts during winter in Arkansas. They found *L. noctivagans* roosted in mature live trees or in burrows as temperatures decreased taking advantage of radiant energy. In Alabama, monitoring surveys of bats occupying karst features has been conducted for several years (M.K. Hudson, pers. comm.). In the past 3 years, monitoring has expanded in response to the spread of the fungus *Geomyces destructans*, which is responsible for killing >1,000,000 bats in the northeastern United States and southeastern Canada (Blehert et al. 2009, Gargas et al. 2009). I recorded activity of bats at temperatures as low as -3.3°C. All three bat frequency groups (≤ 29,

30-39, and ≥40 kHz) were active, and most of the echolocation calls were from the ≥40 kHz frequency group.

I included a model that estimated different rates of use between refuges (Ψ_{refuge}) even though my primary hypotheses were centered on use of different habitats by various groups and species. I found only a slight difference in occupancy between refuges, especially in winter. The most obvious difference between the refuges is the presence of the Cahaba River at Cahaba River NWR, while aquatic resources at Mountain Longleaf NWR are mostly intermittent streams of various sizes. All other attributes were similar. Thus, the models that included the attributes of aquatic resources (Ψ_{river} and $\Psi_{hardwoods+streams}$) explained more of the variation in use of sites by bats than the model comparing the refuges (Ψ_{refuge}).

As expected, the group with frequency ≤29 kHz selected open habitats as evident in the model selection results. This group of bats was predominantly associated with aquatic resources and open fields (Ψ_{field}, Ψ_{river}, $\Psi_{streams}$, Ψ_{YMLP}). These species are morphologically more adapted for open habitats with minimal clutter (Ford et al. 2006). Their use of forested habitats may be indicative of roosting areas (Menzel et al. 2005b, Vonhof and Betts 2010).

Use of habitats also varied among the individual species I analyzed. *Eptesicus fuscus* is common throughout much of North America and is associated with hardwood forest habitats (Kurta et al. 1989). I found that *E. fuscus* use was predicted best by forest structure components basal area and canopy cover, and that it was less likely to use sites as mid-story and canopy cover increased. This is in agreement with the findings of Loeb and O'Keefe (2006), who conducted a similar acoustical study in Oconee County, South Carolina, and found *E. fuscus* to be present in open vegetation areas. Similarly, in the coastal range of Oregon, a habitat use study by Ober and Hayes (2008) indicated that *E. fuscus* preferred open habitats and that activity

increased with a decrease in canopy cover. Additionally, Ford et al. (2006) reported that *E. fuscus* associated more with open habitats compared to forested areas. In another acoustical study, Hein et al. (2009a) found that *E. fuscus* preferred edge and road habitats. However, that study focused solely on use of corridors, whereas my research included all habitats present on the study areas.

Due to its relatively larger size, I expected *T. brasiliensis* to use open habitats, but in my analysis it used hardwood forests with streams ($\Psi_{stream+hardwood}$) more frequently than other sites, including pine stands with streams and the river. This is counter to the findings of Vindigni et al. (2009) who used acoustical detectors to examine natural and modified sources of water in a managed-pine habitat in North Carolina and discovered that *T. brasiliensis* was indifferent to the type of aquatic resource. This may reflect a preference for smaller water bodies over large open water areas like the river. Additionally, my study included a broader range of habitat types and may reflect a preference for hardwoods over pines, which was not considered in Vindigni et al.

