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# BAT, INSECT PREY, AND VEGETATION RESPONSE TO PRESCRIBED FIRE AND OVERSTORY THINNING IN HARDWOOD FORESTS OF TENNESSEE

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To the Graduate Council:

I am submitting herewith a thesis written by Maxwell Rambeau Cox entitled "BAT, INSECT PREY, AND VEGETATION RESPONSE TO PRESCRIBED FIRE AND OVERSTORY THINNING IN HARDWOOD FORESTS OF TENNESSEE." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Wildlife and Fisheries Science.

Emma V. Willcox, Major Professor

We have read this thesis and recommend its acceptance:

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# BAT, INSECT PREY, AND VEGETATION RESPONSE TO PRESCRIBED FIRE AND OVERSTORY THINNING IN HARDWOOD FORESTS OF TENNESSEE

**A Thesis Presented for the**
**Master of Science**
**Degree**
**The University of Tennessee, Knoxville**

**Maxwell Rambeau Cox**
**August 2015**

# DEDICATION

I dedicate this thesis to my wife, Erin, for her love, support, and encouragement throughout my masters, and to my mother and father who taught me to love the outdoors.

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# ABSTRACT

This master's thesis investigates the effects of prescribed fire and overstory thinning on bats and their insect prey in upland hardwood forest stands of Tennessee's Cumberland Plateau. Chapter 1 is a literature review that emphasizes the importance of this research and outlines the objectives and study area for this project. Chapter 2 examines the effect of prescribed fire and overstory thinning on the abundance and biomass of nocturnal flying insects important in the diet of bats. Overall, I found prescribed fire and overstory thinning had little effect on abundance and biomass of nocturnal flying insects, despite changes in vegetation community composition and structure. Chapter 3 examines the effect of prescribed fire and overstory thinning on bat activity. I found activity of bats was greater in hardwood forest stands subject to spring or fall fire in combination with high levels of overstory thinning. This greater activity was tied to reductions in live overstory basal area. My results suggest basal area reductions reduce clutter (physical obstructions to flight and foraging including foliage, branches, and stems), leading to improved foraging and commuting conditions for bats, particularly larger bodied species with lower call frequencies that are adapted to more easily and successfully fly and forage in open conditions.

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# CHAPTER I

# GENERAL INTRODUCTION

## Background

Historically, fire played a critical role in regulating and maintaining the hardwood systems of the Southeastern U.S., including those in Tennessee’s Cumberland Plateau, by creating disturbance that altered forest species composition and structure. However, over the past century, fire suppression in these historically fire-adapted systems has allowed the encroachment of fire-intolerant species and compromised regeneration of once dominant plants, particularly oaks. The resulting loss of important ecosystem elements and creation of a homogeneous, closed-canopy forest structure have led to declines in numerous plant and animal species and diminished wildlife habitat value. Therefore, in more recent years, land managers have increased their use of spring and fall prescribed fire in hardwood forests across the region, both as a fuel reduction treatment and in an attempt to restore the more open woodland and savanna conditions that existed before fire suppression. Prescribed fire is frequently used in combination with overstory thinning to speed up the restoration process by allowing light infiltration that stimulates oak regeneration and the growth of herbaceous plant species (Delecourt and Delecourt 1998, Brose et al. 2001, Brose et al. 2012, Vander Yacht 2013).

The use of prescribed fire and overstory treatments in Tennessee and other Southeastern states as fuel reduction and restoration treatments can modify habitat conditions for numerous wildlife species, including bats. Bats play a significant role in forest ecosystems in North America as a primary predator of nocturnal flying insects, particularly moths (Lepidoptera), beetles (Coleoptera), and true bugs (Hemiptera; Whitaker 1995, Fenton 2003, Lacki et al. 2007). As a result, they can help control and minimize the damage caused by forest pests (Taylor 2006). A big brown bat (*Eptesicus* *fuscus*) colony of 150 individuals in Indiana has been estimated to eat almost 1.3 million insects each year, the majority of which are considered agricultural crop pests. These pests include scarab beetles (Scarabaeidae), the spotted cucumber beetle (*Diabrotica undecimpunctata*, Chrysomelidae), stinkbugs (Pentatomidae), and leafhoppers (Cicadellidae; Whitaker 1995). Boyles et al. (2011) estimated the value of bats to the agricultural industry of the United States, primarily through pest control, at roughly $22.9 billion per year.

Unfortunately, North American bat populations are facing a conservation crisis of unprecedented magnitude because of the cumulative effects of multiple threats. The spread of wind energy installations (i.e., wind turbines) across the U.S. is causing increased mortality of numerous bat species, particularly migratory tree roosting bats such as the eastern red bat *(Lasiurus borealis)*, hoary bat (*Lasiurus cinereus*), and silver-haired bat (*Lasionycteris noctivagans*; Cryan and Barclay 2009). Tennessee is home to the only wind farm in the southeastern US (Southern Alliance for Clean Energy, 2014), the Buffalo Mountain Wind Energy Center in Anderson County, which impacts bats in the state (Fiedler et al. 2007). It is hypothesized that bat mortality at wind energy installations may be a result of bats being attracted to the lights or sounds associated with the turbines and colliding with their blades or towers (Cryan and Barclay 2009). An alternative hypothesis proposes that, as a result of a change in barometric pressure close to the blades, bats approaching turbines suffer fatal internal injuries to the thoracic and abdominal cavities consistent with rapid decompression, or baro-trauma. Regardless the cause of death, by 2020 it is estimated 33,000 to 111,000 bats will be killed annually by wind turbines (Boyles et al. 2011).

