8-8-2023

The response of bats and their insect prey to different coastal upland habitat management techniques

Amanda Nicole Sartain
Mississippi State University, ans889@msstate.edu

The response of bats and their insect prey to different coastal upland habitat management techniques

By

Amanda Nicole Sartain

Approved by:

Eric Sparks (Major Professor)
Jonathan Pitchford
Scott A. Rush
Kevin M. Hunt (Graduate Coordinator)
L. Wes Burger (Dean, College of Forest Resources)

A Thesis
Submitted to the Faculty of
Mississippi State University
in Partial Fulfillment of the Requirements
for the Degree of Master of Science
in Wildlife, Fisheries and Aquaculture
in the Department of Wildlife, Fisheries and Aquaculture

Mississippi State, Mississippi

August 2023

Name: Amanda Nicole Sartain

Date of Degree: August 8, 2023

Institution: Mississippi State University

Major Field: Wildlife, Fisheries and Aquaculture

Major Professors: Eric Sparks

Title of Study: The response of bats and their insect prey to different coastal upland habitat management techniques

Pages in Study: 57

Candidate for Degree of Master of Science

Declining bat populations necessitates a need to understand how different land management techniques influence bat activity. This study assessed the influences of different coastal upland habitat management techniques, such as mulching, prescribed fire, and select cut, on forest bat activity within the Grand Bay National Wildlife Refuge and National Estuarine Research Reserve. Acoustic recorders were used to monitor bat activity and insect and vegetation surveys were used to assess influences on bat activity across different land management techniques. Results demonstrate that overall bat activity was similar across different land management techniques, however larger species adapted for open-space flying were shown to be less active within dense forest such as the select cut technique areas. Findings from this study suggest that various land management techniques can influence bat activity differently.

ACKNOWLEDGMENTS

I would like to give a full-hearted, special thanks to my advisor, Dr. Eric Sparks. This project would not have been possible without his trust and willingness to support me during this adventure. Thank you to Dr. Jonathan Pitchford and Dr. Scott Rush for participating on my committee and providing their expertise along this project.

Thank you to the folks at the Grand Bay National Estuarine Research Reserve who provided assistance and knowledge throughout this project. Special thanks to Kim Cressman for her statistical analysis guidance. Thank you to everyone in the Coastal Conservation and Restoration lab who helped with fieldwork over the course of this project. Special thanks to Shelby Harrier for assisting with the ridiculous number of hours spent identifying and measuring insects. Special thanks to Kristie Gill for her contagious passion for wildlife conservation and assisting with fieldwork.

Finally, I would like to thank my fiancé, Kenneth Rigsby, who provided snacks and encouragement when I needed it most.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

THE RESPONSE OF BATS AND THEIR INSECT PREY TO DIFFERENT COASTAL UPLAND HABITAT MANAGEMENT TECHNIQUES

Introduction

Bats are considered one of the most misunderstood and undervalued animals across the world despite the variety of ecological services they provide such as being predators of night flying insects and indicators of general habitat quality (Ghanem & Voigt, 2012; Fenton 2003). Bats are essential components of forested and agricultural ecosystems throughout the southeast by aiding in plant reproduction by decreasing insect herbivory (Garin et al., 2019). By feeding on flying insects, bats contribute to pest insect suppression, benefiting the agricultural industry, maintaining ecosystem stability, and human health by eating disease vectoring insects such as mosquitoes (Puig-Montserrat et al., 2020). Unfortunately, bats are facing population declines across North America from a variety of threats (Frick et al., 2019). The biggest threats bats face are habitat loss (O'Shea et al., 2016; Frick et al., 2019; Millon et al., 2018), negative human perception (Fagan et al., 2018; Friedenberg & Frick, 2021), wind farm turbines (Friedenberg & Frick, 2021), and white nose syndrome (WNS) (Cheng et al., 2021).

Of the 47 different species of bats found throughout North America, 11 bat species have been documented on the Mississippi Coast including the big brown bat (*Eptesicus fuscus*), little brown bat *(Myotis lucifugus*), tri-colored bat (*Perimyotis subflavus*), evening bat (*Nycticeius humeralis*), Rafinesque big-eared bat (*Corynorhinus rafinesquii*), eastern red bat (*Lasiurus* *borealis*), northern yellow bat (*Lasiurus intermedius*), Seminole bat (*Lasiurus seminolus*), hoary bat (*Lasiurus cinereus*), silver-haired bat (*Lasionycteris noctivagans*), and Mexican free-tailed bat (*Tadarida brasiliensis*) (MSBWG Conservation Strategy, 2020). Due to the 90-100% decrease in populations impacted by white nose syndrome, the tricolored bat (*P. subflavus*) has recently been proposed by US Fish and Wildlife Service to be listed under the Endangered Species Act (Cheng et al., 2021; Perea et al., 2022; USFWS 2022). The big brown bat (*E. fuscus*), an abundant, wide-ranging species commonly found on the coast and presumed to be resistant to WNS (Frank et al. 2014; Lemieux- Labonté et al. 2020), could be more affected by WNS than previously thought (Cheng et al., 2021). While wind energy operations are not currently established in Mississippi, migrating tree-dwelling bats found on the coast, such as eastern red bats (*L. borealis*) and hoary bats (*L. cinereus*), have been severely impacted by the increase in wind farm development in the eastern region (Foo et al., 2017; Thompson et al., 2017). Wind farm activity results in tens of thousands of bat mortalities annually and is projected to decrease the hoary bat (*L. cinereus*) population, an insectivorous migratory bat species found widely throughout the species range, by 50% by the year 2028 (Friedenberg & Frick, 2021). The increased severity of current threats and estimated declines in bat populations caused by the impacts of WNS and wind turbine farms necessitates a need for understanding of bat presence and habitat relationships within unaffected areas such as Mississippi coastal forests.

Coastal Mississippi has a variety of ecosystems including forested uplands, pine savannas, maritime forests, freshwater and salt marsh wetlands, and tidal creeks and bayous. Mississippi coastal forests provide important features for bats including plentiful insect prey on which these bats forage, availability of water, and roost sites. The forests typically have a mix of pine (*Pinus* spp.) and hardwood trees where bats are known to roost and forage (Elmore et al., 2005; Perry & Thill, 2007). The dominant tree species among coastal habitats includes longleaf pine (*Pinus palustris*), Southern live oak (*Quercus virginiana*), bald cypress (*Taxodium distichum*), and black tupelo (*Nyssa sylvatica*) (Peterson et al., 2007) – all of which are known roosting sites for bats (Padgett & Rose, 1991; Menzel et al., 1999; Gooding & Langford, 2004; Lance et al., 2001). Each species of bat found within coastal Mississippi depends on forests for most, if not all, of their lifespan (Whitaker 2004; Miller 2003; Brigham 2007) and in return are a vital component of forested ecosystems (Lacki et al., 2007). Within forested habitats, bats serve as the primary predator of nocturnal flying insects (Fenton 2003). Bats such as *N. humeralis, E. fuscus*, and *L. borealis* forage on commonly occurring insects in the taxonomic orders Lepidoptera (moths), Coleoptera (beetles), Diptera (flies), and Trichoptera (caddisflies) (Whitaker 2004). In temperate areas with mild winters, bat activity has been observed in the winter months while prey is still available (Bernard & McCracken, 2017; Johnson et al., 2016). There is little known about winter bat activity as far south as the Mississippi coast where winters are mild; most studies of bats conducted in Mississippi have focused on summer bat activity (Elmore et al., 2004, 2005; Miller 2003; Trousdale & Beckett, 2005). Mild winter nights in the southern region allow bats to use short stretches of torpor and become active (Grider et al., 2016; Johnson et al., 2012; Sandel et al., 2001). Bats that migrate through the area could possibly use these forest areas for roosting and foraging during migration stop-overs (McGuire et al., 2012; Taylor et al., 2011). There is a large gap in knowledge pertaining to bat species occurrences and activity within coastal Mississippi pine forest ecosystems (Miller et al., 2003). Information about which bat species use coastal Mississippi forests throughout the year could be vital for species recovery (Cornelison et al., 2014). Identifying bat habitats, such as the coastal forests in Mississippi, that are not impacted by current bat population threats (i.e., wind turbines and WNS) could prioritize conservation areas and promote a decrease in threat susceptibility (Grider et al., 2016). Throughout the southeast, many forested areas are managed in efforts to improve overall forest habitat quality and increase biodiversity. Many of these coastal upland areas are the target of habitat management to prevent overgrowth of native and invasive species that degrade ecosystems, but little is known about the bat communities present in these areas (Miller 2003) or how they are affected by land management practices.

Some of the most common large-scale land management techniques in coastal Mississippi include prescribed fire and mechanical removal of vegetation. Prescribed fire is one of the longest used land management practices originating from Native Americans and adopted by European settlers (Johnson & Hale 2002). Prescribed fire has been used to remove native and invasive plant species and increase overall habitat quality (Franklin et al., 2018). Mechanical removal of vegetation through forestry mulching and/or timber removal (e.g., select cutting) are alternative tools used to manage overgrown forests. Both methods are used to promote native tree health and decrease the amount of forest fuel without negatively affecting wildlife, soil structure, and vegetation (Stephens et al., 2012). These approaches are used primarily to decrease the density of midstory vegetation, which promotes growth of herbaceous plant communities by reducing competition and increasing light penetration to the forest floor. These forest changes can have direct and indirect impacts on bat activity (Guldin et al., 2003). Direct mortality can be caused by prescribed fire used to reduce mid-story density resulting in the decrease of bats that use the forest leaf litter as a roosting site, such as the eastern red bat (*L. borealis*) (Mager & Nelson 2001; Saugey et al., 1998). Availability of roost sites are directly affected by land management practices by altering, eliminating, or reducing these resources. The availability of dependable roost sites, such as tree cavities and foliage, plays a key role in bat conservation nationwide (Humphrey 1975). Bat species such as the hoary bat, (*L. cinereus*) use tree foliage for roosting, the Rafinesque's big-eared bat, (*C. rafinesquii*) use tree cavities for day roosts (Fleming et al., 2013), and maternity roosts of the evening bat (*N. humeralis*) are often found in hollow cavities and exfoliating bark of dead and live trees (Menzel et al., 1999; Miles et al., 2006).

Indirect impacts on bat activity can result from changes in forest conditions and resource availability within foraging sites. Forest structure can influence the activity of bats as several studies showing a decrease of forest density (i.e., basal area, canopy cover, physical obstacles) and structural complexity (i.e., clutter; Brigham et al., 1997) promotes increased bat activity (Kalcounis et al., 1999; Lacki et al., 2007; Austin et al., 2018; Bender et al., 2015). Where species of bats forage is influenced based on wing morphologies and echolocation characteristics (Dodd et al., 2012; Britzke et al., 2001; Ober & Hayes, 2008; Fenton & Bogdanowicz, 2002). Studies have revealed that a bat's ability to avoid different levels of physical obstructions in forested habitat is determined by wing shape and size (Aldridge & Rautenbach, 1987; Norberg & Rayner, 1987). Larger bodied bats with longer wings tend to prefer open-space areas, where smaller bodied bats with shorter wings are more maneuverable (Patriquin & Barclay, 2003). Habitat use by bats can be difficult to study, but advancement in acoustic recording technology has made it possible to measure bat activity, enabling researchers to compare activity differences between habitats (Vaughan et al., 1997). Bat species with similar call structure and frequencies are often placed into phonic groups (Bender et al., 2021; Buchalski et al., 2013; Ober & Hayes, 2008). These phonic groups represent groups of bat species that correspond with body morphology and predicted habitat use. Low phonic groups contain larger-bodied bats known to forage in open-space and fly above canopies (Menzel et al., 2005; Ford et al., 2006), while the high and mid phonic group consists of species adapted to flying in denser forest conditions and forest edges (Sleep & Brigham, 2003). Several studies have used these insights to investigate bat activity and habitat use within managed forests (Andersen et al., 2022; Carr et al., 2020; Elmore et al., 2005; Kunberger & Long, 2022; Tibbels & Kurta, 2003). Little is known about the effects of forest management on bat activity within coastal Mississippi. Perceived indirect effects of various management treatments on bat activity include changes in food availability following a burn or clearing event. Through altering the forest structure by thinning and burning, the abundance and diversity of prey insects affected (Loeb & Waldrop, 2008), thus changing foraging opportunities for insectivorous bats (Ketzler et al., 2017). Burford et al. (1999) found that the abundance and diversity of moth species can be influenced by management techniques affecting bat species such as the eastern red bat (*L. borealis*) who feed heavily on moths (Whitaker 2004). The presence of bats and the nocturnal flying insects they prey upon can be key indicators of the health of a diverse ecosystem.

To address some knowledge gaps on how several forms of forest management can affect bat species, an ongoing large-scale habitat management project occurring at the Grand Bay National Wildlife Refuge and National Estuarine Research Reserve in Moss Point, Mississippi was leveraged to assess the impact of different habitat management techniques on bat activity. This study was the first long-term bat activity monitoring taking place in coastal Mississippi. Results from this study can be used to inform coastal restoration, conservation projects, and land managers of the potential benefits and impacts of land management practices on forest bats and their insect prey. The specific hypotheses I am testing are:

1. Determine if the activity and diversity of bats is impacted by different coastal upland land habitat management techniques at the Grand Bay National Estuarine Research Reserve.

H_0: There will be no difference in activity and diversity of bats between the different land habitat management techniques at the Grand Bay National Estuarine Research Reserve.

H_1: There will be a difference in bat activity between the different land habitat management techniques at the Grand Bay National Estuarine Research Reserve.

2. Determine if the abundance and diversity of bat prey (insects) influences bat activity across different coastal upland land habitat management techniques at the Grand Bay National Estuarine Research Reserve.

   H_0: There will be no relationship between bat activity and insect abundance across the different land habitat management techniques at the Grand Bay National Estuarine Research Reserve.

   H_1: There will be a difference between bat activity and insect abundance across the different land habitat management techniques at the Grand Bay National Estuarine Research Reserve.

Methods

Study site and site selection

This study occurred within the Grand Bay National Wildlife Refuge (GNDNWR) in Moss Point, MS (Figure 1). The GNDNWR encompasses 4,123-ha of wet pine savanna and partially overlaps the Grand Bay National Estuarine Research Reserve (GNDNERR). Together these lands encompass 7,284-ha of upland forests, pine savannas, maritime forests, marshes, and bayous. Portions of property within the GNDNWR and GNDNERR boundaries are managed by either the Mississippi Department of Marine Resources (MDMR) or the U.S. Fish and Wildlife Service (USFWS). Specific sites monitored for this study consisted of portions of the GNDNWR managed with either prescribed fire, select cut, or mulching techniques (Figure 2a). The prescribed fire site consisted of 22.53-ha primarily dominated by longleaf pine and slash pine (Figure 2b). Prior to this study, this area was burned in 2008, 2012, 2014, 2018. The select cut site consisted of 31.17-ha of pine forest and hardwood mix (Figure 2c). The latest cutting at this site took place in 2019 where contractors used chainsaws to cut all slash pine <6 inches diameter breast height (dbh). In addition to select cut, this site has also been burned (2014 and 2018) and treated with herbicides targeting invasive Chinese tallow (*Triadica sebifera*), cogon grass (*Imperata cylindrica*), camphor tree (*Cinnamomum camphora*), and Japanese climbing fern (*Lygodium japonicum*). The mulched area consisted of 26.08-ha (Figure 2d) that was mulched using a Gyrotrac mulching machine and skid steer with a mulching head in 2020. This site has also been previously treated with herbicide for invasive Chinese tallow (*T. sebifera*), cogon grass (*I. cylindrica*), camphor tree (*C. camphora*), Japanese climbing fern (*L. japonicum*), and privet (*Ligustrum sinense*). Within each site, 3 plots were selected by overlaying 50m x 50m grids over each site in ArcGIS, assigning each grid a number, and using a random number generator to select plots. To reduce any potential edge effects associated with roads, riparian areas, train tracks, etc., no grids were selected at plots within 50m of the edge of each site.