The frequency 30-39 kHz group selected open habitats in addition to pine and hardwood forests (Ψ_{MLP}, Ψ_{pine}, $\Psi_{stream+hardwood}$, $\Psi_{river+hardwood}$). This group included three species: *N. humeralis, L. borealis*, and *L. seminolus*. Because their calls are similar, I combined *L. borealis* and *L. seminolus* in my analysis, despite known differences in habitats use (Perry et al. 2008). In my study, this species group was found using hardwoods and use increased with decreasing canopy cover ($\Psi_{forest+can-cover}$). Although both species are dependent on forested habitats for roosting, a radiotelemetry study in the Ouachita Mountains in Garland and Perry Counties, Arkansas, found L. seminolus prefers areas near aquatic resources and L. *borealis* prefers sites near roads (Perry et al. 2008). In a predominantly loblolly pine plantation, Hein et al. (2008) determined that *L. seminolus* used tall live pines as day roosts. However, in the Appalachian

Mountains of North Carolina, *L. borealis* commonly roosted in upland hardwood forests (O'Keefe et al. 2009). Given the previous species-specific studies, my analysis would have been more useful if species were not combined.

I found that bats in the frequency ≥40 kHz group more commonly used open areas ($\Psi_{\text{field+ Young MLP}}$, $\Psi_{\text{forest+can-cover}}$). In addition, they avoided cluttered forest, which I thought would have no effect on their habitat use. My hypothesis for ≥40 kHz frequency group was that they would use cluttered environments such as forests and microhabitats would have minimal affect. Among the species in this group *M. septentrionalis* and *M. sodalis* are typically associated with cluttered habitats; other species such as *P. subflavus* are associated with more open riparian areas (Ford et al. 2005). Rogers et al. (2006) acoustical study in Utah classified species into groups and revealed that species with higher-frequency calls preferred riparian forest and edges over other habitats.

In the ≥40 kHz frequency group, I was able to isolate and evaluate use by *P. subflavus*. The best indicator for this species was type of forests, in combination with basal area and canopy cover ($\Psi_{\text{forest+BA}}$, $\Psi_{\text{can-cover}}$, $\Psi_{\text{forest+can-cover}}$). While an increase in basal area decreased occupancy, canopy cover only had a moderate effect on occupancy. Yates and Muzika (2006) reported similar results for the Ozark Mountains in Missouri. In other studies, *P. subflavus* was associated with open sources of water, although more secluded aquatic areas were available (Vindigni et al. 2009). Hein et al. (2009a) reported that *P. subflavus* occupancy was better determined by structures of forests as indicators. They also reported that the species favored edges and roads, which was not supported by my analysis. In the upper coastal plain of South Carolina, *P. subflavus* was predominantly in open compared to forested areas (Ford et al. 2006).

M. spp may represent up to five species, two of which are endangered. The best predictor of occupancy for this group in a habitat was forested roads (Ψ_{roads}). In addition, this group was found more in forested habitats, especially hardwoods and mixed forests ($\Psi_{forest+BA}$, $\Psi_{forest+snags}$, $\Psi_{mixed+snag}$). Further, snags and basal area were the two favored components of microhabitat for the *M*. spp. This is consistent with *M. septentrionalis* dependence on forested habitats (Henderson et al. 2008), and *M. lucifugus* use of edge habitat in a forested landscape in South Carolina (Hein et al. 2009a). In contrast, Ford et al. (2005) noted that *M. lucifugus* and *M. sodalis* selected riparian habitats. They also reported that *M. sodalis* and *M. septentrionalis* were associated with cluttered forests.

Based on previous studies (Menzel et al. 2005a), I hypothesized that probability of use of habitats by bats, regardless of size, would be greater in areas in proximity to aquatic resources (Perry et al. 2008). Seidman and Zabel (2001) evaluated acoustical activity of bats along intermittent streams in northern California. This habitat is similar to some areas at Mountain Longleaf NWR. Their study revealed that activity was greatest along mid-sized to large steams. Low levels of activity along small streams mimicked level of activity in upland locations. Another acoustical study conducted in a managed stand of pines in North Carolina determined that providing open sources of water was an important component of foraging habitat (Vindigni et al. 2009). The physical composition may help in determining the likelihood of a species presence, but abundance of prey and proximity to roosts sites also has a role (Ford et al. 2005, Virdigni et al. 2009). Ober and Hayes (2008) evaluated activity in Oregon detected species-specific use of habitat relative to shrubs and trees surrounding the water. I determined that all three frequency groups, especially the 30-39 and ≥40 kHz frequency bats, preferred riparian

areas. In addition, one-half all observations were recorded at two points associated with the Cahaba River.