Although wind energy installations pose a significant danger to bat populations, the greater immediate threat to this taxon is White-nose Syndrome (WNS), a disease caused by the fungal pathogen *Pseudogymnoascus destructans* (Pd; Minnis and Lindner 2013), which, since 2006, has killed more than 5.7 million cave-hibernating bats across 26 states and 5 Canadian provinces (U. S. Fish and Wildlife Service [USFWS] 2015). WNS was discovered in the winter of 2006/07 in a cave in Schoharie County, New York and is currently known to infect seven, of the ten, cave roosting bat species including the endangered Indiana bat (*Myotis sodalis*,) and gray bat (*Myotis grisescens*), and threatened northern long-eared bat (*Myotis septentrionalis*), as well as the eastern small-footed bat (*Myotis leibii*), little brown bat (*Myotis lucifugus*), tri-colored bat (*Perimyotis subflavus*), and big brown bat. Five additional bat species (Southeastern bat [*Myotis austroriparius*], Rafinesque's big-eared bat [*Corynorhinus rafinesquii*], Eastern red bat, and silver-haired bat, two of which are migratory tree roosters, and one endangered sub-species (Virginia big-eared bat [*Corynorhinus townsendii virginianus*])) have been found with Pd (Reeder et al. 2012, Bernard et al. 2015). WNS was confirmed in Tennessee during the winter of 2009/10 (Carr et al. 2014).

Pd causes WNS in bats by invading the skin's epidermis, connective tissue, and glands during winter hibernation. Although the complete pathogenesis of the disease is still emerging, it appears it likely causes mortality by forcing bats to consume critical body reserves needed to survive this season (Storm and Boyles 2010, Warnecke et al. 2012, Verant et al. 2014), disrupting normal physiological process such as water balance (Cryan et al. 2010) and/or preventing gas exchange across the wing membranes resulting in severe acidosis (Verant et al. 2014). Laboratory studies indicate that death frequently occurs within 2-3 months of initial fungal infection (Warnecke et al. 2012). If bats survive WNS during hibernation, they often go on to suffer from Immune Reconstitution Inflammatory Syndrome, displaying intense inflammation at Pd infection sites and severe wing damage (Meteyer et al. 2012). Clinical signs of WNS infection in some bat species include the presence of the white fungus on the nose, wings, or ears during hibernation; emaciation; and damaged and scarred wings. In addition, individuals of some species develop a number of aberrant behaviors, including altered torpor patterns, increased frequency of emergence from hibernacula, and changes in roosting location and sociality (Blehert et al. 2009, Boyles and Willis 2010, Cryan et al. 2010, Reeder et al. 2012, Warnecke et al. 2012, Wilcox et al. 2014, Carr et al. 2014). If WNS persists, it could result in declines in the populations of 25 species of hibernating bats and threaten numerous once abundant colonial, cave-hibernating bat species with extinction (Frick et al. 2010). In addition, climate change, habitat destruction, and environmental contaminants, the effects of which are difficult to quantify, all threaten multiple bat species (Hutson et al 2001, Racey and Entwistle 2003, Weller et al. 2009).

Sixteen species of bat occur in Tennessee including Indiana bat, gray bat, northern long-eared bat, little brown bat, eastern small-footed bat, tricolored bat, big brown bat, Southeastern bat, eastern red bat, silver-haired bat, Townsend’s big-eared bat (*Corynorhinus townsendi*), Rafinesque’s big-eared bat, Seminole bat (*Lasiurus seminolus*), evening bat (*Nycticeius humeralis*), and Brazillian free-tailed bat (*Tadarida brasiliensis*). Of these, 3 species (Indiana bat, gray bat, and Townsend’s big eared bat) are federally listed as endangered, 1 species (northern long-eared bat) is listed as federally threatened, and 2 species (little brown bat and tricolored bat) are being considered for possible federal listing (USFWS 2015). Many of these bat species are forest-dwelling, utilizing hardwood systems for foraging, especially during the late spring, summer, and early fall pre/post-hibernation and maternity periods. This is an exceptionally important time in the life-history of bats because of the energetics associated with reproduction and entering and recovering from hibernation. Therefore managing hardwood forests to provide suitable foraging conditions during this period may be critical for population persistence and species recovery (Johnson et al. 2010). This is especially true in the forested regions of Tennessee that are in close proximity to major cave hibernacula infected with WNS and where a number of species subject to mortality at wind turbine facilities are found. Prescribed fires and overstory thinning in this region may benefit bat species by enhancing foraging conditions through changes in forest structure and increased insect nocturnal prey abundance and biomass (Humes et al.1999, Lacki et al. 2009, Armitage and Ober 2012).

The historical forest structure to which many of Tennessee's bats are likely adapted included substantial components of more disturbed open stands, the sparse canopies of which were maintained by wildfires, insect outbreaks, ice storms, and high wind events (Brose et al. 2001, USFWS 2013). In flight, bats must contend with physical obstructions that impede flight such as foliage, branches, and stems. Collectively, these forest structures and related obstructions are referred to as clutter. More disturbed open stands have less clutter than do those that have experienced little disturbance and are more closed. A bat's ability to maneuver in clutter and capture insect prey depends on a number of factors including body size and wing morphology, particularly wing aspect ratio (AR; length of the wing squared divided by its surface area) and wing loading (WL;

mass of the bat divided by its total wing area). Larger-bodied bat species with high WLs or ARs tend to be less maneuverable and more adapted to flight in more open, less cluttered areas than smaller-bodied bat species with low WLs or ARs, which exhibit greater maneuverability and are more able to use foraging space that is cluttered with vegetation (Findley and Black 1983, Aldridge and Rautenbach 1987, Crome and Richards 1988; Kalcounis et al. 1999, Kingston et al. 2000, Lee and McCracken 2004). A bat's capacity to maneuver in and capture insect prey in clutter also depends on its echolocation call capabilities. The structure of search-phase calls emitted by bats when looking for prey are related to habitat and foraging strategy (Schnitzler and Kalko 1998). Low frequency, narrow bandwidth calls are effective at detecting objects at long distances, but are confounded by even low degrees of clutter. Alternatively, high-frequency, broad-bandwidth calls are effective at detecting objects at short distances and can contend with higher degrees of clutter (Aldridge and Rautenbach 1987, Crome and Richards 1988). Therefore, species with narrowband calls of low frequency are more suited to open locations (Neuweiler 1983). In contrast, species with broadband calls of high frequency are better suited to foraging in more cluttered forest locations (Simmons and Stein 1980). All this said, the majority of bat species in North America avoid using highly cluttered habitat. For example, little brown bats forage most frequently in areas with low levels of clutter (Adams 1997) despite having low WLs, and ARs and relatively high frequency calls.