Measurements

Within each of the 9 plots (3 per habitat management treatment; Figures 2b, 2c, 2d) bat, insect, and vegetation surveys were completed quarterly between March 2021 and February 2022.

Acoustic surveys

Over the duration of this study, acoustic recorders were deployed to quantify bat activity and diversity. For this study, bat activity is defined as the pulses recorded during each bat survey period. Bat surveys were completed using passive Song Meter Mini Bat ultrasonic recorders (Wildlife Acoustics, Song Meter Mini Bat, Firmware 2.9). One recorder was placed at each of the plots (n=9), secured to a tree at least two meters off the ground following the USFWS 2020 Range-Wide Indiana Bat Survey Guidelines. All recorder microphones faced forest openings and were oriented at a 45° angle toward canopy openings to maximize the likelihood of high-quality bat call recordings (Figure 3a; De La Cruz et al., 2020). Recording began 30 minutes prior to sunset and 30 minutes following sunrise. Recorders remained at the same location for the duration of this study and were frequently maintained (battery changes, water-proof checks, and microphone calibrations). Call recordings were retrieved from the recorder on memory cards and downloaded to a computer for analysis. Data collected for all survey nights were evaluated to find a window of time within each season where all recorders were simultaneously recording and rain was absent. There was no visual confirmation for bat identification (i.e., mist netting) due to the research constraints placed during the development of this project.

Insect surveys

Insect surveys were conducted seasonally by simultaneously deploying flight intercept traps and bucket light traps a minimum of 10 meters apart (Muirhead-Thomson 2012) near the acoustic recorder in each plot (Figure 3b and 3c). Two methods of insect trapping were used to prevent capture biases (Kunz 1988). Both the flight intercept traps and the bucket light traps were placed within the location of the recorders the morning of the same day to begin the sampling period. Insect sampling took place for a continuous four days and four nights to passively collect insects in spring (April 24–27, 2021), summer (August 24–27, 2021), fall (November 9–12, 2021), and winter (January 17–20, 2022) over the study duration.

Flight intercept traps

Flight intercept traps were used to passively collect flying insects (Tripplehorn & Johnson, 2005) with a modified version of the Composite Insect Trap design described in Russo et al. (2011) (Figure 3b). Traps consisted of vertical mesh barriers functioning as a malaise trap forcing the insects to fly upwards avoiding the mesh into a collection container, and a pan trap below the mesh to capture insects that fly downward (Figure 3b; Russo et al., 2011). The traps were constructed to be assembled and disassembled in the field. The top section of the trap was securely connected creating a tent-like shape for the collection funnel to hang (Figure 3b). The collection funnel was created using a disposable fly trap funnel (Starbar Trap 'N Toss Fly Trap; Tractor Supply) that consisted of an inverted funnel encompassed by a clear plastic dome. To retrieve the insects collected, a 5 cm by 7.6 cm door was cut into the upper side of the plastic dome and secured closed with tape. The funnel trap was filled to the pre-indicated "fill" line of the fly trap funnel with of soapy water solution (approximately 16 oz) and secured through the 17 cm mesh cutout to hang from the connected 36 cm PVC pipes with zip ties. (Figure 3b). The bottom section of the flight intercept trap was constructed using two pieces of rectangular mesh netting (Phifer BetterVue Insect Screen; Home Depot) measuring 142 cm height by 91 cm wide. These mesh pieces were sewn together, connecting in the middle to form an "X" shape with four corners. Next, 142 cm height by 15 cm wide canvas strips were folded over and sewn to the longitudinal ends of the mesh to create pockets to hold the four 152 cm by 1.3 cm PVC pieces. The 152 cm PVC pipes were then inserted through each of the canvas pockets allowing for the top section of the trap, previously described, to be attached via the four open elbows. The two sections of the flight intercept trap described above were transported to each sampling location where they were connected. To securely position the trap for surveying, a 24 cm by 2.5 cm metal stake was hammered into the ground where each of the four PVC pipes will stand. With the trap secured on to the stakes in the ground, a string was tied around each of the four vertical PVC pipes through a hole in the canvas pocket approximately 76 cm from the bottom of the pipe. The other end of the string was tied to a garden stake and pulled taut then hammered into the ground to stabilize the trap. Lastly, the 32 cm by 32 cm by 5.4 cm three-quart galvanized pan, spray painted yellow as described in Russo et al. (2011), was placed below the trap and filled with soapy water solution to catch any insects that flew down the vertical mesh (Figure 3b).

Bucket light traps

Bucket light traps, a common and successful method to capture night flying insects, were used to passively collect night flying insects using UV light (Figure 3c; Dodd et al., 2008, 2012; Jonason et al., 2014; Ketzler et al., 2017). The night traps used for this study were a modified version of the low-cost light traps described in White et al. (2016). Each trap consisted of a battery-powered string of UV lights contained within the center of three, clear plastic vanes placed on top of a bucket containing a funnel for collection (Figure 3c). The bucket light trap vanes were made using 28 cm by 36 cm clear acrylic sheets. Nine sheets were used to cut three 28 cm by 10 cm vanes for each trap. The three vanes for a trap were connected via a three-way connector piece created using a white PLA on a Qidi X Max 3D printer. At the center of the vanes was a 27 cm by 6 cm clear plastic cylinder made from clear acrylic sheeting. This cylinder is where the light source described next will be encased (Figure 3c). Flexible 12V LED blacklights were used as the light source for each bucket light trap. These lights come in a spool designed to be cut into smaller sections. For each trap, 30 cm strips of LED lights were cut and folded in half and connected with double sided tape creating a strip of lights with nine on the front and nine on the back. These light strips had a viewing angle of 120-degrees and light wavelength of 395–405nm (White et al., 2016). The lights were powered by four 9-volt batteries that were snapped together and connected to the lights using snap connectors. The wire ends of the snap connectors were soldered to the light strips and covered with heat-shrink tubing. The light strips were placed in the clear cylinder between the vanes through a hole in the center of the three-way connector. Prior to placing the traps in the field, each light strip and its corresponding power source (batteries) were checked to ensure proper and secure connections. New batteries were used each time the bucket light traps were deployed to ensure maximum power and longevity for surveying (96 hours). The completed vane assembly was attached to the collection bucket portion of the trap through slits correlating with each vane into the lip of the bucket. A lid was placed over the top of the vane assembly and securely attached to the collection bucket using bungee cords. The collection bucket portion of the bucket light trap was constructed using a funnel and bucket. Black poster board was used to make the funnels consisting of a 11 cm radius at the top and 5 cm at the spout opening at the bottom. In addition to the paper funnel, a clear plastic funnel of the same dimensions was made from clear plastic sheets and fitted into the top of the paper funnel to promote a more slippery funnel surface. A 23 cm by 23 cm (5 quarts) bucket was used as the collection bucket for the bucket light traps. The funnel was set in the bucket and connected to the bucket via nuts and bolts through two holes punched at opposite sides of the top of the bucket. A soapy water solution was used in the collection buckets to kill any insects collected. Using 1.3 cm PVC pipe, a stand was made to elevate each bucket trap off the ground. The top of the stand was made using four pieces of 1.3 cm PVC pipe and 1.3 cm three-way PVC elbows connected into a 23 cm by 23 cm square to allow the bucket to sit in. The four legs of the stand were made using two pieces of 1.3 cm PVC connected with a 45-degree elbow fitting. Each bucket light trap was set on a stand elevating the trap to approximately 1 meter off the ground at each sample location (Figure 3c).

At the conclusion of the sample period, collected samples were retrieved from both the flight intercept traps and bucket lights and the traps were taken out of the field. The trapped insects were collected from each of the collection containers; 1) hanging collection funnel and 2) pan (flight intercept traps), and 3) collection bucket (bucket light trap). Since the insects were trapped in a water solution, each container was emptied into a separate collection jar to be transported to the lab for processing. Once in the lab, insects were immediately separated from the water solution by gently pouring the sample through a 55 µm sieve. All easily identifiable and large insects (>20 mm) were pulled from the sieved sample to be pinned and placed into a temporary holding box for identification. The remaining insects in the sieve were picked out with forceps to be preserved in 70% ethanol while awaiting identification (Dodd, Chapman, et al., 2012). All insects were measured (mm) and identified down to order using identification keys (McGavin 2002; Leckie and Beadle, 2012). Relative abundance (RA) of insect orders was calculated for each order within each treatment by dividing the number of individuals of a taxonomic order (n_i) by the total number of individuals within the treatment (Σn_t) multiplied by 100 for percentage.

$$RA\% = \frac{n_i}{\Sigma n_t} * 100 \tag{1}$$

Habitat Characteristics

For each plot, canopy cover, canopy height, shrub layer height, vegetation species counts, basal area, and distance to water measurements were taken in early June 2021. Canopy cover was assessed using an ocular tube with a crosshair at the end to visually measure the percentage of sky obscured by tree canopy branches (Rodewald & Abrams 2002; James & Shugart, 1970). Measurements were taken within a 10-meter radius in each cardinal direction every 2 meters from the recorder as the center point (for a total of 20 points each site, n=180). Using a second person to ensure a straight vertical line of sight to the sky, the ocular tune was pointed to the sky and looked through. Presence or absence readings for canopy cover were recorded if the cross hairs were obscured by vegetation (James & Shugart, 1970). Percent canopy cover measurements were calculated using the number of presence readings (P) divided by the total number of observations (n) multiplied by 100. Measurements taken within each treatment site were averaged.

$$\%\ Canopy\ cover = \left(\frac{P}{n}\right) * 100 \qquad (2)$$

To determine tree density within each treatment site, basal area was measured using an BAF-10 angle gauge. Using the tree with the recorder as a center point, a 360-degrees sweep was preformed measuring the diameter breast height (DBH at 1.5 meters) of each tree that fell within the BAF-10 angle gauge (Bender et al., 2015). Each tree that fell within the gauge was also identified down to the lowest taxonomic level. Basal area measurements were taken at each recorder location (n=9) and averaged across the sites. To determine the estimated basal area (BA) per meter squared (m^2) per hectare (ha) of each treatment site, calculations were performed using the function from the R package ‘basifoR’ below.

$$BA\ m^2/ha = (pi * (dbh)^2) * 0.0004 \tag{3}$$

The vertical heights of the shrub layer were measured using a 2 m Robel pole at a random location around each recorder location in each treatment (James & Shugart, 1970). Measurements of the tallest vertical herbaceous or woody vegetation were taken at five points two meters apart in each cardinal direction from the center point. The Robel pole was taped off prior to the field day at 10 cm intervals (0.1 meter) with a 25 cm wire cylinder extending from the pole. This wire cylinder could move up and down the pole freely to adjust for each measurement. The tallest herbaceous or woody vegetation that fell within the wire cylinder's radius were measured to the closest 0.1-meter interval. If no herbaceous vegetation was present, only woody was measured and vice versa. Measurements of tallest heights were averaged to get plot shrub layer height. Vertical heights were then averaged across each treatment site. Vegetation species diversity was assessed at the same random locations as previously described for the vertical vegetation height measurements. Within the 10-meter radius, present vegetation species were visually assessed and counts were recorded (Tibbels & Kurta, 2003; Titchenell et al., 2011). At each recorder location, canopy heights (m) of the 3 tallest trees were estimated using a combination of RTK elevation points and drone imagery of each plot (Lim et al., 2015) and averaged for the mean canopy height surrounding each recorder location. Distance to water was measured to the closest meter from each plot to the nearest water source (stream, bayou, pond) using the measurement tool in ArcGis Pro. All vegetation measurements were taken once throughout the duration of this project since there was no active land management taking place.

Statistical analysis

Bat activity

Surveyed nights were targeted to a continuous timeframe within each season where the acoustic recorders were all simultaneously recording and rain was absent for the same amount of nights – leading to eight consecutive nights of recording each season for a total of 32 surveyed nights for the duration of this study. Recording from those 32 survey nights were processed using Kaleidoscope Pro software (Wildlife Acoustics Inc., Concord, MA, USA) using the automatic identification function that identifies bat species based on call characteristics (minimum and maximum frequencies, shape, pattern). Kaleidoscope Pro was run on its default settings with the North American species classifier with Mississippi species selected for the species reference library. Post processing with Kaleidoscope, call files were manually checked for identification accuracy. Recordings listed as “No ID” or “Noise” were omitted from statistical analysis. To increase confidence in bat species presence, all call files identified as species with a geographical range not known to be on the Mississippi coast (MSBWG Bat Conservation Strategy 2020) were omitted from analysis (i.e., little brown bat, *Myotis lucifugus*, and Indiana bat, *Myotis sodalis*). Species were grouped into common phonic groups (Bender et al., 2021; Buchalski et al., 2013; Ober & Hayes, 2008) due to similarities in recorded calls among species with similar call structures and frequency ranges. These phonic groups included species with call frequency ranges of high (40 kHz), mid (30 kHz), and low (20 kHz) (Betts, 1998; Britzke et al., 2011; Dodd, Lacki, et al., 2012; Yates & Muzika, 2006). Bat activity was defined as the number of pulses in a call file during the survey event (Dodd, Lacki, et al., 2012).

Statistical analysis of bat activity was performed in Program RStudio (V. 4.1.0; R Core Team). Total bat activity data were run through a Shapiro-Wilk normality test to assess normality followed by a natural log (ln) transformation to meet normality assumptions. The transformed data were used in further statistical analyses and all tests had statistical significance set at $\alpha < 0.05$. Season was included as a factor in analyses to account for temporal variation and each season was considered a surveying event. A two-way ANOVA was used to test for the effect of land management treatment (hereafter, referred to as treatment) and season on bat activity followed by a Tukey's multiple comparison test. A two-way ANOVA was used to test for the effect of phonic group and treatment on bat activity. When there was a statistically significant interaction between phonic group and treatment on bat activity, one-way ANVOAs were run for each treatment. A two-way ANOVA was used to test for the effect of phonic group and season on bat activity. When there was a statistically significant interaction between phonic group and season on bat activity, one-way ANVOAs were run for each season. To further look at the differences between the effect of treatment and season on phonic group activity, each phonic group (high, mid, low) activity was analyzed individually. Prior to running statistical analyses, each set of phonic group data were tested for normality. For normally distributed data, a two-way ANOVA was used to test for differences. If there was a significant interaction between treatment and season on phonic group activity, a one-way ANOVA was run for each season and if the interactions were significant, a Tukey's multiple comparison test was used to identify individual differences between treatments and season. When data could not be normalized through transformations, the non-parametric Kruskal-Wallis test was used, followed by the Dunn's Multiple Comparison test to identify individual pairwise differences between treatments and season on phonic group activity.

Insect abundance on bat activity

All insects were measured to the nearest millimeter, identified to order, and counts (n) were averaged across treatments for the sum of individuals to be used to estimate insect relative abundance (Akasaka et al., 2009; Müller et al., 2012). Non-winged organisms (i.e., spiders, earwigs, caterpillars) were omitted from statistical analysis. To be as representative as possible of potential bat prey in this study, insects were placed into size classes to test for a relationship between bat activity to insect size. Foraging limitations from low echolocation detectability of small insects, ecomorphology, and energetic demands can limit foraging opportunities (Norberg & Rayner, 1987; Barclay & Brigham, 1991; Waters et al., 1995). To meet assumptions of normality, insect count data were transformed by natural log (ln). Since bat activity has shown no preference to insect size between 3 mm to 30 mm, any insect smaller than 3 mm and larger than 30 mm were omitted from insect abundance statistical analysis. Insect abundance was used as a predictor variable for bat activity during statistical analysis. Linear regressions were used to examine the relationship between insect abundance and bat activity across the land management treatments. Linear regression was also used to examine the relationship between insect abundance and phonic group activity across the land management treatments.