I also hypothesized that species preferred diverse habitats more so than mono-cultural stands. In my analysis, no species selected mono-cultural habitats over other forest types. This is important given the large proportion of forests in the southeast that are managed as monocultures. Both, frequency ≤29 and 30-39 kHz groups of bats use the even-aged, single-species stands that should have made maneuvering difficult for these species, which are not adapted for cluttered environments (Adams et al. 2009). However, given the approximate 12m height of the stands associated with these plots, these particular species of bats may have been detected while flying above the canopy (Menzel et al. 2005b, Yates and Mazuka 2006). In the two refuges, even if the restoration actions of returning the areas to habitat dominated by mountain longleaf pines take time to materialize, the areas will be used.

In other similar habitat studies, researchers have examined presence of bats in plantations of pine trees (Hein et al. 2009b, Miles et al. 2006, Miller 2003, Morris et al. 2010). Morris et al. (2010) focused on foraging activities in a managed pine forest in North Carolina. They found six species and *Myotis*, all of which I detected. Smaller species and *L. borealis* were associated with unmanaged stands about one-half of the time, the other one-half was divided among open, pre-thinned, and thinned stands depending on the species. Miller (2003) used mist nets to evaluate diversity of species in a managed pine forest in Mississippi. The site was 75% plantation and the remainder consisted of a mature-riparian hardwood forest. His study sites were distributed evenly among habitats, and he also detected six species during a 3-year period, predominantly *L. borealis*, *L. seminolus*, *N. humeralis*, and *P. subflavus*. Miles et al. (2006) found *N. humeralis* selected forked topped loblolly pines in managed forests. Hein et al. (2009b) found *N. humeralis*

roosting in tree cavities in mature stands of pine, hardwood, and mixed. Both studies

recommended incorporating mature stands into heavily managed stands to allow for greater

diversity. Nonetheless, as suggested by some studies, species of bats are utilizing mono-culture

stands (Hein et al. 2009b, Miles et al. 2006, Miller 2003, Morris et al. 2010, Vindigni et al.

2009).

Another of my hypotheses evaluated the presence of bats in response to management

activities related to maintaining and restoring stands of mountain longleaf pines. Both refuges

have active restoration and management of longleaf stand involving control of hardwoods and

prescribed fires. Control of hardwoods opens up the canopy and creates snags. The

management plan calls for burning about 800 ha per year on a 3-5 year rotation. The young

stands of mountain longleaf pines are in an early successional stage, with trees <3 m tall and

spaced 5 m apart. All three bat frequency groups ($\leq$29, 30-39, and $\geq$40 kHz) responded

favorably to the YMLPs in restoration sites, which essentially mimicked an open uncluttered

habitat.

Mature forests consisting of stands of mountain longleaf pines created open canopies.

Only the frequency 30-39 kHz group of bats had high rates of occupancy in mature stands of

mountain longleaf pines. Given the open nature of the habitat, I expected both the $\leq$29 and 30-

39 kHz frequency groups would be present, but not necessarily the $\geq$40 kHz frequency group.

However, no species or group, with the exception of the 30-39 kHz frequency group indicated

any preference for that habitat.

In my study, the use of prescribed fire did not seem to affect any of the groups or

individual species considerably. However, some previous studies have evaluated a more direct

relationship between prescribed fires and bat activity. The consensus was the long-term positive