Prescribed fire in combination with overstory thinning can mimic historical disturbance regimes in hardwood stands and enhance foraging conditions for some bat species by reducing structural clutter and creating an open stand for foraging. Little brown bats have been found to forage more in burned stands than unburned stands of mixed hardwood forest, with differences attributed to the less cluttered canopies occurring in burned areas (Lacki et al. 2009). Other studies examining the effects of fire on bats have mostly been conducted in pine forests. Bat activity was higher in recently burned Florida longleaf pine-wiregrass stands and was positively associated with height of canopy closure, suggesting benefits to certain species of reduced clutter. Activity levels of poorly maneuverable bats with high wing loadings and aspect ratios declined below the canopy with increasing time between fire due to the development of a hardwood midstory and increased clutter (Armitage and Ober 2012). Humes et al. (1999) found bat activity was higher in thinned Douglas fir (*Pseudotsuga menziesii*) stands than un-thinned stands of the same age. They concluded that the structural changes resulting from thinning may benefit bats by creating a habitat structure they are able to use more effectively. Loeb and Waldrop (2008) also found that total bat activity was higher in thinned southern pine stands than in control stands, but stands that were burned and thinned didn’t vary from that of controls. However, thinning of red pine (*Pinus resinosa*) stands in Michigan did not lead to an increase in their use by bats, despite significant changes in their structural complexity. It was suggested that, even after thinning, red pine plantations are too structurally complex for use by foraging bats (Tibbels and Kurta 2003). Another study, conducted in boreal forest, also found thinning had minimal effect on habitat use by bats. However, this study did emphasize the practice may have different effects on different species that may be obscured if the community is studied as a single entity (Patriquin and Barclay 2003).

Prey availability may alternatively or additionally shape habitat quality for bats. Therefore, prescribed fire in combination with overstory thinning in hardwood stands may also affect bat populations by altering food availability. Many insect groups decline immediately after and for a short time (1-2 months) following fire, with the magnitude of the decline closely related to the intensity of the fire and the proximity of insects to the flame (Swengel 2001). In the longer-term (<2 months) insect response appears to be highly variable. Some studies indicate insect orders such as the grasshoppers (Orthoptera), true flies (Diptera), and beetles respond positively to fire in the long-term and increase in abundance following prescribed fire, while others such as the true bugs (Hemiptera) respond negatively (Swengel 2001, Lacki et al. 2009). However, another study found few differences in abundance or biomass of most insect orders with the exception of the Lepidoptera, which had a lower biomass on sites subject to frequent fire (Armitage and Ober 2012). The effect of overstory thinning on insects is also highly variable depending on the intensity of tree removal. According to Grindal and Brigham (1998), when patches of trees are removed in areas of 0.5 ha, 1.0 ha, and 1.5 ha, insect availability is unaffected and remains similar to that of un-cut areas. However, Burford et al. (1999) reported there was lower insect availability, particularly moths, in cleared areas with no trees compared to that of moderately mature (30-59 years old) or mature (>60 years old) stands. Examination of fecal samples of northern long-eared bat in hardwood forest found lepidopterans, coleopterans, and dipterans are the three most important groups of insect prey to this species, with consumption of dipterans increasing following fire (Lacki et al. 2009). This species appears to shift the location of its foraging activity to track changes in insect availability (Lacki et al. 2009), suggesting changes in insect prey availability following prescribed fire and overstory thinning treatments may be important to foraging bats.

The limited knowledge on the effects of prescribed fire and overstory thinning in upland hardwood forest limits mangers ability to implement these treatments to benefit bats in conservation need. Therefore, the goal of my study was to examine the effects of prescribed fire (i.e., fall and spring prescribed fire) and overstory thinning treatments (i.e., savanna and woodland) on bat foraging behavior in upland hardwood forest of Tennessee's Cumberland plateau during late spring and summer. My study results are likely to be important to the effective management of bats in such forests.

## Study Objectives

The objectives of my study were to:

1. Examine the impact of prescribed fire and overstory thinning on upland hardwood forest clutter (structural complexity).
2. Determine how abundance and biomass of nocturnal flying insects differs in response to prescribed fire and overstory thinning in upland hardwood forest.
3. Assess the effects of prescribed fire and overstory thinning treatments on bat activity (i.e., relative use of an area for foraging and commuting) in upland hardwood forest.
4. Explore the relative contributions of nocturnal flying insect prey availability and upland hardwood forest structural complexity in explaining bat activity in hardwood forest.

I address these objectives in the subsequent 2 chapters. Chapter 2 examines the effects of prescribed fire and overstory thinning of upland hardwood forests on nocturnal flying insects important in the diet of bats and Chapter 3 examines bat response to prescribed fire and overstory thinning in upland hardwood forest.

## Study Area

I conducted my research at Catoosa Wildlife Management Area (CWMA), managed by the Tennessee Wildlife Resources Agency (TWRA) which encompasses 32,374 ha in Cumberland, Morgan, and Fentress Counties, TN (Figure 1.1), within the Cumberland Plateau and Mountainous physiographic province (DeSelm 1994). During spring of 2008, 10 research stands were delineated at CWMA. These stands were configured to minimize topographic variation and maximize core area. Using a completely randomized design with two replicates, we assigned one of 4 prescribed fire and overstory thinning treatments to 8 stands: spring prescribed fire and low overstory thinning (woodland with a target residual basal area of 14 m$^2$ha$^1$; SpL), spring prescribed fire and high overstory thinning (savanna with a target residual basal area of 7 m$^2$ha$^{-1}$; SpH), fall prescribed fire and low overstory thinning (FaL), and fall prescribed fire and high overstory thinning (FaH). The remaining 2 stands were left as untreated controls (Figure 1.2).