Habitat characteristics on bat activity

Vegetation measurements were taken within each treatment and used as predictor variables in linear regression to examine the relationship between habitat characteristic across the treatments to bat activity. Vegetation measurements were averaged across the treatments and used as predictor variables separately in linear regressions to examine which habitat characteristics influenced bat activity. The same models were used to analyze relationships between the activity of each phonic group.

Results

Recording summary and species diversity

This study ensued in a total of 36 surveyed nights that included spring (March 6-14, 2021), summer (August 19-27, 2021), fall (November 8-16, 2021), and winter (January 4-12, 2022). There was a total of 6,446 identified bat call files (123,558 pulses) and 6680 unidentified files recorded over the duration of the study. Of those bat call files identified, 513 were big brown bat (*Eptesicus fuscus*, EPTFUS), 290 were eastern red bat (*Lasiurus borealis*, LASBOR), 1,456 were hoary bat (*Lasiurus cinereus*, LASCIN), 126 were northern yellow bat (*Lasiurus intermedius*, LASINT), 124 were silver-haired bat (*Lasionycteris noctivagans*, LASNOC), 795 were Seminole bat (*Lasiurus seminolus*, LASSEM), 406 were evening bat (*Nycticeius humeralis*, NYCUM), 415 were tri-colored bat (*Perimyotis subflavus*, PERSUB), and 2,321 were Mexican free-tailed bat (*Tadarida brasiliensis*, TADBRA) (Table 1). Any call files identified as species with a geographical range not known to be in this project area (MSBWG Bat Conservation Strategy 2020) were omitted from analysis (i.e., little brown bat (*M. lucifugus* (n=9) and Indiana bat (*M. sodalis* (n=1)).

Phonic groups

Acoustically identified bat species were placed into phonic groups based on similar call characteristics and frequency ranges. Phonic groups comprised of the high phonic group included the tri-colored bat (*P. subflavus*), eastern red bat (*L. borealis*), Seminole bat (*L. seminolus*), and the evening bat (*N. humeralis*); mid phonic group included the northern yellow bat (*L. intermedius*), big brown bat (*E. fuscus*), and the silver-haired bat (*L. noctivagans*); and low phonic group included the hoary bat (*L. cinereus*) and Mexican free-tailed bat (*T. brasiliensis*) (Table 1). Bat activity for each frequency group was averaged across plots for each habitat management treatment. Of the recorded call files, 235 (4,989 pulses) were from the high phonic group, 142 (2,869 pulses) were from the mid phonic group, and 193 (2,057 pulses) were from the low phonic group (Table 2).

Bat activity across treatments

Total bat activity data were run through a Shapiro-Wilk normality test to assess normality followed by a log transformation to meet normality assumptions ($p = 0.08$). These transformed data were used for the statistical analysis on total bat activity and each season was considered a surveying event. A two-way ANOVA revealed that both treatment ($p = 0.012$) and season ($p < 0.001$) had a significant impact on total bat activity but there wasn't a significant interaction between treatment and season ($p = 0.885$) (Figure 4). Pairwise post hoc Tukey tests showed that bat activity was significantly different between select cut and prescribed fire treatments ($p = 0.007$) and that was driven primarily by the lower activity in the select cut treatment in the spring and winter seasons. Pairwise comparisons between spring and fall showed significant differences ($p = 0.003$) with spring having more bat activity. Other pairwise comparisons between summer and fall ($p = 0.007$), and winter and summer ($p = 0.015$) showed significant differences with summer having more activity compared to each, and winter and spring ($p = 0.006$) with spring having more activity (Table 3).

Phonic group activity

A two-way ANOVA (phonic group ~ treatment) showed that bat activity varied significantly by both phonic group ($p < 0.001$) and treatment ($p = 0.008$). Additionally, there was a significant interaction between the phonic group and treatment on bat activity ($p = 0.047$). Due to this interaction, one-way ANOVAs were run to assess differences among phonic group activity by treatment. Results of these one-way ANOVAs showed that phonic group activity was significantly different for each treatment ($p < 0.001$). Pairwise post hoc Tukey tests showed that phonic group activity was significantly different between select cut and prescribed fire treatments ($p = 0.005$) and that was driven primarily by the lower activity of the low phonic group in the select cut treatment (Figure 5).

To account for seasonal variability on phonic group activity, another two-way ANOVA (phonic group x season) showed that bat activity varied significantly by both phonic group ($p < 0.001$) and season ($p < 0.001$). Additionally, there was a significant interaction between the effect phonic group and season on bat activity ($p = 0.011$). Due to this significant interaction, one-way ANOVAs were conducted to look at the effect of season on phonic group activity for each season individually. Results of the one-way ANOVAs showed that bat activity was significantly different among phonic groups in all seasons except for fall ($F = 1.718$, $df = 2$, $p = 0.188$) (Figure 6). Given the strong differences between phonic groups, each phonic group (high, mid, and low) was analyzed individually as described below.

High phonic group

Both raw and natural log (ln) transformed activity data for the high phonic group of bats were tested for normality and were found not to be normal (Shapiro-Wilk normality test, $p < 0.05$). Due to lack of normality, non-parametric Kruskal-Wallis tests were used for further analyses. Results of this test showed that high phonic group bat activity was not different among habitat management treatments ($p = 0.422$) but was for season ($p = 0.002$). The Dunn's Multiple Comparison post-hoc test showed that high phonic group bat activity was significantly lower in fall than spring ($p = 0.003$) and summer ($p = 0.033$) (Figure 7a). Given the differences in high phonic group bat activity among seasons, a Kruskal-Wallis test was run for each season to assess the differences among high phonic group bat activity in habitat management treatments, but no differences were found.

Mid phonic group

Similar to the high phonic group, neither raw nor natural log (ln) transformed bat activity data for the mid phonic group was found to be normally distributed (Shapiro-Wilk normality tests, $p < 0.001$). The non-parametric Kruskal-Wallis test showed that neither treatment ($p = 0.795$) nor season ($p = 0.080$) impacted mid phonic group bat activity (Figure 7b).

Low phonic group

Raw low phonic group bat activity data were not normal ($p < 0.001$), but natural log (ln) transformed data were ($p = 0.109$). A two-way ANOVA (treatment x season) showed that low phonic bat activity varied significantly by both treatment ($p < 0.001$) and season ($p < 0.032$). However, there was a significant interaction between the effect of treatment and season on low phonic group bat activity ($p = 0.004$). Due to this significant interaction, one-way ANOVAs were conducted for each season to assess habitat management treatment affects by season. Results of these one-way ANOVAs showed that there were significant differences among treatments in all seasons except for winter ($p = 0.224$). Post-hoc Tukey tests showed that the select cut treatment had significantly less low phonic group bat activity than the prescribed fire treatment in spring, ($p < 0.001$), summer ($p = 0.020$), and fall ($p < 0.001$). Pairwise comparisons between prescribed fire and mulch treatments only showed significant differences in fall ($p = 0.003$) with the prescribed fire treatment having more bat activity. The only other pairwise comparison was between the select cut and mulched treatments and the only season where they were significantly different was summer ($p = 0.004$) with mulched having more activity (Figure 7c).

Insect abundance & habitat characteristics on bat activity

Sampling events took place each season (n=4) for a total of 16 surveying periods resulting in 16,002 winged insects collected the duration of the project to estimate relative insect abundance across land treatments (Table 4; Figure 8). To meet assumptions of normality, insect data were transformed by natural log (ln). Since bat activity showed no preference to insect size between 3 mm to 30 mm, any insect smaller than 3 mm and larger than 30 mm were omitted, and the remaining sum of insects (n= 9,277) were used in statistical analysis of relationships between insect abundance and bat activity. Linear regression analysis showed a significant positive relationship between insect abundance and total bat activity when pooled across all land management treatments ($R^2 = 0.34$, $p < 0.001$; Table 5; Figure 9a). Linear regression showed no relationship between individual phonic group activity and insect abundance (Table 5).

Various vegetation and habitat characteristic measurements were taken within each treatment (Table 6). Each of these measurements were used as predictor variables in linear regressions to test for relationships to bat activity (Table 5). Linear regression showed a significant negative relationship between mean tree diameter (dbh) and total bat activity ($R^2 = 0.13$, $p < 0.027$, Table 5; Figure 9b). Linear regression showed a significant negative relationship between canopy height and total bat activity ($R^2 = 0.16$, $p < 0.014$, Table 5; Figure 9c). Also, linear regression showed a significant negative relationship between basal area (m^2) on total bat activity as basal area increased, bat activity decreased ($R^2 = 0.14$, $p < 0.025$, Table 5; Figure 9d). The same models were used to analyze relationships between the activity of each phonic group. Linear regression only showed significant relationships between mean tree diameter ($R^2 = 0.12$,

$p < 0.036$), canopy cover ($R^2 = 0.21$, $p < 0.005$), canopy height ($R^2 = 0.15$, $p < 0.002$), and basal area ($R^2 = 0.1225$, $p < 0.036$) within the low phonic group (Table 5, Figure 10).

Discussion

This study is the first to assess the influence of different coastal upland habitat management techniques over an entire year on bat activity along the northern Gulf of Mexico coast. In this study, bat activity was shown to be different across management techniques, supporting the first hypothesis predicting there would be a difference in bat activity between the different land management treatments. These findings are consistent with other studies that showed variations in habitat could play a role in influencing bat activity (Tibbels & Kurta, 2003). Additionally, increased bat activity in management techniques with reduced vegetation (i.e., stem thinning, clear cuts, open pine savanna conditions) has been documented in a variety of forested landscapes (Ford et al., 2006; Loeb & O'Keefe, 2006; Loeb & Waldrop 2008; Bender et al., 2015; Wegiel et al., 2019). For total bat activity, there was a general preference for prescribed fire than select cut techniques; however, these preferences weren't consistent across seasons.

The difference in bat activity across the land management treatments across seasons is supported by previous studies on varying bat activity across landscape use (Vaughn et al., 1997) as diet, habitat requirements, and resource availability changes across seasons (Kuenzi & Morrison, 2003; Taylor et al., 2013; Kunberger & Long, 2022). Unsurprisingly, bat activity was highest during summer and lowest during winter with 41.6% and 11.7% of pulses from identified recordings during this study, respectively. During the winter survey, bat activity was measured across all land management treatments. Determining how bats are using these areas during the winter was beyond the scope of this study but considering that winter insect samples contained potential bat prey, it is possible that bats take advantage of the mild winter temperatures on the Mississippi coast to forage. This study supports the hypothesis that bats use torpor on the coast where winters are mild and foraging opportunities emerge on warm nights (Grider et al., 2016; Johnson et al., 2012; Sandel et al., 2001; Bernard & McCracken, 2017; Johnson et al., 2016). While the results from this study cannot indicate whether residential bats are staying in the area year-round or if bats are stopping in along migration routes (Furmankiewicz & Kucharska, 2009; McGuire et al. 2012), it provides new insights into bat presence and activity throughout the seasons along the northern Gulf of Mexico coast.

Phonic groups allowed for a representative look at the diversity of bat species activity within the habitat treatments within the scope of this study. These groups have similar call characteristics and morphologies that indicate habitat preference (Dodd et al., 2012; Britzke et al., 2001; Ober & Hayes, 2008; Fenton & Bogdanowicz, 2002). Differences in activity across habitat management treatments by different phonic groups is supported by studies where differences in habitat preference amongst bats was driven by morphological differences (Gonçalves et al., 2017; Buchalski et al., 2013; Aldridge & Rautenbach, 1987). The results from this study showed that increase in forest structure density (i.e., higher basal area, larger diameter trees, taller canopy) had a negative relationship to overall bat activity. When compared among phonic groups, forest structure was particularly important to the low phonic group. The low phonic group contains larger-bodied bats known to forage in open-space and fly above canopies (Menzel et al., 2005; Ford et al., 2006), while the high and mid phonic group consists of species adapted to flying in denser forest conditions (Sleep & Brigham, 2003).

The largest overall difference between phonic group activity was between the prescribed fire and select cut habitat treatment sites. The difference in phonic group activity between these treatments was influenced by greater bat activity levels for the high (39.1% of pulses) and low phonic group (38.7% of pulses) in the prescribed fire treatment. Higher bat activity by multiple species in open rather than dense forest habitats could be attributed to open-space for easier movement and flight (Grindal and Brigham, 1998). In addition to the open-space habitat characteristics, prescribed fire habitats may also provide more foraging and roosting opportunities (Tibbles & Kurta, 2003; Boyles & Aubrey, 2006; Jorge et al., 2021). An increase in availability of potential insect prey consumed by bats has shown to increase following a burn event (Lacki et al., 2009).

It was not surprising to find no difference in high phonic group activity across treatments when compared to the other phonic groups. Bats with higher frequency calls are smaller-bodied and better adapted to maneuver within dense forest enabling these bats to utilize different forest conditions (Ford et al., 2005; Menzel et al., 2005). The mid phonic group showed no preference for any habitat management treatment but was most active within the mulched habitat treatment when compared to the other phonic groups. The mulched treatment area exhibited a fragmented forest habitat with patches of mulched areas adjacent to unmulched areas with dense stands of slash pine. The higher activity seen by the mid phonic group in this treatment could suggest that this group of bats is adapted to both densely forested and open habitats (Armitage & Ober 2012; Fenton 1990) and possibly use this area to forage with the high relative abundance of insects found within this treatment. The low phonic group activity was found to be the highest in the prescribed fire habitat treatment and was lowest in the select cut treatment. This group consists of bats with echolocation and morphological characteristics better suited for habitats with more open space (Aldridge & Rautenbach, 1987; Hodgkison et al., 2004; Patriquin & Barclay, 2003).

As predicted, the results from this study showed a difference between insect abundance and bat activity across habitat management techniques, supporting the second hypotheses of this study, with a positive relationship between insect abundance and bat activity across habitat management techniques. The most abundant insect orders collected during this study represent common bat prey including Coleoptera (beetles), Diptera (flies), Hemiptera (true bugs), and Lepidoptera (moths) (Bernard & McCracken, 2017; Ruadreo et al., 2018; Whitaker 2004). Relative insect abundance (RA%) varied across the land management treatments with the mulch site having the most relative insect abundance and consisting of 64% of total sampled insects. Although dense forest ecosystems tend to have greater abundance of insects (Hanula et al., 2000), the select cut treatment had the lowest relative insect abundance in this study. Even with the vastness of relative insect abundance, the mulch site did not contain the highest measurements of bat activity indicating that insect abundance alone does not determine bat activity across these land management sites. Vegetation is often a strong indicator of insect availability for bats (Müller et al., 2012) and the combination of insects and vegetation, with vegetation likely influencing insects, could be what drove differences in bat activity across habitat management treatments in this study (Bender et al., 2021; Grindal & Brigham 1999). Further investigation into the combination of vegetation characteristics and prey abundance is warranted as previous studies have observed management techniques to contribute to and reduce foraging habitat of bats (Aldridge & Rautenbach, 1987; Bender et al., 2021; Salcedo et al., 1995, Patriquin & Barclay, 2003; Armitage & Ober, 2012) and the extent of the combination of forest characteristics and prey abundance on habitat use by bats is species-specific (Caldwell et al., 2019).

Management Recommendations

In summary, heterogeneity in forest structure provided by the use of different habitat management techniques could provide habitat for several species of bats present along the northern Gulf Coast throughout the year. Findings from this study further supports other research that has shown the importance of diverse habitat to support a diverse bat community (Ober & Hayes, 2008; Lundy & Montgomery, 2010). The ecomorphological and species-specific responses (Owen et al., 2004; Cox et al., 2016) to habitat management techniques should be considered to help maximize suitable habitat for bats. Lands that are targeted for broad-scale habitat management should consider resident and transient bat species and seasonal foraging requirements when developing habitat management plans and coordinating management actions.