impacts were worth the short-term disturbance (Johnson et al. 2009, Lacki et al. 2009, Loeb and Waldrop 2008). For example, a study conducted in a mixed forest in Kentucky evaluated the possible disturbance that prescribed burns may have on activity of *M. septentrionalis* (Lacki et al. 2009). They examined foraging behavior and selection of roost sites. They discovered a greater incidence of roost sites in burned areas compared to unburned areas, including the selection of trees with cavities and bark. Their study also revealed an increase in activity of insects in post-burn areas. They concluded that *M. septentrionalis* was tolerant of prescribed fire under some conditions. In another study using radiotelemetry, also involving *M. septentrionalis*, in a hardwood forest in the Appalachian Mountains in West Virginia, maternity colonies were monitored to determine their response to prescribed burns (Johnson et al. 2009). Although colonies selected roost trees based on different attributes, there was no apparent difference in occupancy between burned plots and controls. The species appeared to take advantage of the newly created snags and abundance of prey after burning. In addition, a study set in a pine stand in South Carolina evaluated the effects of thinning and prescribed fires on bat diversity (Loeb and Waldrop 2008). They conducted experiments on various management applications. They found that *E. fuscus* and *L. borealis* responded favorably to thinned stands compared to the control and burn stands. Management applications did not affected *P. subflavus*. They concluded that removing clutter from an area increases bat activity in that habitat.

IMPLICATIONS FOR CONSERVATION

The habitat characteristics that showed the most influence on bat use were related to forest structure. The presence of snags was a good indicator for some species, showing a positive relationship between certain species and snag density. An increase in basal area was either a positive or a negative indicator of presence of species of bats. In addition, canopy cover was another forest structure component that consistently appeared in the best models for bat occupancy. Most species' occupancy decreased with an increase in canopy cover, just at different scales. Thus, managers interested in providing bat habitat should consider retaining snags, providing stands with variable basal area, and relatively open canopies.

Based on my results, the even-aged, single-species stands had little influence on occupancy of species. The frequency groups did show some preference among the broad results, but the individual species showed none. Species or individuals that preferred these habitats my not have been identifiable in the recordings I captured, or there may have been too much heterogeneity with the groups I analyzed to estimate relationships precisely. Had I specifically targeted that question, the results may have been more dependable.

In addition to considering individual species, my analysis incorporated grouping echolocation calls into three major frequency groups. This analysis was not as productive as I had hoped because results for two of the three groups were very broad. The ≤29 and 30-39 kHz frequency groups were so general in their model selections that it made inferences difficult.

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However, the broad model selection may have resulted from the grouped species different habitat requirements. Conversely, there was not strong support for a number of models, the ≥40 kHz group had similar covariates within the models. Because there were so many species within frequency groups, I question whether my results would have been more precise if I had monitored additional sites. However, I found clear habitat preferences within individual species.

Management actions, such as prescribed burns and control of hardwoods, at Cahaba River NWR and Mountain Longleaf NWR directly influence habitats. Actions taken to restore mountain longleaf pines did not appear to affect bats. There is a large-scale effort to restore longleaf pines across the southeast. As a result, open-canopy stands are replacing dense-forest stands. In many of these stands hardwoods are reduced or eliminated. Because some species of bats prefer hardwoods, my results suggest that the practice of controlling hardwoods may negatively affect their use of those sites. Where appropriate, stands of hardwoods should be maintained as roosting and foraging habitat. Allowing certain stands of hardwoods to remain creates a mosaic of habitats increasing species richness; especially in areas where hardwoods are a natural component of the landscape.

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Appendix A. Species of bats that potentially occur in central Alabama with the Alabama Comprehensive Wildlife Conservation Strategy greatest conservation need ranking (Alabama Department of Conservation and Natural Resources 2005).

Taxon	Common name	kHz[1]	Priority rank in Alabama[2]	Federal rank[3]
Family Molossidae				
Tadarida brasiliensis	Brazilian free-tailed bat	20	P2	
Family Vespertilionidae				
Eptesicus fuscus	Big brown bat	20		
Lasionycteris noctivagans	Silver-haired bat	20		
Lasiurus borealis	Eastern red bat	30		
Lasiurus cinereus	Hoary bat	20		
Lasiurus seminolus	Seminole bat	30		
Myotis austroriparius	Southeastern myotis	40	P2	
Myotis grisescens	Gray myotis	40	P1	E
Myotis lucifugus	Little brown myotis	40	P2	
Myotis septentrionalis	Northern long-eared myotis	40	P2	
Myotis sodalis	Indiana myotis	40	P1	E
Nycticeius humeralis	Evening bat	30		
Perimyotis subflavus	Tri-colored bat	40	P2	
Corynorhinus rafinesquii	Rafinesque's big-eared bat	40	P1	