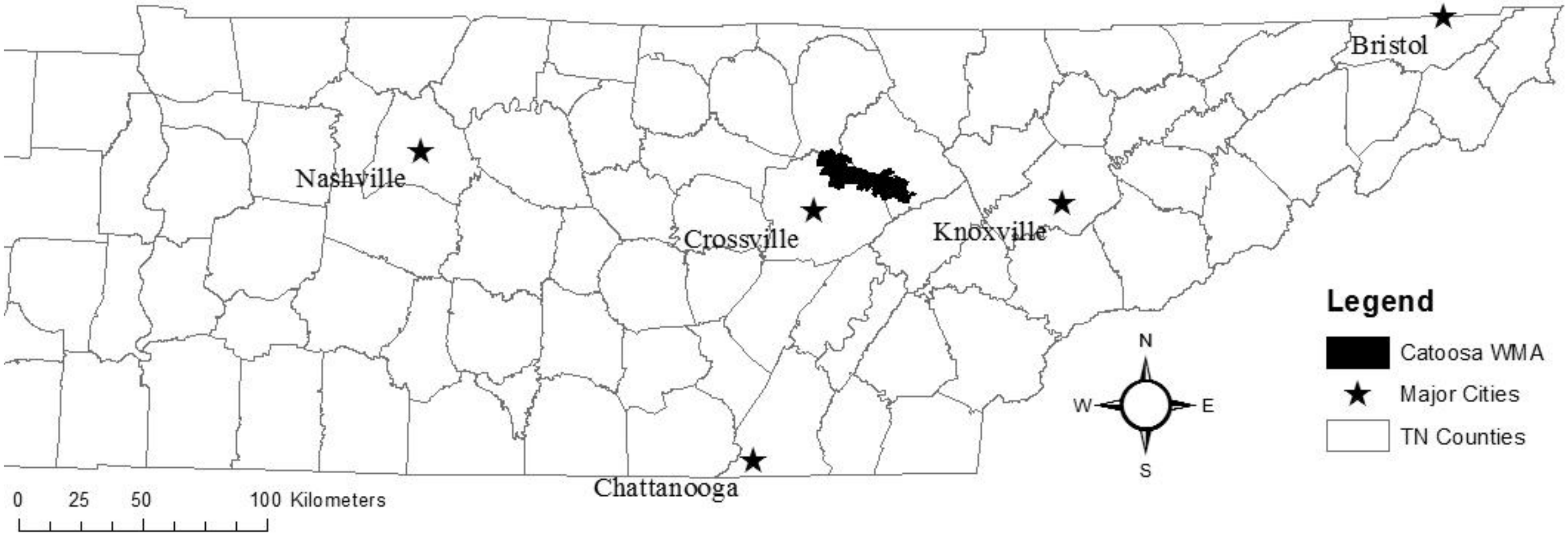

Figure 1.1: Catoosa Wildlife Management Area, Cumberland, Morgan, and Fentress Counties, Tennessee, USA, the location of a study examining bat response to prescribed fire and overstory thinning in hardwood forest stands, 2013−2014.