Acoustic monitoring of activity and habitat use of bats is an inexpensive method used widely in bat research (Hayes 2000; Parsons & Szewczak, 2009; Kungerger & Long, 2002). Due to research and permitting constraints during the implementation of this study, visual verification of active bat species was limited to passive acoustic recording. Using advanced software and visuals to identify recorded bat calls to species-specific detail is challenging due to the variation and similarity of bat echolocation calls (Hayes et al., 2009; Parsons & Szewczak, 2009). However, these techniques were suited to address the objectives of this study.

While a strong relationship between insect abundance and bat activity was observed, this relationship could potentially have been stronger with more comprehensive insect monitoring. Surveying insects using trapping methods measures insect availability to the researcher and is possibly not completely indicative of insects available to bats (Whitaker 1994). It was beyond the scope of this study to determine if bats were performing specific activities (e.g., foraging, commuting, roosting, etc.) and if those varied by habitat management treatment. While it is possible bats are foraging in these areas where insect prey is available, it can also be possible that bats use these areas as a commuting route to foraging areas (Verboom et al., 1999; Van de Sijpe et al., 2004). Further research is required to analyze bat diet to establish whether bats are using these areas to forage on available insects across habitat management treatments.

Conclusion

Despite the limitations of acoustic monitoring and insect surveying, this study is useful for concluding the presence and activity of bats and their insect prey across different land management habitats within the northern Gulf of Mexico coast. Future studies could leverage these results to increase research on habitat use for foraging bats within habitat management areas prior to and following habitat management.

Tables

Table 1 Summary of bat activity recorded at the Grand Bay National Wildlife Refuge during this study.

Phonic Group	Common name	Scientific name	Call frequency range (kHz)	Foraging habitat	# of call files	# of pulses
High	Tri-colored bat	*Perimyotis subflavus*	41-44	Forest edges	415	9,889
	Eastern red bat	*Lasiurus borealis*	37-44	Forest edges	290	5,984
	Seminole bat	*Lasiurus seminolus*	36-44	Forest edges	795	10,636
	Evening bat	*Nycticeius humeralis*	31-43	Forest edges	406	14,062
Mid	Northern yellow bat	*Lasiurus intermedius*	27-30	Open space	126	2,618
	Big brown bat	*Eptesicus fuscus*	26-30	Open space	513	16,200
	Silver-haired bat	*Lasionycteris noctivagans*	23-31	Open space	124	1,908
Low	Mexican free-tailed bat	*Tadarida brasiliensis*	22-26	Open space	2,321	44,811
	Hoary bat	*Lasiurus cinereus*	18-22	Open space	1,456	17,450
				Unidentified	6,680	-
				Total:	6,446	123,558

Summary of bat species recorded during this study and processed using Kaleidoscope Pro software (Wildlife Acoustics Inc.). Identified species were placed into phonic groups based on similar call characteristics and call frequency ranges (kHz). Bat activity is determined by analyzing the number (#) of pulses from recorded call files.

Note: Foraging habitat informed by Norberg and Rayner (1987), Lacki et al. (2007), and Denzinger and Schnitzler (2013); call frequencies informed by Humboldt State University Bat Lab Echolocation Call Characteristics of Eastern US Bats (2011).

Table 2 Summary of total bat activity and phonic group activity each season across the land management techniques during this study.

				Mulch		Select Cut		Prescribed Fire	
Group	Season	# of call files	# of pulses	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
High	Spring	42	1054	21.11	2.16	27.75	7.24	29.65	2.09
	Summer	105	2388	22.80	2.29	22.66	1.29	25.78	4.06
	Fall	64	1096	23.56	5.96	14.46	3.15	14.59	3.77
	Winter	24	451	19.59	5.00	13.60	3.83	25.05	3.45
	Total	235	4989	24.78	0.4	20.79	0.22	19.94	0.36
Mid	Spring	41	840	23.42	3.27	17.07	2.87	21.33	2.34
	Summer	62	1313	20.63	1.68	26.57	3.08	21.04	2.27
	Fall	24	428	11.48	4.10	24.42	8.48	16.71	3.68
	Winter	15	288	20.48	3.42	18.19	4.67	17.00	2.00
	Total	142	2869	20.18	0.57	32.03	0.36	19.79	0.44
Low	Spring	54	618	12.42	0.28	10.01	0.66	14.05	0.86
	Summer	41	421	16.56	4.61	5.34	0.67	11.62	1.95
	Fall	54	602	9.17	0.65	8.76	0.99	15.49	1.31
	Winter	44	416	8.25	1.32	8.95	1.38	11.95	1.70
	Total	193	2057	18.79	0.35	10.29	0.12	16.97	0.19
Total	Spring	137	2512	18.81	1.53	16.12	2.15	21.69	1.65
	Summer	208	4122	20.00	1.81	18.69	2.13	19.48	1.99
	Fall	142	2126	14.64	2.59	14.38	2.61	15.40	1.68
	Winter	83	1155	13.79	2.06	12.22	1.74	15.58	2.06
	Grand total	570	9915	17.2	1.03	15.7	1.12	18.6	0.974

Summary of total bat activity and phonic group activity each season across the land management techniques. Bat activity was measured by the number (#) of pulses averaged across the land management plots during each season. Seasons were measured as a survey event (Spring – March 6 to 14; Summer – August 19 to 27; Fall – November 8 to 16; Winter – January 4-12). Total number (#) of pulses for each phonic group each season with the mean ($\bar{x}$) # of pulses and standard error (SE) within each technique.

Table 3 Results of pairwise post-hoc Tukey test on significant differences from two-way ANOVA on total bat activity across land management techniques.

	Comparisons	Diff	Lower	Upper	p-adj
Treatment	PF – ML	0.117	-0.083	0.318	0.354
	SC – ML	-0.146	-0.348	0.055	0.201
	SC – PF	-0.264	-0.469	-0.058	***0.007****
Season	Spring – Fall	0.342	0.093	0.590	***0.003****
	Summer – Fall	0.308	0.064	0.553	***0.007****
	Winter – Fall	-0.015	-0.301	0.271	0.999
	Summer – Spring	-0.033	-0.271	0.204	0.984
	Winter – Spring	-0.357	-0.637	-0.076	***0.006****
	Winter – Summer	-0.323	-0.599	-0.046	***0.015****

The results from the pairwise post-hoc Tukey test on significant difference from two-way ANOVA on total bat activity across treatments and interactions with season (activity ~ treatment * season). This data were natural log (ln) transformed for analysis. Significant p-values at the <0.05 level are indicated starred in bold. Treatment legend indicates ML = mulch, PF = prescribed fire, SC = select cut.

Table 4 Summary of insect data collected within each land management technique at the Grand Bay National Wildlife Refuge during this project.

Treatment	Order	n	RA %	$\bar{x}$ length (mm)	$\bar{x}$ minimum length (mm)	$\bar{x}$ maximum length (mm)
Mulch	Blattodea	10	0.10	5.82	2.00	8.00
	Coleoptera	7700	75.31	3.80	1.00	22.30
	Diptera	1734	16.96	3.37	1.00	16.20
	Hemiptera	389	3.80	4.31	2.00	15.00
	Hymenoptera	134	1.31	4.12	1.00	27.00
	Lepidoptera	232	2.27	14.54	4.50	46.00
	Neuroptera	1	0.01	6.60	6.60	6.60
	Odonata	1	0.01	21.00	21.00	21.00
	Orthoptera	3	0.03	24.40	8.00	33.00
	Trichoptera	20	0.20	5.35	3.00	6.00
	Total (Σn_t)	10,224				
Prescribe Fire	Coleoptera	1554	49.70	3.67	1.50	30.00
	Diptera	1197	38.28	3.11	1.00	25.00
	Hemiptera	157	5.02	4.26	2.00	14.00
	Hymenoptera	36	1.15	4.38	2.00	18.00
	Lepidoptera	174	5.56	14.07	4.00	44.00
	Odonata	1	0.03	21.80	21.80	21.80
	Orthoptera	5	0.16	15.56	5.00	49.00
	Psocoptera	1	0.03	3.00	3.00	3.00
	Trichoptera	2	0.06	3.90	3.60	4.20
	Total (Σn_t)	3,127				
Select Cut	Coleoptera	464	17.50	4.14	1.20	32.00
	Diptera	1665	62.81	3.26	1.50	13.00
	Hemiptera	124	4.68	3.61	2.00	11.00
	Hymenoptera	168	6.34	3.75	2.00	15.00
	Lepidoptera	212	8.00	16.51	3.00	50.00
	Orthoptera	9	0.34	8.51	5.00	20.00
	Psocoptera	4	0.15	2.88	2.50	3.00
	Trichoptera	5	0.19	4.88	3.00	9.00
	Total (Σn_t)	2,651				
	Grand total	16,002				

Insects were collected using flight intercept and bucket light traps in each plot within each land management technique each season. The summary of the insect data collected within each land management technique includes the taxonomic Order, number of specimens (n), relative abundance (RA%), mean ($\bar{x}$) length to the nearest millimeter (mm), and mean ($\bar{x}$) maximum and minimum lengths from measurement data.

Table 5 Results from linear regression models of the relationships between bat activity to insect abundance and habitat characteristic variables.

Group	Variables	R^2	F-statistic	P-value
Total activity	Insect abundance	0.3414	17.62	***< 0.001****
	Mean tree dbh (cm)	0.1349	5.303	***0.028****
	Canopy cover (%)	0.0627	2.276	0.141
	Canopy height (m)	0.1638	6.659	***0.014****
	Basal area (m^2/ha)	0.1442	5.727	***0.022****
	Shrub height (m)	0.002	0.068	0.796
	Vegetation diversity	0.0385	1.361	0.251
	Distance to water (m)	0.002	0.071	0.792
High phonic	Insect abundance	0.0225	0.784	0.382
	Mean tree dbh (cm)	0.0406	1.441	0.238
	Canopy cover (%)	0.0404	1.432	0.24
	Canopy height (m)	0.0474	1.691	0.202
	Basal area (m^2/ha)	0.0383	1.355	0.253
	Shrub height (m)	0.0034	0.118	0.734
	Vegetation diversity	0.0200	0.695	0.41
	Distance to water (m)	0.0041	0.137	0.714
Mid phonic	Insect abundance	0.0096	0.330	0.5692
	Mean tree dbh (cm)	0.0103	0.354	0.556
	Canopy cover (%)	0.0255	0.892	0.352
	Canopy height (m)	0.0229	0.799	0.377
	Basal area (m^2/ha)	0.0117	0.400	0.531
	Shrub height (m)	0.0039	0.135	0.716
	Vegetation diversity	0.0110	0.379	0.542
	Distance to water (m)	0.0536	1.925	0.174
Low phonic	Insect abundance	0.0262	0.915	0.3455
	Mean tree dbh (cm)	0.1226	4.753	***0.0363****
	Canopy cover (%)	0.2087	8.97	***0.0051****
	Canopy height (m)	0.1513	6.061	***0.019****
	Basal area (m^2/ha)	0.1225	4.744	***0.0364****
	Shrub height (m)	0.0192	0.666	0.420
	Vegetation diversity	0.0200	0.694	0.411
	Distance to water (m)	0.0081	0.277	0.602

Linear regression models were used to test relationships between total bat activity and phonic group activity to insect abundance and habitat characteristic variables. Bold and starred (*) p-values are significant.

Table 6 Habitat characteristic measurements taken within each land management technique site.

Treatment	Size (ha)	Previous treatment description	Habitat description	$\bar{x}$ dbh	BA (m^2/ha)	$\bar{x}$ canopy height (m)	$\bar{x}$ canopy cover (%)	$\bar{x}$ shrub height (m)	Ground cover diversity (∑)	$\bar{x}$ distance to water (m)
Mulched	26.08	In 2020, mulched using a GyroTrac and skid steer with a mulching head. This area was also previously treated with herbicide targeting invasive vegetation.	Pine savanna and pine flatwood. Ground cover included mulch pieces from woody vegetation, grasses, and small shrubs.	92.26	13.71	22.85	14.33	0.40	18	225.86
Prescribed Fire	22.53	This area was burned in 2008, 2012, 2014, and 2018.	Pine savanna primarily with low densities of longleaf and slash pine. Ground cover of grasses, wildflowers, and shrubs bordered by firebreaks and more densely forested areas.	77.19	7.85	20.51	14.83	1.38	9	430.38
Select Cut	31.17	This area received a select cut in 2019 targeting slash pine <6 inches in diameter breast height (dbh). This site was also burned in 2014 and 2018 and treated with herbicides targeting invasive vegetation.	Pine flatwood with shrubs and with some forest gaps bordered by firebreaks and roads.	94.91	11.31	23.73	57.83	0.88	16	574.80

Habitat characteristic measurements were taken at each plot (n=9) and averaged across the treatments to represent the overall habitat land management sites.

Figures

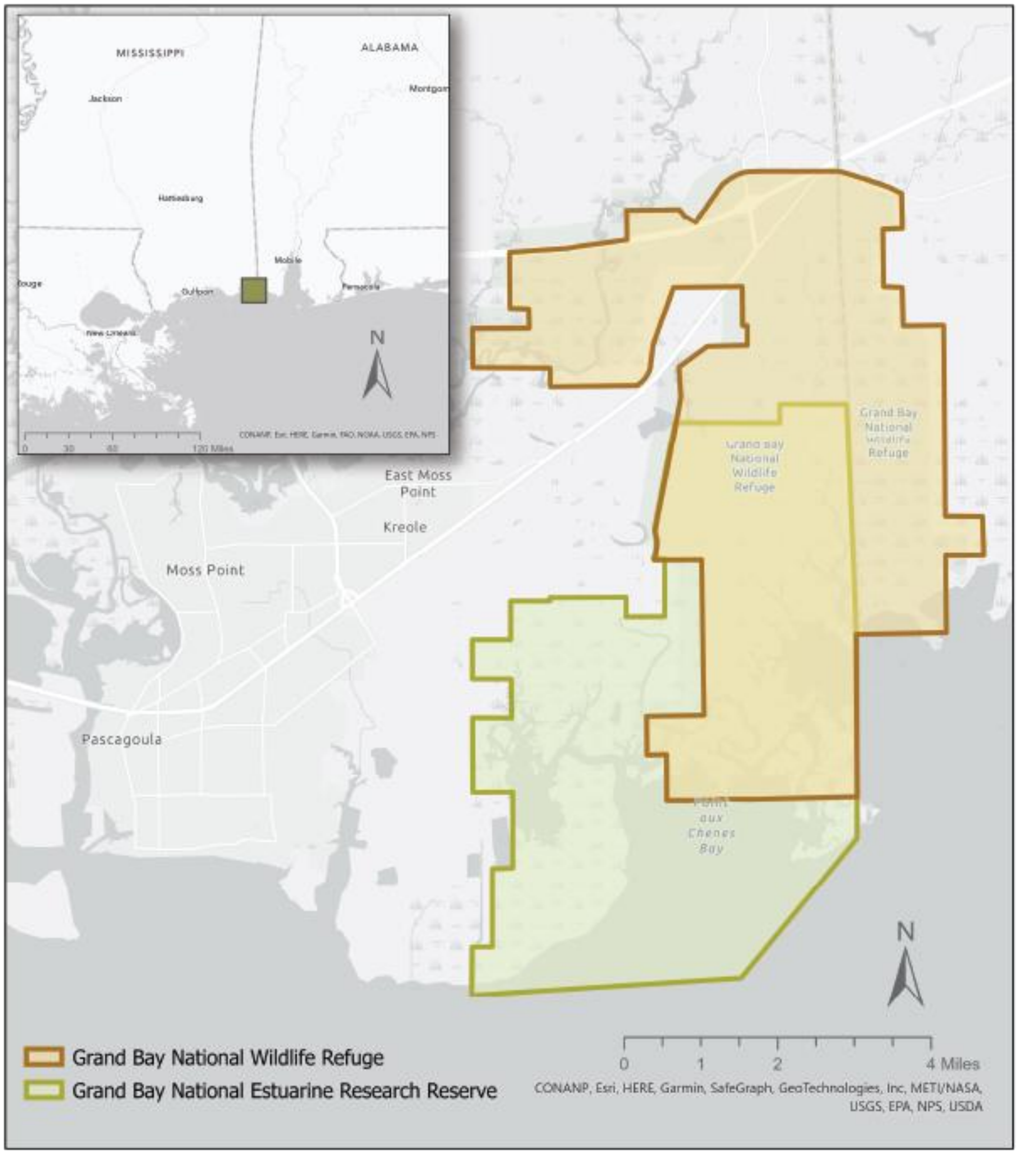

Figure 1 Map of Grand Bay National Wildlife Refuge, Moss Point, Mississippi.