[1]Frequency group based on echolocation calls

[2]P1 - Highest conservation concern, P2 - High conservation concern

[3]E - Federally listed as endangered

Appendix B. Summary of vegetation survey forest structure data from Cahaba River National Wildlife Refuge, Bibb County, and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama, 2009-2010. The mean is displayed for the forest structure covariates.

	Forest Structure				
Refuge[1]	Snag[2]	Basal Area[3]	Average Canopy Height[4]	Percent Canopy Cover[5]	Percent Mid-story Cover[6]
CR01	0.04	0.05	0.43	0.33	0.45
CR02	0.40	0.07	0.43	0.31	0.55
CR03	0.32	0.08	0.60	0.37	0.88
CR05	0.04	<0.01	0.33	0.39	0.12
CR07	0.12	0.09	0.40	0.51	0.65
CR08	0.12	0.05	0.45	0.14	0.41
CR09	0.08	<0.01	0.54	0.33	0.27
CR10	0.24	0.10	0.57	0.78	0.57
CR11	0.28	0.13	0.57	0.61	0.73
CR13	0.04	0.04	0.63	0.86	0.47
CR14	0.28	0.23	0.59	0.35	0.55
CR15	0.08	0.06	0.53	0.51	0.69
ML01	0.40	0.08	0.51	0.94	0.37
ML02	0.12	0.09	0.48	0.57	0.80
ML04	0.20	0.11	0.48	0.33	0.10
ML05	0.40	0.20	0.45	0.86	0.41
ML06	0	<0.01	0.29	0.02	0.37
ML07	0.12	0.14	0.45	0.65	0.24
ML10	0.12	0.13	0.58	0.16	0.73
ML11	0.36	0.14	0.58	0.96	0.51
ML12	0.08	0.18	0.38	0.90	0.57
ML13	0.04	0.30	0.65	1.00	0.73
ML14	0.16	0.10	0.49	0.96	0.39
ML15	0.20	0.29	0.62	0.98	0.61
ML16	0.32	0.20	0.55	0.94	0.55
ML17	0.28	0.24	0.54	0.78	0.43
ML18	0.12	0.15	0.57	0.80	0.53
ML19	0.04	0.11	0.40	0.20	0.80
ML20	0.32	0.12	0.43	0.86	0.55
ML22	0.04	<0.01	0.38	0.33	0.39
ML23	0.08	0.21	0.56	0.90	0.78
ML24	0.12	0.20	0.43	0.98	0.63
ML25	0.04	0.06	0.43	0.71	0.57
ML26	0.40	0.20	0.52	0.96	0.49
ML27	0.32	0.03	0.38	0.76	0.49

Appendix B. Summary of vegetation survey forest structure data from Cahaba River National Wildlife Refuge, Bibb County, and Mountain Longleaf National Wildlife Refuge, Calhoun County, Alabama, 2009-2010. The mean is displayed for the forest structure covariates.

Refuge[1]	Forest Structure Snag[2]	Basal Area[3]	Average Canopy Height[4]	Percent Canopy Cover[5]	Percent Mid-story Cover[6]
ML28	0.32	0.10	0.58	0.55	0.80
ML29	0.20	0.14	0.60	0.90	0.59
ML30	0.40	0.09	0.57	0.20	0.65

[1]Cahaba River National Wildlife Refuge and Mountain Longleaf National Wildlife Refuge
[2]Density of (snags/ha)/1000
[3]Basal Area (BA/ha)/100
[4]Average canopy height (n/100)
[5]Percent canopy cover (cover data/49)/100
[6]Percent mid-story cover (mid-story data/49)/100