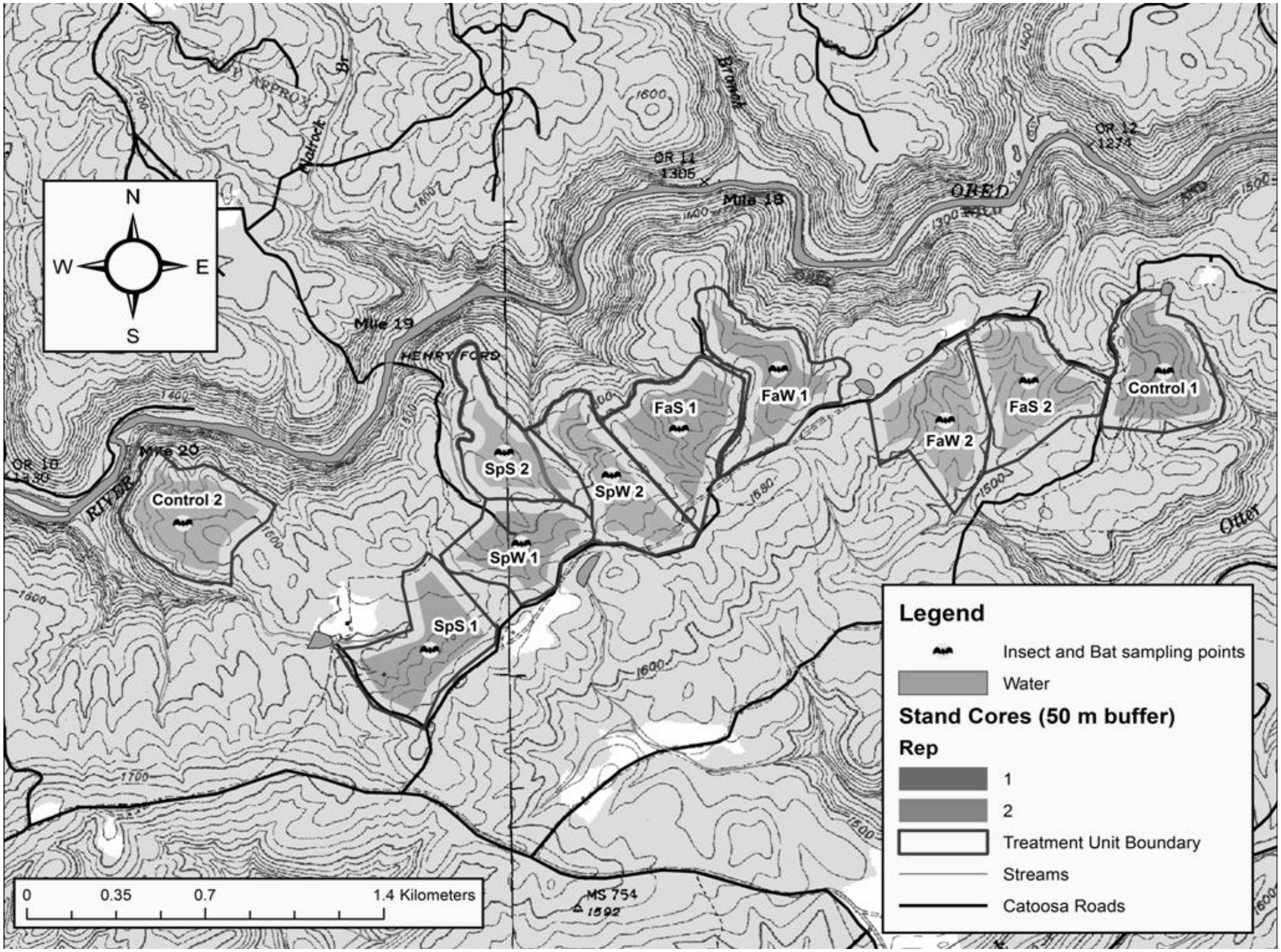

Figure 1.2: Layout of 10 20-ha experimental hardwood forest stands, used to examine bat response to prescribed fire and overstory thinning, at Catoosa Wildlife Management Area, Cumberland County, TN, USA 2013−2014

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# CHAPTER II

# THE EFFECTS OF PRESCRIBED FIRE AND OVERSTORY THINNING OF HARDWOOD FORESTS IN THE CUMBERLAND PLATEAU ON NOCTURNAL FLYING INSECTS IMPORTANT IN THE DIET OF BATS

This chapter is slightly modified from a manuscript that is being prepared for submission and potential publication:

Cox, M.R., E.V. Willcox, P.D. Keyser, and A.L. Vander Yacht, The Effects of Prescribed Fire and Overstory Thinning of Hardwood Forests in The Cumberland Plateau on Nocturnal Flying Insects Important in The Diet of Bats

My consistent use of "we" throughout this chapter is in reference to my co-authors and myself. I was the primary contributor to this work, which involved the following tasks: (1) development of project design and all data collection, (2) acoustic and statistical analyses, (3) gathering and interpretation of the relevant literature, and (4) all writing.

## ABSTRACT

All bats inhabiting hardwood forest systems of the Southeastern U.S. are insectivorous. Insect prey availability can be influenced by prescribed fire and overstory thinning treatments being used across the region, including the Cumberland Plateau of Tennessee, to create and restore the open woodland and savanna conditions that historically existed. Adequate prey availability following these treatments is important to the reproduction and survival of bats, particularly those threatened by the fungal disease White-nose Syndrome. Therefore, we examined abundance and biomass of nocturnal flying insects in upland hardwood forest stands subject to 4 prescribed fire and overstory thinning treatments (spring fire with high [SpH] and low overstory thinning [SpL], and fall fire with high [FaH] and low overstory thinning [FaL]), as well as untreated controls. We found treatments had no effect on abundance or biomass of Coleoptera, Diptera, or Lepidoptera ($P \geq 0.220$). Abundance of Other (Blattodea, Ephemeroptera, Hymenoptera, Neuroptera, Odonata, Orthoptera, Plecoptera, Trichoptera combined) was lower in FaH stands ($P = 0.024$). Abundance of Hemiptera was affected by treatment*year ($P = 0.014$) and treatment*sample period ($P = 0.032$) interactions, being lower on FaH stands than controls in 2013 and fluctuating in SpL, SpH, and FaH stands compared to controls in some sample periods. However, overall, abundance and biomass of insects were not affected by treatments, despite changes in plant community composition and structure, including lower live overstory basal area (*P* = 0.09) and greater understory density (*P* = 0.037) and percent cover of litter and coarse woody debris (*P* ≤ 0.001), forbs (*P* = 0.004), graminoids (*P* ≤ 0.001), and woody vegetation (*P* ≤ 0.001) in some treatment stands compared to controls. These results suggest, at least in our study area, that the availability of nocturnal flying insect prey important in the diet of bats is not influenced by the implementation of prescribed fire and overstory thinning treatments.

## INTRODUCTION

Across the Southeastern U.S., including the Cumberland Plateau of Tennessee, prescribed fire and overstory thinning are being increasingly used in upland hardwood forest systems to create and restore the open woodland and savanna conditions that historically existed in the region. The use of these treatments in combination, rather than the application of prescribed fire alone, speeds up the restoration process by increasing light infiltration that stimulates oak regeneration and the growth of herbaceous plant species (Delecourt and Delecourt 1998, Brose et al. 2001, Brose et al. 2012, Vander Yacht 2013).

Insects play a critical role in upland hardwood forests as a food source for numerous wildlife species, including bats, and can be influenced by prescribed fire and overstory thinning treatments (Grindal and Brigham 1998, Burford et al. 1999, Swengel 2001, Dodd et al. 2012, Willcox and Giuliano 2015). All bats inhabiting North American forests are insectivorous and rely on insects as a prey base (Lacki et al. 2007). Although specializations have been reported, most species consume insects from multiple orders, their diet varying by geographic location, time of night, season, and year, presumably as a result of shifts in the availability of insects of different types (Whitaker 1972, Whitaker and Clem 1992, Kurta and Whitaker 1998, Murray and Kurta 2002, Lee and McCracken 2001, Lacki et al. 2007).