The Grand Bay National Wildlife Refuge encompasses 4,123-ha and partially overlaps the Grand Bay National Estuarine Research Reserve. Together they encompass 7,284-ha of protected land with a variety of habitats including upland forests, pine savanna, maritime forests, marshes, and bayous.

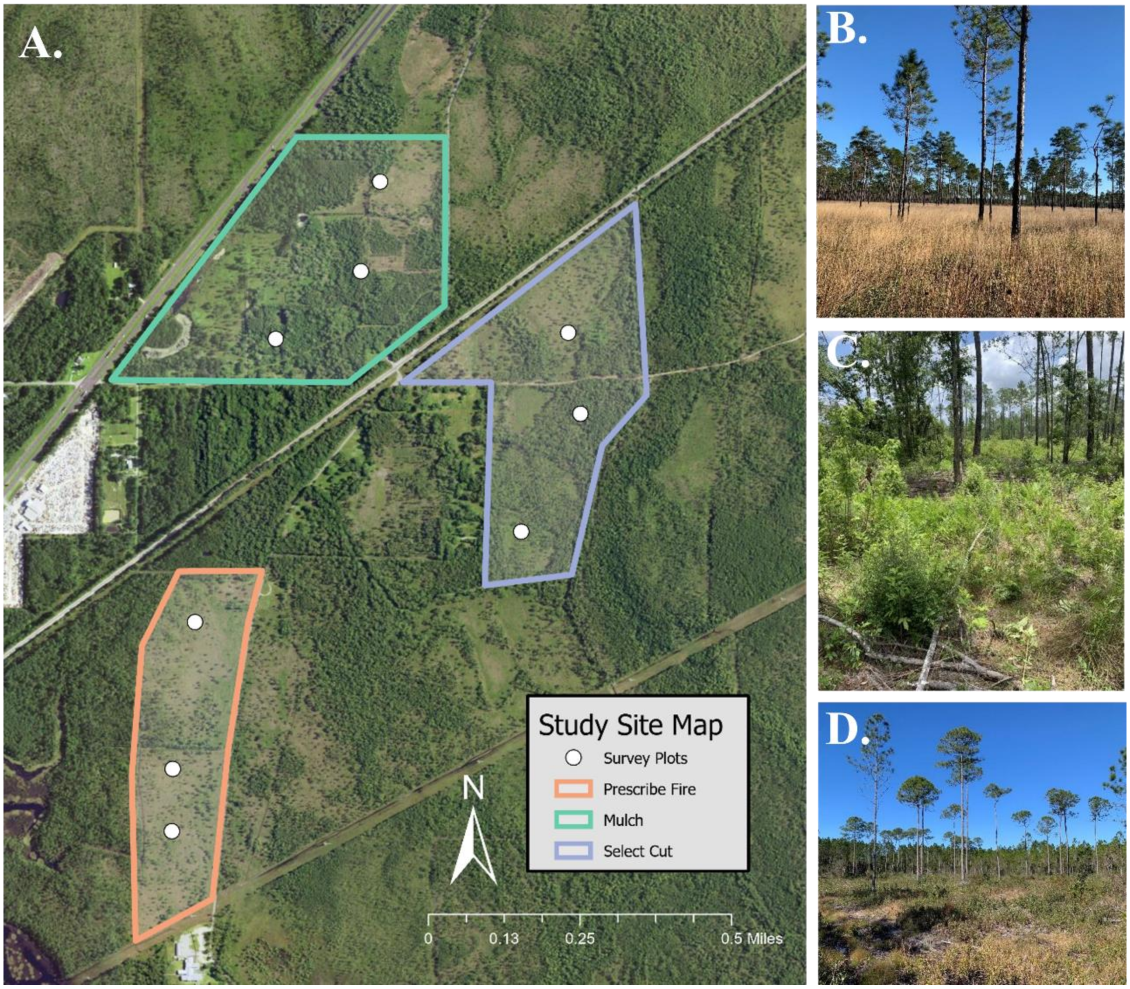

Figure 2 Map of the study sites at Grand Bay National Wildlife Refuge.

A) Surveys were completed at three plots within each of the land management technique study sites (n=9): B) prescribed fire site consists of open-space pine savanna and flatwoods; C) select cut site consists of pine flatwoods with downed trees from the land management treatment; and D) mulch site consists of pine flatwoods with mulch on the ground from the land management treatment.

Figure 3 Methods used to complete acoustic and insect surveys.

A.) Wildlife Acoustics Song Meter Mini Bat passive acoustic recorder placed at least 2 meters off the ground on a tree with microphones facing forest openings and oriented at a 45° toward canopy openings to maximize the likelihood of high-quality bat call recordings; B) Flight intercept trap deployed in a prescribed fire plot to collect samples of flying insects; and C) Bucket light trap deployed in a prescribed fire plot to collect samples of flying insects.
complete acoustic surveys

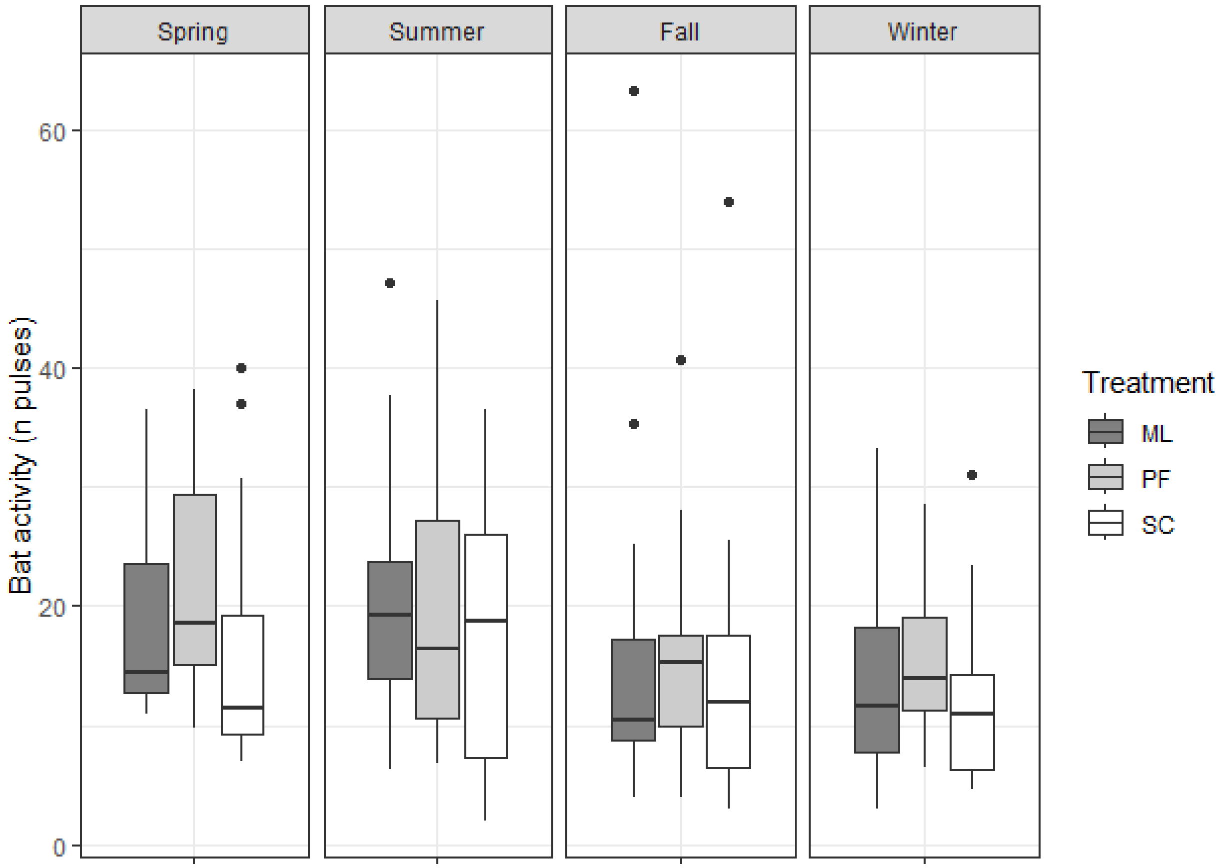

Figure 4 Box and whisker plots showing total bat activity distribution across the land management techniques each season.

Box and whisker plot display of total bat activity within the treatment sites over the duration of the study. Each season was a survey event. Treatment legend indicates ML = mulch, PF = prescribe fire, SC = select cut.

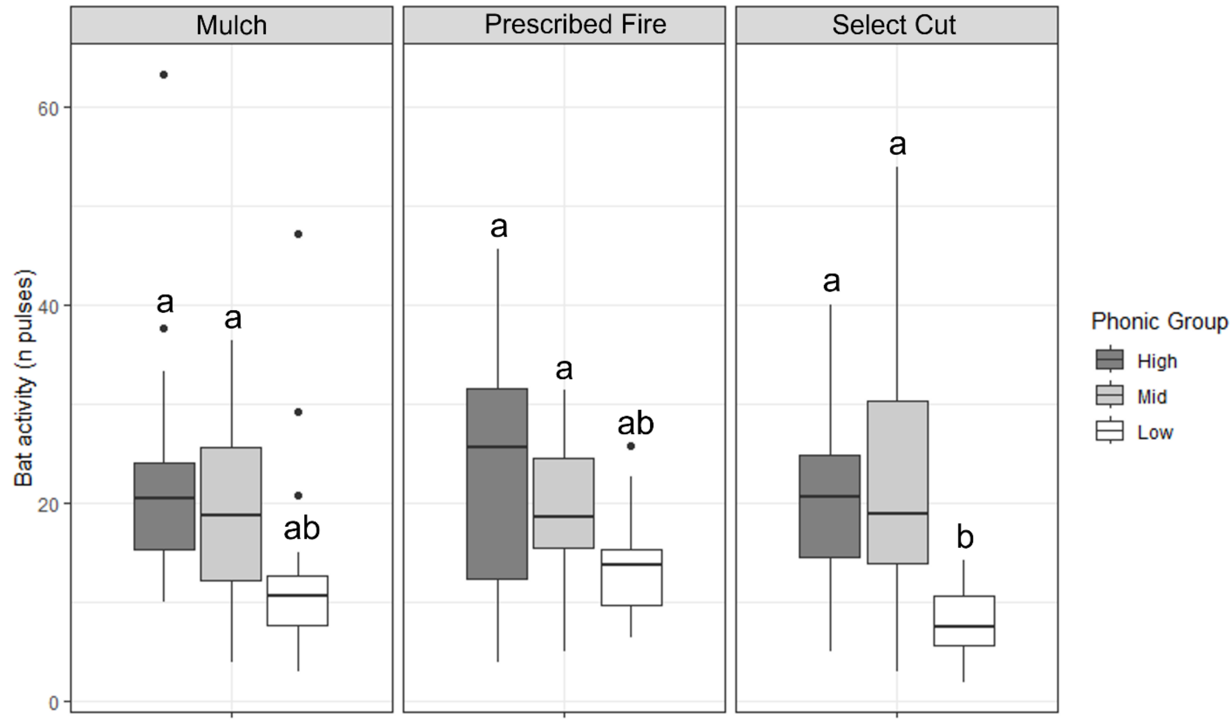

Figure 5 Box and whisker plots showing phonic group activity distribution across the land management techniques.

Box and whisker plot display showing phonic group activity distribution within each land management technique site. Techniques are represented by treatments in each panel. Pairwise post-hoc Tukey tests shown a significant difference between the select cut and prescribed fire treatments ($p = 0.005$) primarily driven by the low phonic group activity in the select cut site.

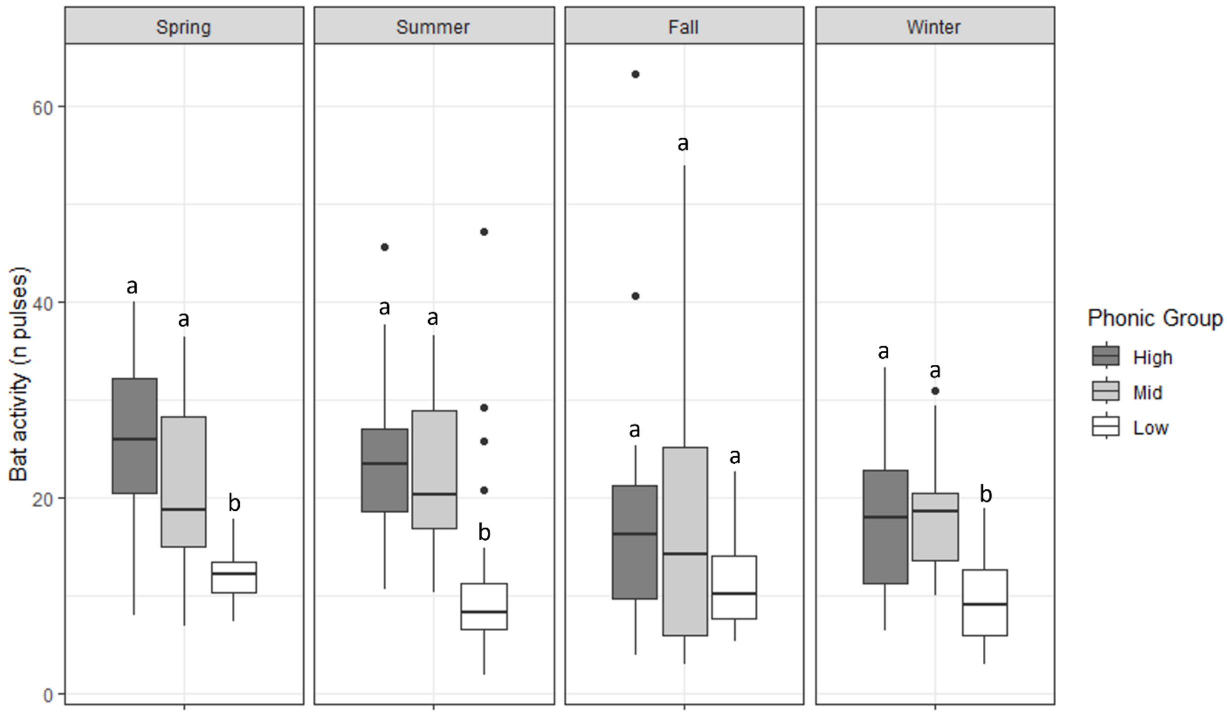

Figure 6 Box and whisker plots showing phonic group activity distribution for each season.

Box and whisker plots display phonic group activity across seasons. Due to there being a significant interaction between the effect phonic group and season on bat activity (p = 0.01), one-way ANOVAs were conducted to further look at the effect of season on phonic group activity so each season individually. Results of the one-way ANOVA tests showed that there was a significant difference between phonic group activity in all seasons except fall (p = 0.188).

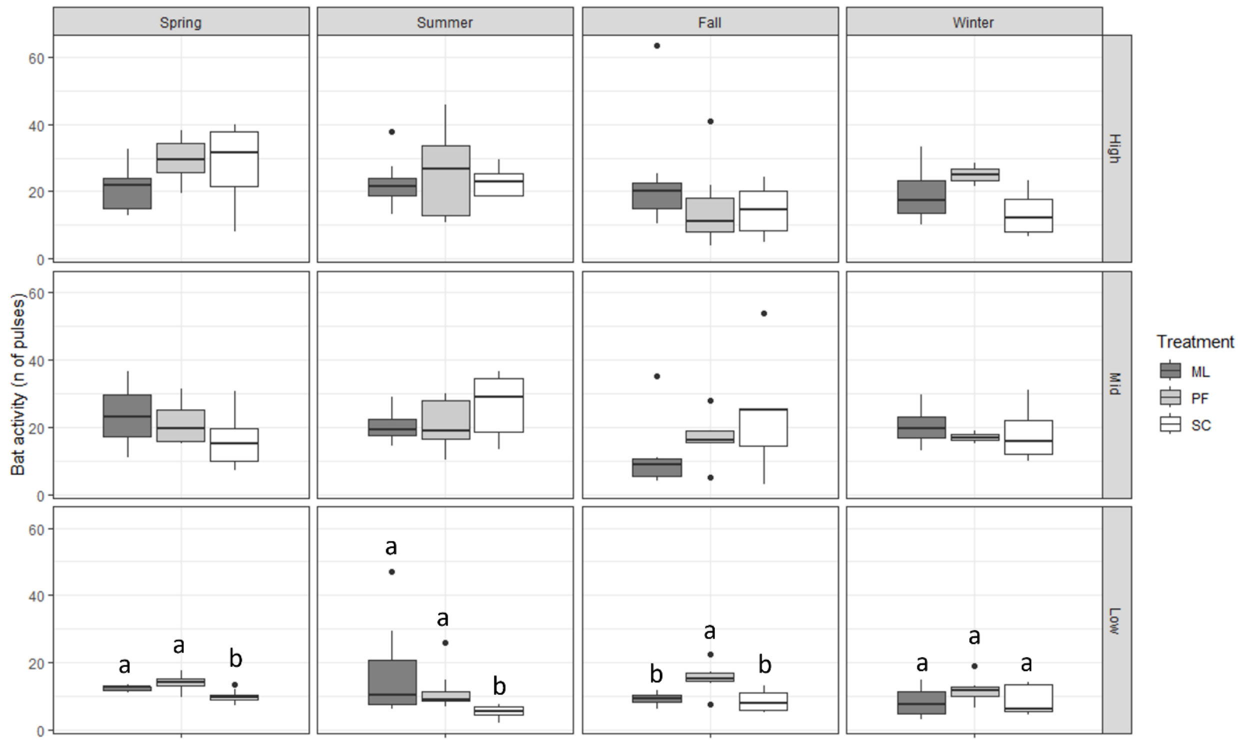

Figure 7 Box and whisker plot panel showing seasonal phonic group activity across the land management techniques.

Box and whisker plots showing bat activity seasonally across treatments for the (A) high, (B) mid, and (C) low phonic groups. Species recorded during survey events were grouped based on similar call structures and frequency ranges into common phonic groups. Seasons were measured as a survey event (spring – March 6 to 14; summer – August 19 to 27; fall – November 8 to 16; winter – January 4-12). Post-hoc Tukey comparisons showed that the select cut site had significantly less low phonic group activity than the prescribe fire sire for all seasons except winter. Treatment legend indicates ML = mulch, PF = prescribed fire, and SC = select cut.

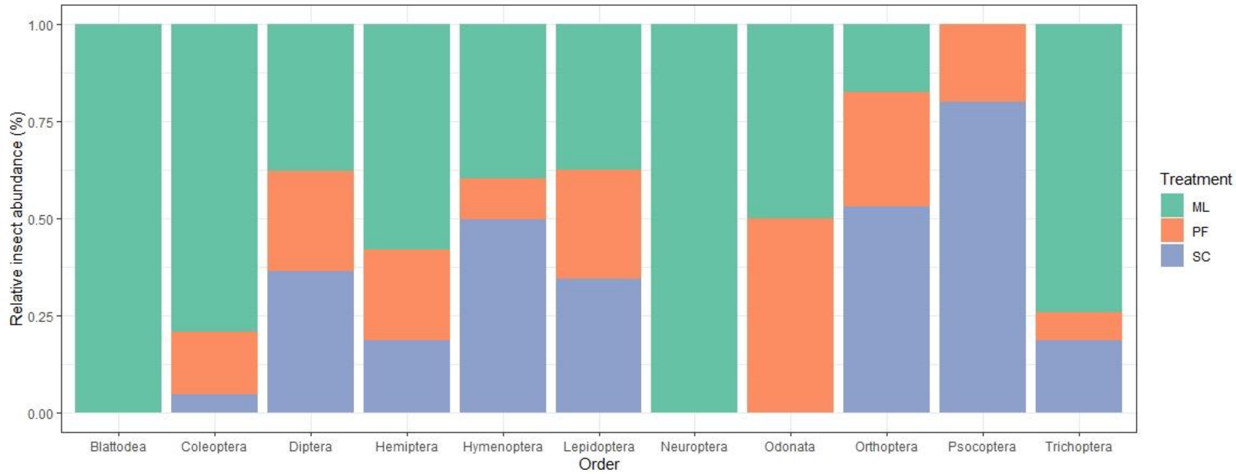

Figure 8 Relative abundance of insects sampled across land management techniques.

Relative abundance of insect orders sampled across the treatments during the duration of the project. Insects were collected using flight intercept and bucket-light traps during each season. Insect sampling took place for a continuous four days and four nights to passively collect insects in spring (April 24-27, 2021), summer (August 24-27, 2021), fall (November 9-12, 2021), and winter (January 17-20, 2022) over the study duration. All seasons are combined in this figure to give an overall glance at insect diversity across treatments. Treatment legend indicates ML = mulched; PF = prescribed fire; and SC = select cut.

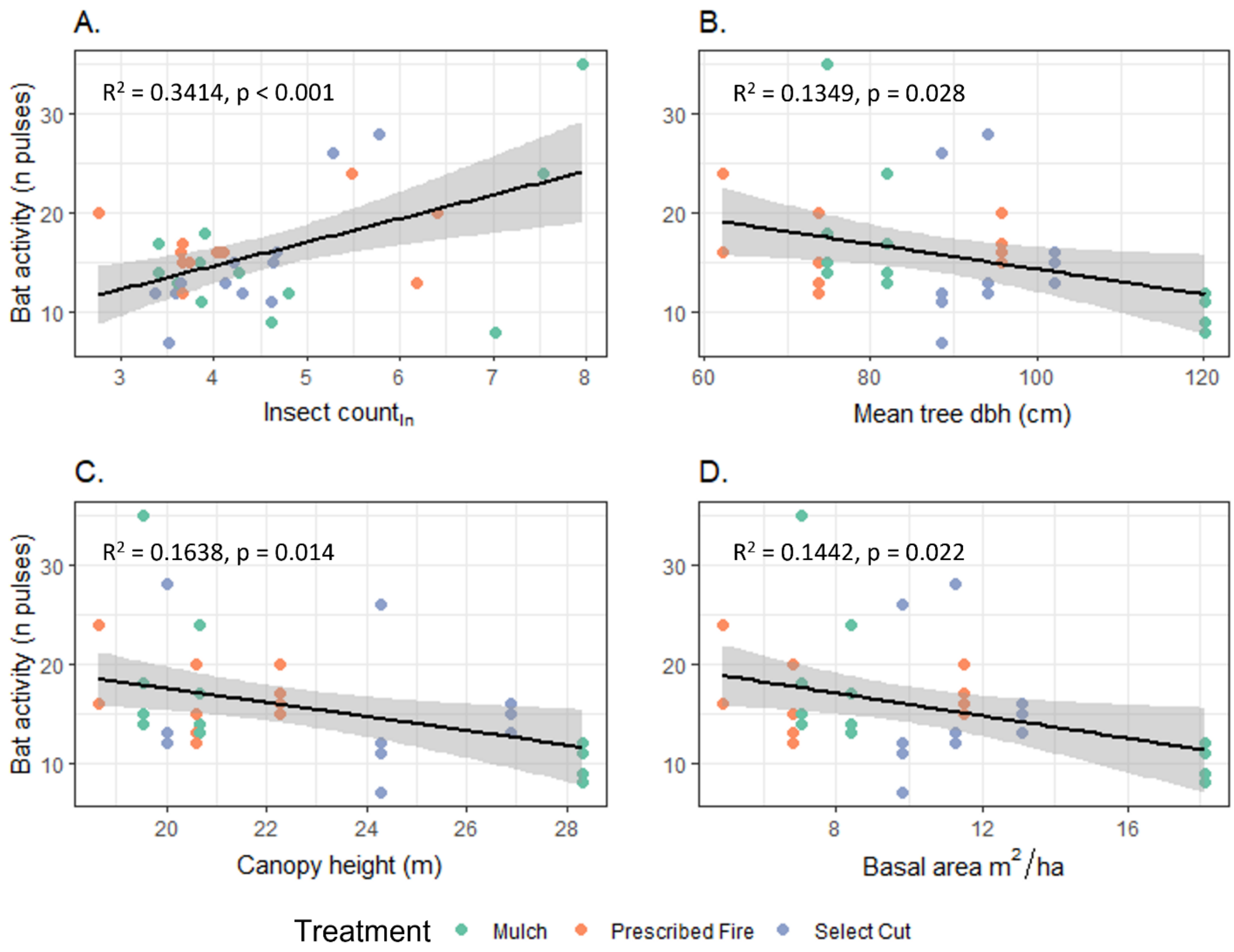

Figure 9 Linear regression figures of significant relationships between total bat activity across the land management techniques.

Linear regression figures of significant relationships between total bat activity across the treatment sites. Bat activity is defined as the number of pulses (n pulses) recorded during an acoustic survey event; A) bat activity increased as insect abundance increased; B) bat activity showed a decrease as mean tree diameter at diameter breast height increased; C) bat activity showed a decrease as canopy height increased; and D) bat activity decreased as average basal area per meter squared per hectare (BA m^2/ha) across the different land management treatments increased.

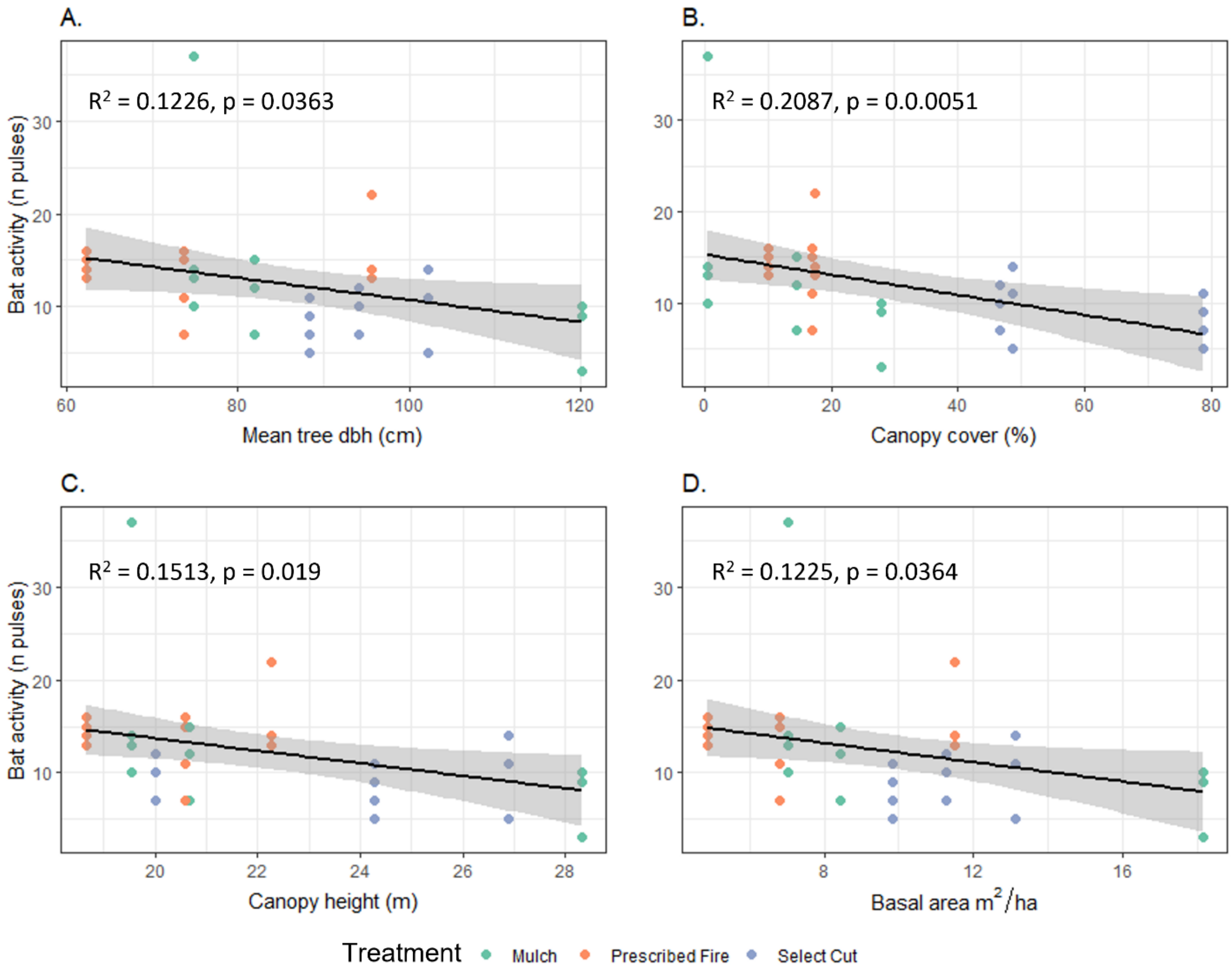

Figure 10 Linear regression figures of significant relationships between low phonic group activity and different habitat characteristics.

Linear regression of the significant negative relationships between low phonic group bat activity and; A) mean tree diameter at diameter breast height (dbh); B) percent canopy cover; C) canopy height across the different land management treatments; and D) basal area per meter squared per hectare (BA m^2/ha) across the different land management treatments increased. The low phonic group consisted of bats known to prefer to fly in open-space and above canopies.

REFERENCES

Adam, M. D., & Hayes, J. P. (2000). Use of bridges as night roosts by bats in the Oregon Coast Range. *Journal of Mammalogy*, *81*(2), 402-407.

Akasaka, T., Nakano, D., & Nakamura, F. (2009). Influence of prey variables, food supply, and river restoration on the foraging activity of Daubenton's bat (*Myotis daubentonii*) in the Shibetsu River, a large lowland river in Japan. *Biological Conservation*, *142*(7), 1302-1310.

Aldridge, H. D. J. N., & Rautenbach, I. L. (1987). Morphology, echolocation and resource partitioning in insectivorous bats. *The Journal of Animal Ecology*, 763-778.

Andersen, B. R., McGuire, L. P., Wigley, T. B., Miller, D. A., & Stevens, R. D. (2022). Habitat associations of overwintering bats in managed pine forest landscapes. *Forests*, *13*(5), 803.

Armitage, D. W., & Ober, H. K. (2010). A comparison of supervised learning techniques in the classification of bat echolocation calls. *Ecological Informatics*, *5*(6), 465-473.