Studies suggest prescribed fire and overstory thinning can have positive, negative, or neutral effects on insects depending on the order, family, genus, or species examined, as well as mobility and life stage at time of treatment, and treatment frequency (Warren et al. 1987, Siemann et al. 1997, Grindal and Brigham 1998, Burford et al. 1999, Hanula and Wade 2003, Swengel 2001, Willcox and Giuliano 2015,). One way in which these treatments may influence insect communities is through changes in vegetation community composition and structure (Herman et al. 1998, Armitage and Ober 2012). The majority of insects either consume plants directly through herbivory or detritovory, or indirectly by predating on herbivores or detritivores. Plants also provide insects with shelter and sites for oviposition (Strauss and Zangerl 2001). Therefore, changes in vegetation composition and structure in upland hardwood forest stands treated with prescribed fire and overstory thinning likely alter their insect carrying capacity, potentially affecting the abundance and biomass of insects available to bats as prey.

Understanding the response of insects important in the diet of bats to restoration and management treatments, such as prescribed fire and overstory thinning, has become increasingly important due to the numerous threats faced by this taxa, including habitat loss, wind energy installations (Cryan and Veilleux 2007, Cryan and Barclay 2009, Lacki at al. 2007), and, most recently, the fungal disease White-nose Syndrome (WNS), which has caused population declines in numerous cave hibernating bat species, threatening once abundant populations with regional extirpation (Frick et al. 2010, Turner et al. 2011, Langwig et al. 2012). Many of the species affected by WNS use upland hardwood forest systems for foraging during the pre- and post-hibernation and maternity periods (i.e., spring, summer, and early fall; Barclay and Kurta 2007, Lacki et al. 2007) when food requirements are high due to the energetics associated with reproduction and entering and recovering from hibernation, especially if affected by WNS. Therefore, ensuring adequate prey availability during this period is crucial to bat reproduction and survival.

Limited knowledge on the effects of prescribed fire, in combination with overstory thinning, on insect prey availability in upland hardwood forest currently limits managers' ability to implement these treatments to benefit imperiled bat species. Therefore, we experimentally assessed nocturnal flying insect prey response to prescribed fire and overstory thinning treatments. The objectives of our study were to 1) compare nocturnal flying insect prey availability (biomass and abundance) among 4 prescribed fire and overstory thinning treatments and untreated controls in upland hardwood forest stands of Tennessee's Cumberland Plateau and 2) determine the influence of vegetation composition and structure on nocturnal flying insect prey availability (abundance and biomass).

# METHODS

## Study Area

We conducted our research at Catoosa Wildlife Management Area (CWMA). This public land is managed by the Tennessee Wildlife Resources Agency (TWRA) and encompasses 32,374 ha in Cumberland, Morgan, and Fentress Counties, TN, within the Cumberland Plateau and Mountainous physiographic province (DeSelm 1994). It is comprised of oak-hickory dominated upland hardwood and pine-hardwood stands, approximately 80–100 years old. Short-leaf pine (*Pinus echinata*) was a major overstory component at CWMA until a pine bark beetle (*Dendroctonus frontalis*) outbreak in 1999–2000. In 2002, TWRA began salvage cutting short-leaf pine damaged or killed during this outbreak and shortly after initiated an oak savanna restoration project involving prescribed fire and overstory thinning. Restoration activities began on our study area in 2008. At the initiation of this restoration, the overstory was comprised primarily of red maple (*Acer rubrum*; 2.89 $m^2ha^{-1}$), white oak (*Quercus alba*; 2.85 $m^2ha^{-1}$) sourwood (*Oxydendrum arboreum*; 1.86 $m^2ha^{-1}$), hickory (*Carya spp*; 1.13 $m^2ha^{-1}$), scarlet oak (*Q. coccinea*; 0.99 $m^2ha^{-1}$), blackgum (*Nyssa sylvatica*; 0.83 $m^2ha^{-1}$), and post oak (*Quercus stellata*; 0.83 $m^2ha^{-1}$). The midstory layer was dominated by blackgum, downy serviceberry (*Amelanchier arborea*), red maple, sourwood, and sassafras (*Sassafras albidum*). Groundcover consisted of a mixture of native grasses, forbs, legumes, and woody plant regeneration. At the start of the study, mean canopy cover within treatment units was >80%, mean live basal area >14 $m^2$ $ha^{-1}$, and mean live overstory stem density (trees >12.7 cm diameter at breast height [dbh]) >270 stems $ha^{-1}$ (Vander Yacht 2013). Elevations within the study area range from 437−521 m above sea-level, slopes from 1−60%, and average stand aspects from 131−267°. The average annual precipitation in the area is 153 cm and the average annual temperature 12 °C (NOAA 2013).

### Experimental Design

During spring of 2008, 10 20-ha study stands were delineated at CWMA. These stands were configured to minimize topographic variation and maximize core area. Using a completely randomized design with two replicates, we assigned one of 4 prescribed fire and overstory thinning treatments to 8 stands: spring prescribed fire and low overstory thinning (woodland with a target residual basal area of 14 $m^2ha^1$; SpL), spring prescribed fire and high overstory thinning (savanna with a target residual basal area of 7 $m^2ha^{-1}$; SpH), fall prescribed fire and low overstory thinning (FaL), fall prescribed fire and high overstory thinning (FaH). The remaining two stands were assigned as untreated controls. Commercial loggers completed overstory thinning in June 2008. We conducted fall prescribed fire treatments 11 October, 2010 and 15 October, 2012 and for the spring treatments 22 March, 2011 and 20 March, 2013.

### Nocturnal Flying Insect Abundance and Biomass

In each research stand, we sampled nocturnal flying insects 3 times each summer (May−July) for 2 years (2013−2014) using Universal Black Light Traps (BioQuip Products Inc., Rancho Dominquez, California, USA) powered by rechargeable 12-volt batteries. We deployed light traps at the center of each study stand, suspended 3 m above the ground (Armitage and Ober 2012). We deployed light traps every other night from sunset to sunrise over a 7 day period in 5 study stands (1 detector in each treatment type collecting 4 insect sub-samples/7 night sample period). At the end of the 7 nights, we relocated light traps to the remaining 5 study stands and collected insects every other night over a further 7 nights. We repeated this process over an additional 2 sampling periods each summer.