Armitage, D. W., & Ober, H. K. (2012). The effects of prescribed fire on bat communities in the longleaf pine sandhills ecosystem. *Journal of Mammalogy*, *93*(1), 102-114.

Austin, L. V., Silvis, A., Ford, W. M., Muthersbaugh, M., & Powers, K. E. (2018). Bat activity following restoration prescribed burning in the central Appalachian upland and riparian habitats. *Natural Areas Journal*, *38*(2), 183–195. https://doi.org/10.3375/043.038.0208

Barclay, R. M., & Brigham, R. M. (1991). Prey detection, dietary niche breadth, and body size in bats: why are aerial insectivorous bats so small? *The American Naturalist*, *137*(5), 693-703.

Bender, M. J., Castleberry, S. B., Miller, D. A., & Bently Wigley, T. (2015). Site occupancy of foraging bats on landscapes of managed pine forest. *Forest Ecology and Management*, *336*, 1–10. https://doi.org/10.1016/j.foreco.2014.10.004

Bender, M. J., Perea, S., Castleberry, S. B., Miller, D. A., & Wigley, T. B. (2021). Influence of insect abundance and vegetation structure on site-occupancy of bats in managed pine forests. *Forest Ecology and Management*, *482*, 118839. https://doi.org/10.1016/j.foreco.2020.118839

Bernard, R. F., & McCracken, G. F. (2017). Winter behavior of bats and the progression of white-nose syndrome in the southeastern United States. *Ecology and Evolution*, *7*(5), 1487–1496. https://doi.org/10.1002/ece3.2772

Betts, B. J. (1998). Effects of interindividual variation in echolocation calls on identification of big brown and silver-haired bats. *The Journal of Wildlife Management*, *62*(3), 1003. https://doi.org/10.2307/3802553

Bogdanowicz, W., Fenton, M. B., & Daleszczyk, K. (1999). The relationships between echolocation calls, morphology and diet in insectivorous bats. *Journal of Zoology*, *247*(3), 381-393.

Boyles, J. G., & Aubrey, D. P. (2006). Managing forests with prescribed fire: implications for a cavity-dwelling bat species. *Forest Ecology and Management*, *222*(1-3), 108-115.

Brigham, R.M. (2007). Bats in forests: what we know and what we need to learn. In: Lacki, M.L., Hayes, J.P., Kurta, A. (Eds.), Bats in forests: conservation and management. Johns Hopkins, Baltimore, Maryland, USA, pp. 1–15.

Brigham, R. M., Grindal, S. D., Firman, M. C., & Morissette, J. L. (1997). The influence of structural clutter on activity patterns of insectivorous bats. Canadian journal of zoology, 75(1), 131-136.

Britzke, E. R., Duchamp, J. E., Murray, K. L., Swihart, R. K., & Robbins, L. W. (2011). Acoustic identification of bats in the eastern United States: A comparison of parametric and nonparametric methods. *The Journal of Wildlife Management*, *75*(3), 660–667. https://doi.org/10.1002/jwmg.68

Buchalski, M. R., Fontaine, J. B., Heady, P. A., Hayes, J. P., & Frick, W. F. (2013). Bat response to differing fire severity in mixed-conifer forest California, USA. *PLoS ONE*, *8*(3), e57884. https://doi.org/10.1371/journal.pone.0057884

Burford, L. S., Lacki, M. J., & Covell Jr., C. V. (1999). Occurrence of moths among habitats in a mixed mesophytic forest: implications for management of forest bats. *Forest Science*, *45*(3), 323–332.

Calderón-Capote, M. C., Dechmann, D. K., Fahr, J., Wikelski, M., Kays, R., & O'Mara, M. T. (2020). Foraging movements are density-independent among straw-coloured fruit bats. *Royal Society Open Science*, *7*(5), 200274.

Caldwell, K. L., Carter, T. C., & Doll, J. C. (2019). A comparison of bat activity in a managed central hardwood forest. *The American Midland Naturalist*, *181*(2), 225-244.

Campbell, J. W., Hanula, J. L., & Waldrop, T. A. (2007). Effects of prescribed fire and fire surrogates on floral visiting insects of the blue ridge province in North Carolina. *Biological Conservation*, *134*(3), 393-404.

Carr, A., Weatherall, A., & Jones, G. (2020). The effects of thinning management on bats and their insect prey in temperate broadleaved woodland. *Forest Ecology and Management*, *457*, 117682.

Cheng, T. L., Reichard, J. D., Coleman, J. T. H., Weller, T. J., Thogmartin, W. E., Reichert, B. E., Bennett, A. B., Broders, H. G., Campbell, J., Etchison, K., Feller, D. J., Geboy, R., Hemberger, T., Herzog, C., Hicks, A. C., Houghton, S., Humber, J., Kath, J. A., King, R. A., & Frick, W. F. (2021). The scope and severity of white-nose syndrome on hibernating bats in North America. *Conservation Biology*, *35*(5), 1586–1597. https://doi.org/10.1111/cobi.13739

Cornelison, C. T., Keel, M. K., Gabriel, K. T., Barlament, C. K., Tucker, T. A., Pierce, G. E., & Crow, S. A. (2014). A preliminary report on the contact-independent antagonism of *Pseudogymnoascus destructans* by *Rhodococcus rhodochrousstrain* DAP96253. *BMC Microbiology*, *14*(1), 246. https://doi.org/10.1186/s12866-014-0246-y

Cox, M. R., Willcox, E. V., Keyser, P. D., & Vander Yacht, A. L. (2016). Bat response to prescribed fire and overstory thinning in hardwood forest on the Cumberland Plateau, Tennessee. *Forest Ecology and Management*, *359*, 221-231.

De La Cruz, J.L., True, M., Taylor, H., Brown, D., & Ford, W.M. (2020). Occupancy and roost ecology of the northern long-eared and Indiana bat on the coastal plain of North Carolina. US Geological Survey Science Support Project G17AC00288 Final Report, Reston, VA, USA.

Denzinger, A., & Schnitzler, H. U. (2013). Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. Frontiers in physiology, 4, 164.

Dodd, L. E., Chapman, E. G., Harwood, J. D., Lacki, M. J., & Rieske, L. K. (2012). Identification of prey of *Myotis septentrionalis* using DNA-based techniques. *Journal of Mammalogy*, *93*(4), 1119–1128. https://doi.org/10.1644/11-MAMM-A-218.1

Dodd, L. E., Lacki, M. J., Britzke, E. R., Buehler, D. A., Keyser, P. D., Larkin, J. L., Rodewald, A. D., Wigley, T. B., Wood, P. B., & Rieske, L. K. (2012). Forest structure affects trophic linkages: How silvicultural disturbance impacts bats and their insect prey. *Forest Ecology and Management*, *267*, 262–270. https://doi.org/10.1016/j.foreco.2011.12.016

Dodd, L. E., Lacki, M. J., & Rieske, L. K. (2008). Variation in moth occurrence and implications for foraging habitat of Ozark big-eared bats. *Forest Ecology and Management*, *255*(11), 3866–3872. https://doi.org/10.1016/j.foreco.2008.03.034

Elmore, L. W., Miller, D. A., & Vilella, F. J. (2004). Selection of diurnal roosts by red bats (Lasiurus borealis) in an intensively managed pine forest in Mississippi. *Forest Ecology and Management*, *199*(1), 11–20. https://doi.org/10.1016/j.foreco.2004.03.045

Elmore, L. W., Miller, D. A., & Vilella, F. J. (2005). Foraging area size and habitat use by red bats (Lasiurus borealis) in an intensively managed pine landscape in Mississippi. *The American Midland Naturalist*, *153*(2), 405–417. https://doi.org/10.1674/0003-0031(2005)153[0405:FASAHU]2.0.CO;2

Fagan K.E., Willcox E.V., & Willcox A.S. (2018). Public attitudes toward the presence and management of bats roosting in buildings in Great Smoky Mountains National Park, Southeastern United States. Biological Conservation. 220(1), 132-139. DOI: 10.1016/j.biocon.2018.02.004

Fenton, M.B. (2003). Science and the conservation of bats: where to next? *Wildlife Society Bulletin*, *31*:6-15.

Fenton, M. B., & Bogdanowicz, W. (2002). Relationships between external morphology and foraging behaviour: bats in the genus Myotis. *Canadian Journal of Zoology*, *80*(6), 1004-1013.

Fleming, H. L., Jones, J. C., Belant, J. L., & Richardson, D. M. (2013). Multi-scale roost site selection by Rafinesque's Big-eared Bat (*Corynorhinus rafinesquii*) and southeastern myotis (*Myotis austroriparius*) in Mississippi. *The American Midland Naturalist*, *169*(1), 43–55. https://doi.org/10.1674/0003-0031-169.1.43

Foo, C. F., Bennett, V. J., Hale, A. M., Korstian, J. M., Schildt, A. J., & Williams, D. A. (2017). Increasing evidence that bats actively forage at wind turbines. *PeerJ*, *5*, e3985. https://doi.org/10.7717/peerj.3985

Ford, W. M., Menzel, M. A., Rodrigue, J. L., Menzel, J. M., & Johnson, J. B. (2005). Relating bat species presence to simple habitat measures in a central Appalachian forest. *Biological Conservation*, *126*(4), 528-539.

Ford, W. M., Menzel, J. M., Menzel, M. A., Edwards, J. W., & Kilgo, J. C. (2006). Presence and absence of bats across habitat scales in the upper coastal plain of South Carolina. *The Journal of Wildlife Management*, *70*(5), 1200-1209.

Frank, C. L., Michalski, A., McDonough, A. A., Rahimian, M., Rudd, R. J., & Herzog, C. (2014). The resistance of a North American bat species (*Eptesicus fuscus*) to white-nose syndrome (WNS). *PLoS One*, *9*(12), e113958.

Franklin, J.F., Johnson, K.N., & Johnson, D.L. (2018). Ecological forest management. Long Grove, Illinois: Waveland Press.

Frick, W. F. (2013). Acoustic monitoring of bats, considerations of options for long-term monitoring. *Therya*, *4*(1), 69-70.

Frick, W. F., Kingston, T., & Flanders, J. (n.d.). (2019) A review of the major threats and challenges to global bat conservation. *Annals of the New York Academy of Sciences*. 1469(1), 5-25. https://doi.org/10.1111/nyas.14045

Frick, W. F., Pollock, J. F., Hicks, A. C., Langwig, K. E., Reynolds, D. S., Turner, G. G., Butchkoski, C. M., & Kunz, T. H. (2010). An emerging disease causes regional population collapse of a common North American bat species. *Science*, *329*(5992), 679–682. https://doi.org/10.1126/science.1188594

Friedenberg, N. A., & Frick, W. F. (2021). Assessing fatality minimization for hoary bats amid continued wind energy development. *Biological Conservation*, *262*, 109309. https://doi.org/10.1016/j.biocon.2021.109309

Furmankiewicz, J., & Kucharska, M. (2009). Migration of bats along a large river valley in southwestern Poland. *Journal of Mammalogy*, *90*(6), 1310–1317.

Garin, I., Aihartza, J., Goiti, U., Arrizabalaga-Escudero, A., Nogueras, J., & Ibáñez, C. (2019). Bats from different foraging guilds prey upon the pine processionary moth. *PeerJ*, *7*, e7169. https://doi.org/10.7717/peerj.7169

Ghanem, S. J., & Voigt, C. C. (2012). Increasing Awareness of Ecosystem Services Provided by Bats. In *Advances in the Study of Behavior* (Vol. 44, pp. 279–302). Elsevier. https://doi.org/10.1016/B978-0-12-394288-3.00007-1

Gonçalves, F., Fischer, E., & Dirzo, R. (2017). Forest conversion to cattle ranching differentially affects taxonomic and functional groups of Neotropical bats. *Biological conservation*, *210,* 343–348.

Gooding, G., & Langford, J.R. (2004). Characteristics of tree roosts of Rafinesque's big-eared bat and southeastern bat in northeastern Louisiana. *Southwestern Naturalist*, *49*:61–67.

Grider, J. F., Larsen, A. L., Homyack, J. A., & Kalcounis-Rueppell, M. C. (2016). Winter Activity of Coastal Plain Populations of Bat Species Affected by White-Nose Syndrome and Wind Energy Facilities. *PLOS ONE*, *11*(11), e0166512. https://doi.org/10.1371/journal.pone.0166512

Grindal, S. D., & Brigham, R. M. (1999). Impacts of forest harvesting on habitat use by foraging insectivorous bats at different spatial scales. *Ecoscience*, *6*(1), 25–34.

Guldin, J.M. & Guldin, R.W. (2003). Forest management and stewardship, pp. 179-220, in Introduction to forest ecosystem science and management: third edition (R.A. Young and R.L. Giese, eds). John Wiley and Sons, New York.

Haddad, N.M., Tillman, D., Haarstad, J., Ritchie, M., & Knops, J.M. (2001). Contrasting effects of plant richness and composition on insect communities: a field experiment. *The American Naturalist, 158*:17–35.

Hartley, M. K., Rogers, W. E., Siemann, E., & Grace, J. (2007). Responses of prairie arthropod communities to fire and fertilizer: balancing plant and arthropod conservation. *The American Midland Naturalist*, *157*(1), 92–105.

Hodgkison, R., Balding, S. T., Zubaid, A., & Kunz, T. H. (2004). Temporal variation in the relative abundance of fruit bats (Megachiroptera: Pteropodidae) in relation to the availability of food in a lowland Malaysian rain forest. *Biotropica*, *36*(4), 522–533.

Humphrey, S.R. (1975). Nursery roosts and community diversity of nearctic bats. *Journal of Mammalogy*, *56*(2):321–346.

James, F. C., & Shugart Jr, H. H. (1970). A quantitative method of habitat description. *Audubon Field Notes*, *24*(6), 727–736.

Jantzen, M. K., & Fenton, M. B. (2013). The depth of edge influence among insectivorous bats at forest–field interfaces. *Canadian Journal of Zoology*, *91*(5), 287–292.

Johnson, S.A. & Hale, P.E. (2002). The historical foundations of prescribed burning for wildlife: a southeastern perspective. In: W.M. Ford, K.R Russell, C.E. Moorman (eds.), The role of fire in nongame wildlife management and community restoration: traditional uses and new directions. USDA Forest Service Gen. Technical Report NE-288:11–23.

Johnson, J. S., Lacki, M. J., Thomas, S. C., & Grider, J. F. (2012). Frequent arousals from winter torpor in Rafinesque's big-eared bat (Corynorhinus rafinesquii). PLoS ONE, 7(11), e49754. https://doi.org/10.1371/journal.pone.0049754

Johnson, J. S., Scafini, M. R., Sewall, B. J., & Turner, G. G. (2016). Hibernating bat species in Pennsylvania use colder winter habitats following the arrival of white-nose syndrome. In C. M. Butchkoski, D.M. Reeder, G.G. Turner, & H.P. Whidden (Eds.), *Conservation and ecology of Pennsylvania's bats*, 181–199.

Johnson, J. S., Treanor, J. J., Lacki, M. J., Baker, M. D., Falxa, G. A., Dodd, L. E., Waag, A. G., & Lee, E. H. (2016). Migratory and winter activity of bats in Yellowstone National Park. *Journal of Mammalogy*, gyw175. https://doi.org/10.1093/jmammal/gyw175

Jonason, D., Franzén, M., & Ranius, T. (2014). Surveying moths using light traps: effects of weather and time of year. *PLoS ONE*, *9*(3), e92453. https://doi.org/10.1371/journal.pone.0092453

Jorge, M. H., Ford, W. M., Sweeten, S. E., Freeze, S. R., True, M. C., St. Germain, M. J., & Cherry, M. J. (2021). Winter roost selection of Lasiurine tree bats in a pyric landscape. *PLoS One*, *16*(2), e0245695.

Kalcounis, M.C., Hobson, K.A., Brigham, R.M., & Hecker, K.R. (1999). Bat activity in the boreal forest: importance of stand type and vertical strata. *Journal of Mammalogy*, *80*:673–682.

Ketzler, L. P., Comer, C. E., & Twedt, D. J. (2017). Nocturnal insect availability in bottomland hardwood forests managed for wildlife in the Mississippi Alluvial Valley. *Forest Ecology and Management*, *391*, 127–134. https://doi.org/10.1016/j.foreco.2017.02.009

Knuff, A. K., Staab, M., Frey, J., Dormann, C. F., Asbeck, T., & Klein, A. M. (2020). Insect abundance in managed forests benefits from multi-layered vegetation. *Basic and Applied Ecology*, *48*, 124-135.

Kuenzi, A. J., & Morrison, M. L. (2003). Temporal patterns of bat activity in southern Arizona. *The Journal of wildlife management*, *67*, 52-64.

Kunberger, J. M., & Long, A. M. (2022). The influence of forest management practices on seasonal bat species occurrence and activity at the Kisatchie National Forest in Louisiana, USA. *Forest Ecology and Management*, *526*, 120579.

Kunz, T. H. (1988). Methods of assessing the availability of prey to insectivorous bats. In: T.H. Kunz (ed.), *Ecological and behavioral methods for the study of bats*. 191-210. Smithsonian Institution Press, Washington, D.C.

Lacki, M. J., Cox, D. R., Dodd, L. E., & Dickinson, M. B. (2009). Response of northern bats (*Myotis septentrionalis*) to prescribed fires in eastern Kentucky forests. *Journal of Mammalogy*, *90*(5), 1165-1175.

Lacki, M. J., Hayes, J. P., & Kurta, A. (2007) Bats in Forests: Conservation and Management. *John Hopkins University Press.* Baltimore, Maryland.

Lance, R.F., Hardcastle, B., Talley, A., & Leberg, P.L. (2001). Day-roost selection by Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) in Louisiana forests. *Journal of Mammalogy*, *82*:166-172.

Lara, W., Ordonez, C., & Bravo, F. (2021). *basifoR*: Retrieval and processing of the Spanish National Forest. https://cran.r-project.org/package=basifoR

Lemieux-Labonté, V., Dorville, N. A. Y., Willis, C. K., & Lapointe, F. J. (2020). Antifungal potential of the skin microbiota of hibernating big brown bats (*Eptesicus fuscus*) infected with the causal agent of white-nose syndrome. *Frontiers in Microbiology*, *11*, 1776.

Lim, Y. S., La, P. H., Park, J. S., Lee, M. H., Pyeon, M. W., & Kim, J.-I. (2015). Calculation of tree height and canopy crown from drone images using segmentation. *Journal of the Korean Society of Surveying, Geodesy, Photogrammetry and Cartography*, *33*(6), 605–614. https://doi.org/10.7848/ksgpc.2015.33.6.605

Loeb, S. C., & O'keefe, J. M. (2006). Habitat use by forest bats in South Carolina in relation to local, stand, and landscape characteristics. *The Journal of Wildlife Management*, *70*(5), 1210-1218.

Loeb, S. C., & Waldrop, T. A. (2008). Bat activity in relation to fire and fire surrogate treatments in southern pine stands. *Forest Ecology and Management*, *255*(8–9), 3185–3192. https://doi.org/10.1016/j.foreco.2007.10.060

Lundy, M., & Montgomery, I. (2010). Summer habitat associations of bats between riparian landscapes and within riparian areas. *European Journal of Wildlife Research*, *56*, 385-394.

Mager, K.J. & Nelson, T.A. (2001). Roost-site selection by eastern red bats (*Lasiurus borealis*). *American Midland Naturalist*, *145*:120-126.

McGavin, G.C. (2002). Smithsonian Handbooks: Insects. DK Publishing. *256*. ISBN-10: 0789493926.

McGuire, L. P., Guglielmo, C. G., Mackenzie, S. A., & Taylor, P. D. (2012). Migratory stopover in the long-distance migrant silver-haired bat, *Lasionycteris noctivagans*. *Journal of Animal Ecology*, *81*(2), 377–385. https://doi.org/10.1111/j.1365-2656.2011.01912.x

Menzel, J. M., Menzel Jr, M. A., Kilgo, J. C., Ford, W. M., Edwards, J. W., & McCracken, G. F. (2005). Effect of habitat and foraging height on bat activity in the coastal plain of South Carolina. *The Journal of Wildlife Management*, *69*(1), 235-245.

Menzel, M. A., Krishon, D. M., Carter, T. C., & Laerm, J. (1999). Notes on tree roost characteristics of the northern yellow bat (*Lasiurus intermedius*), the seminole bat (*L. Seminolus*), the evening bat (*Nycticeius humeralis*), and the eastern pipistrelle (*Pipistrellus subflavus*). *Biological Sciences*, *62*(3–4), 185–193.

Miles, A. C., Castleberry, S. B., Miller, D. A., & Conner, L. M. (2006). Multi-scale roost-site selection by evening bats on pine-dominated landscapes in southwest Georgia. *Journal of Wildlife Management*, *70*(5), 1191–1199. https://doi.org/10.2193/0022-541X(2006)70[1191:MRSBEB]2.0.CO;2

Miller, D. A. (2003). Species diversity, reproduction, and sex ratios of bats in managed pine forest landscapes of Mississippi. *Southeastern Naturalist*, *2*(1), 59–72. https://doi.org/10.1656/1528-7092(2003)002[0059:SDRASR]2.0.CO;2

Millon, L., Colin, C., Brescia, F., & Kerbiriou, C. (2018). Wind turbines impact bat activity, leading to high losses of habitat use in a biodiversity hotspot. *Ecological Engineering*, *112*, 51–54. https://doi.org/10.1016/j.ecoleng.2017.12.024

Mississippi Bat Working Group (2020). Mississippi Bat Conservation Strategy. Mississippi Bat Working Group. Jackson, Mississippi. https://msbats.org/wp-content/uploads/MSBatConservationStrategy20200810.pdf

Muirhead-Thompson, R. C. (2012). Trap responses of flying insects: the influence of trap design on capture efficiency. Academic Press, London, 287 pp. ISBN 0-12-509755-7.

Müller, J., Mehr, M., Bässler, C., Fenton, M. B., Hothorn, T., Pretzsch, H., ... & Brandl, R. (2012). Aggregative response in bats: prey abundance versus habitat. *Oecologia*, *169*, 673-684.

Norberg, U. M., & Rayner, J. M. (1987). Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *316*(1179), 335-427.

O'Shea, T. J., Cryan, P. M., Hayman, D. T., Plowright, R. K., & Streicker, D. G. (2016). Multiple mortality events in bats: a global review. *Mammal Review*, *46*(3), 175-190.

Ober, H. K., & Hayes, J. P. (2008). Influence of vegetation on bat use of riparian areas at multiple spatial scales. *Journal of Wildlife Management*, *72*(2), 396–404. https://doi.org/10.2193/2007-193

Ober, H. K., & Hayes, J. P. (2008). Prey selection by bats in forests of western Oregon. *Journal of Mammalogy*, *89*(5), 1191-1200.

Owen, S. F., Menzel, M. A., Edwards, J. W., Ford, W. M., Menzel, J. M., Chapman, B. R., & Miller, K. V. (2004). Bat activity in harvested and intact forest stands in the Allegheny Mountains. *Northern Journal of Applied Forestry*, *21*(3), 154-159.

Padgett, T.M. & Rose, R.K. (1991). Bats (Chiroptera: Vespertilionidae) of the Great Dismal Swamp of Virginia and North Carolina. *Brimleyana*, *17*:17-25.

Parsons, S., & Szewczak, J. (2009). Detecting, recording and analysing the vocalisations of bats. *Ecological and behavioral methods for the study of bats*, *2nd edition*, 91-111.

Patriquin, K. J., & Barclay, R. M. (2003). Foraging by bats in cleared, thinned and unharvested boreal forest. *Journal of Applied Ecology*, *40*(4), 646-657.

Perea, S., Yearout, J., Ferrall, E., Morris, K., Pynne, J., & Castleberry, S. (2022). Seven-year impact of white-nose syndrome on tri-colored bat (*Perimyotis subflavus*) populations in Georgia, USA. *Endangered Species Research*, *48*, 99–106. https://doi.org/10.3354/esr01189

Perry, R. W., & Thill, R. E. (2007). Roost characteristics of hoary bats in Arkansas. *The American Midland Naturalist*, *158*(1), 132–138. https://doi.org/10.1674/0003-0031(2007)158[132:RCOHBI]2.0.CO;2

Person, P. (1961). Fish and Wildlife Service. *The Journal of the American Dental Association*, *62*(2), 260–261. https://doi.org/10.14219/jada.archive.1961.0023

Peterson, M.S., Waggy, G.L., & Woodrey, M.S. (2007). Grand Bay National Estuarine Research Reserve: An Ecological Characterization. Grand Bay National Estuarine Research Reserve, Moss Point, Mississippi, (268).

Puig-Montserrat, X., Flaquer, C., Gómez-Aguilera, N., Burgas, A., Mas, M., Tuneu, C., Marquès, E., & López-Baucells, A. (2020). Bats actively prey on mosquitoes and other deleterious insects in rice paddies: Potential impact on human health and agriculture. *Pest Management Science*, *76*(11), 3759–3769. https://doi.org/10.1002/ps.5925

Redgwell, R. D., Szewczak, J. M., Jones, G., & Parsons, S. (2009). Classification of echolocation calls from 14 species of bat by support vector machines and ensembles of neural networks. *Algorithms*, *2*(3), 907-924.

Rodewald, A. D., & Abrams, M. D. (2002). Floristics and avian community structure: implications for regional changes in eastern forest composition. *Forest Science*, *48*(2), 267-272.

Ruadreo, N., Voigt, C. C., & Bumrungsri, S. (2018). Large dietary niche overlap of sympatric open-space foraging bats revealed by carbon and nitrogen stable isotopes. *Acta Chiropterologica*, *20*(2), 329-341.

Russo, L., Stehouwer, R., Heberling, J. M., & Shea, K. (2011). The composite insect trap: an innovative combination trap for biologically diverse sampling. *PLoS ONE*, *6*(6), e21079. https://doi.org/10.1371/journal.pone.0021079

Sandel, J. K., Benatar, G. R., Burke, K. M., Walker, C. W., Lacher, T. E., & Honeycutt, R. L. (2001). Use and selection of winter hibernacula by the eastern pipistrelle (*Pipistrellus subflavus*) in Texas. *Journal of Mammalogy*, *82*(1).

Salcedo, H. D. L. C., Fenton, M., Hickey, M., & Blake, R. (1995). Energetic consequences of flight speeds of foraging red and hoary bats (*Lasiurus borealis* and *Lasiurus cinereus*; Chiroptera: Vespertilionidae). *The Journal of Experimental Biology*, *198*(11), 2245-2251.

Saugey, D.A., Crump, B.G., & Heidt, G.A. (1998). Notes on the natural history of *Lasiurus borealis* in Arkansas. *Journal of the Arkansas Academy of Science*, 52:92-98.

Sleep, D. J., & Brigham, R. M. (2003). An experimental test of clutter tolerance in bats. *Journal of Mammalogy*, *84*(1), 216-224.

Smith, D. A., & Gehrt, S. D. (2010). Bat response to woodland restoration within urban forest fragments. *Restoration Ecology*, *18*(6), 914-923.

Stephens, S.L., Mclver, J.D., Boerner, R.E.J., Fettig, C.J., Fontaine, J.B., Hartsough, B.R., Kennedy, P.L., & Schwilk D.W. (2012). Effects of forest fuel-reduction treatments in the United States. *Bioscience*, 63:549-560.

Szewczak, J.M., Corcoran, A., Kennedy, J.P., Ormsbee, P.C., & Weller, T.J. (2011). Echolocation call characteristics of eastern US bats. Humbolt State University Bat Lab. https://www.sonobat.com/download/EasternUS_Acoustic_Table_Mar2011.pdf

Taylor, P. D., Mackenzie, S. A., Thurber, B. G., Calvert, A. M., Mills, A. M., McGuire, L. P., & Guglielmo, C. G. (2011). Landscape movements of migratory birds and bats reveal an expanded scale of stopover. *PLoS ONE*, *6*(11), e27054. https://doi.org/10.1371/journal.pone.0027054

Taylor, P. J., Monadjem, A., & Nicolaas Steyn, J. (2013). Seasonal patterns of habitat use by insectivorous bats in a subtropical African agro-ecosystem dominated by macadamia orchards. *African Journal of Ecology*, *51*(4), 552-561.

Thompson, M., Beston, J. A., Etterson, M., Diffendorfer, J. E., & Loss, S. R. (2017). Factors associated with bat mortality at wind energy facilities in the United States. *Biological Conservation*, *215*, 241–245. https://doi.org/10.1016/j.biocon.2017.09.014

Tibbels, A. E., & Kurta, A. (2003). Bat activity is low in thinned and unthinned stands of red pine. *Canadian Journal of Forest Research*, *33*(12), 2436–2442. https://doi.org/10.1139/x03-177

Titchenell, M. A., Williams, R. A., & Gehrt, S. D. (2011). Bat response to shelterwood harvests and forest structure in oak-hickory forests. *Forest Ecology and Management*, *262*(6), 980–988. https://doi.org/10.1016/j.foreco.2011.05.032

Tripplehorn, C.A., & Johnson, N.F., Editors. (2005). Borror and DeLong's introduction to the study of insects. Seventh edition. Thomson Brooks/Cole, Belmont, CA.

Trousdale, A. W., & Beckett, D. C. (2005). Characteristics of tree roosts of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) in Southeastern Mississippi. *The American Midland Naturalist*, *154*(2), 442–449. https://doi.org/10.1674/0003-0031(2005)154[0442:COTROR]2.0.CO;2

US Fish and Wildlife Services. (2022). Proposed Rules. Federal Register, *87*(177), 56381-56393. https://www.fws.gov/sites/default/files/federal_register_document/2022-18852.pdf

Vaughan, N., Jones, G., & Harris, S. (1997). Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. *Journal of Applied Ecology*, 716-730.

Verboom, B., & Spoelstra, K. (1999). Effects of food abundance and wind on the use of tree lines by an insectivorous bat, *Pipistrellus pipistrellus*. *Canadian Journal of Zoology*, *77*(9), 1393-1401.

Waters, D. A., Rydell, J., & Jones, G. (1995). Echolocation call design and limits on prey size: a case study using the aerial-hawking bat *Nyctalus leisleri*. *Behavioral Ecology and Sociobiology*, *37*, 321-328.

Węgiel, A., Grzywiński, W., Ciechanowski, M., Jaros, R., Kalcounis-Rüppell, M., Kmiecik, A., & Węgiel, J. (2019). The foraging activity of bats in managed pine forests of different ages. *European Journal of Forest Research*, *138*, 383-396.

Whitaker Jr, J. O. (1994). Food availability and opportunistic versus selective feeding in insectivorous bats. *Bat Research News*, *35*, 75-77.

Whitaker, J. O. (2004). Prey selection in temperate zone insectivorous bat community. *Journal of Mammalogy*, *85*(3), 460–469.

White, P. J. T., Glover, K., Stewart, J., & Rice, A. (2016). The technical and performance characteristics of a low-cost, simply constructed, black light moth trap. *Journal of Insect Science*, *16*(1), 25. https://doi.org/10.1093/jisesa/iew011

Yates, M. D., & Muzika, R. M. (2006). Effect of forest structure and fragmentation on site occupancy of bat species in Missouri Ozark forests. *Journal of Wildlife Management*, *70*(5), 1238–1248. https://doi.org/10.2193/0022-541X(2006)70[1238:EOFSAF]2.0.CO;2