We used Nuvan Prostrip© (Amvac Chemical Corp., Los Angeles, California) kill strips to euthanize all trapped insects and collected captured individuals after each trap night. After collection, insects were placed in containers of 70% isopropyl alcohol until they could be sorted to order, using a dissecting microscope and appropriate identification keys (Triplehorn and Johnson 2005), and counted. We measured the body length (mm) of each individual insect collected using calipers, from the anterior of the head to the posterior of the last abdominal segment. From these body length measurements, biomass of insects (g) was estimated using order-specific length-mass equations derived from other studies conducted in the United States (Sample et al. 1993, Benke et al. 1999, Sabo et al. 2002, and Ober and Hayes 2008).

### Vegetation Characteristics

From May−July of 2013 and 2014, we sampled overstory, midstory, understory, and ground cover characteristics at up to 15 randomly located sampling points in each of our study stands. Sampling points were located in the core (50m buffer) of each 20 ha stand to reduce the bias associated with edge effects.

***Live overstory basal area***: To determine live overstory basal area ($m^2ha^{-1}$), we measured dbh of all live overstory trees with a dbh ≥12.7 cm within an 11.3-m radius subplot centered on each vegetation sampling point (Figure 2.1).

***Midstory stem density:*** To assess midstory stem density (stems/$m^2$), we counted all tree saplings, shrubs, woody vines, and semi-woody plants >1.4 m tall and with a dbh <12.7 cm within 7 3-m radius subplots. Five of the subplots were located at 12.5-m intervals along the 50-m transect used to measure groundcover. Two additional subplots (one upslope and one down slope) were located 12.5 m from the vegetation sampling point and perpendicular to the transect line (Figure 2.1).

***Understory stem density:*** To estimate understory stem density (stems/$m^2$), we counted all tree seedlings, shrubs, woody vines, and semi-woody plants (e.g., brambles and greenbriers) >0.35 m but <1.4 m tall within 7 1-$m^2$ subplots, centered on the 3-m radius understory subplots used to estimate understory density (Figure 2.1).

***Ground cover:*** We determined ground cover (%) along a 50-m transect, centered on each sampling point and run perpendicular to slope, using the point-intercept method (Owensby 1973; Figure 2.1). At 1-m intervals along each transect, we categorized all intersecting vegetation <0.35-m tall as: 1) graminoid, 2) forb, 3) woody vegetation (trees, vines, shrubs, brambles, and greenbriars), or 4) other vegetation (moss, lichen, fern, or fungus). At intervals where no vegetation was present, we categorized cover as: 1) rock or bare ground, or 2) leaf litter or coarse woody debris.

### Data Analysis

We used repeated measures, mixed-model regressions with sample period and year as repeated measures to compare insect abundance and biomass among our 4 prescribed fire and overstory thinning treatments and untreated controls. The same procedure was used to compare vegetation characteristics among treatments and controls but, as these characteristics were measured just once each summer, only year was used as a repeated measure. We interpreted a significant treatment effect, treatment * year interaction effect, or, as applicable, treatment * sampling period interaction effect as evidence of an insect abundance, insect biomass, or vegetation response to treatment. We performed post-hoc tests using a Fisher's LSD comparison procedure. We rank-transformed all data prior to analyses to meet normality and homogeneity of variance assumptions (Conover 1999, Zar 1999, SYSTAT 2007). We concluded statistical significance for all tests at $P \leq 0.05$ (Zar 1999). All analyses were performed using SYSTAT 13 (Systat Software Inc., San Jose, CA).

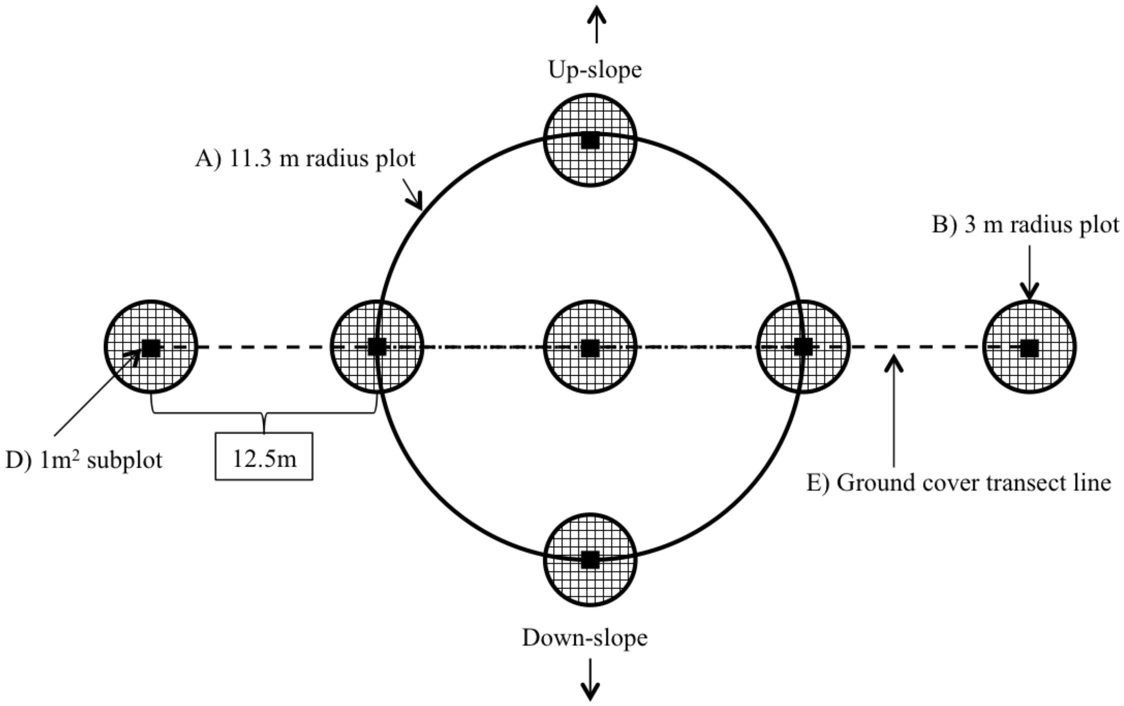

Figure 2.1: Sampling layout for assessing vegetation characteristics in hardwood forest stands used to examine response of nocturnal flying insects to prescribed fire and overstory thinning at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013−2014. A) 11.3 m radius plot used to measure live overstory basal area(stems >12.7 cm dbh; $m^2 ha^-1$), B) 3 m radius plot used to assess midstory stem density (stems >1.4 m tall and <12.7 cm dbh; stems/$m^2$), D) $1m^2$ subplot used to measure understory density (stems >0.35 m but <1.4 m tall; stems/$m^2$), and E) 50 m transect line used to measure percent ground cover (graminoids, forbs, woody vegetation, other vegetation, rock and bare ground, and litter and course woody debris; %).

# RESULTS

## Nocturnal Flying Insect Abundance and Biomass

We collected nocturnal flying insects within our 10 study stands for 120 nights from May–July 2013 and 2014 (12 nights/stand/year), for a total of 2,880 collection hours (12 hours/night) over 2 years. A total of 40,220 individuals were captured (18,309 [45.52%] in 2013 and 21,911 [54.48%] in 2014), with a combined biomass of 242.95 g (105.61 g [43.47%] in 2013 and 137.34 g [56.53%] in 2014). Captured individuals were identified as belonging to one of twelve orders. We grouped any order that had ≤250 total captures across both study years for analysis purposes due to low sample size (Morris et al. 2010). This left us with 4 insect orders and one insect group: 1) Coleoptera, 2) Diptera, 3) Hemiptera, 4) Lepidoptera, or 5) Other (Blattodea, Ephemeroptera, Hymenoptera, Neuroptera, Odonata, Orthoptera, Plecoptera, and Trichoptera). Of identified individuals, Coleoptera constituted 53% (n = 21,316) of total insects collected followed by Lepidoptera 34.74% (n = 13,972), Diptera 9.15% (n = 3,680), Hemiptera 1.77% (n = 710), and Other 1.35%(n = 546). In terms of biomass, Lepidoptera constituted 135.86 g (55.92%), Coleoptera 94.43 g, (38.87%), Other 3.15% (7.64 g), Diptera 1.07 % (2.61 g), and Hemiptera 0.99 % (2.40 g) of insects collected.

Total insect abundance and abundance of Coleoptera, Diptera, and Lepidoptera were not affected by prescribed fire and overstory thinning and did not differ among treatment and control stands ($P \geq 0.220$, Appendix Table A.1, A.2, and A.3). Abundance of Other was affected by treatment alone (Table 2.1, Appendix Table A.2, and A.3). There was no difference in Other abundance between control, SpL, FaL, and FaH stands. However, Other abundance was lower in SpH compared to control, FaL, and

FaH stands. Hemiptera abundance was affected by a treatment * year and treatment * sample period interaction (Table 2.2 and 2.3, respectively, Appendix Table A.1). In 2013, Hemiptera abundance was similar among control, SpL, SpH, and FaL stands. However, Hemiptera abundance was greater in FaH compared to all other treatment and control stands. In 2014 there was no difference in Hemiptera abundance between control and all treatment stands. During the May sampling period there was no difference in Hemiptera abundance among control and all treatment stands. Hemiptera abundance was similar in control, SpL, SpH, and FaL stands, but greater in FaH compared to control and SpL stands during the June sampling period. During the July sampling period Hemiptera abundance was similar in control, SpH, FaL, and FaH stands but greater in SpL than control stands. Total insect biomass and biomass of Coleoptera, Diptera, Hemiptera, and Lepidoptera were not affected by prescribed fire and overstory thinning and did not differ between treatment stands ($P \geq 0.290$, Appendix Table A.1, A.2, and A.3).

Table 2.1: Effect of treatment on nocturnal flying Other (orders= Blattodea, Ephemeroptera, Hymenoptera, Neuropetera, Odonta, Orthoptera, Plecoptera, and Trichoptera) abundance in hardwood forest stands subject to prescribed fire and overstory thinning at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013−2014.

| Mean Other Abundance (no. of individuals)/Treatment ($\bar{x}$ ± SE)[a] | | | | | |
|---|---|---|---|---|---|
| Control | SpL[b] | SpH[b] | FaL[b] | FaH[b] | *P* |
| $15.17 \pm 4.30_{A}$ | $7.75 \pm 2.81_{ABC}$ | $3.17 \pm 1.41_{C}$ | $9.33 \pm 2.71_{AB}$ | $9.75 \pm 2.49_{AB}$ | 0.024 |

[a] Means followed by the same uppercase letter not different (*P* > 0.05)

[c] Treatment: SpL = spring prescribed fire and low overstory thinning (woodland with a target residual basal area of 14 $m^2ha^{-1}$), SpH = spring prescribed fire and high overstory thinning (savanna with a target residual basal area of 7 $m^2ha^{-1}$), FaL = fall prescribed fire and low overstory thinning, FaH = fall prescribed fire and high overstory thinning.

Table 2.2: Effect of a treatment * year interaction on nocturnal flying Hemiptera abundance in hardwood forest stands subject to prescribed fire and overstory thinning at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013−2014.

| | Hemiptera Abundance (no. of individuals)/Treatment ($\bar{x}$ ± SE)[a] | | | | | |
|---|---|---|---|---|---|---|
| Year | Control | SpL[b] | SpH[b] | FaL[b] | FaH[b] | *P* |
| 2013 | $5.17 \pm 2.10_A$ | $5.50 \pm 1.91_A$ | $2.00 \pm 1.26_A$ | $5.33 \pm 2.79_A$ | $32.5 \pm 11.85_B$ | 0.014 |
| 2014 | $8.67 \pm 4.22_A$ | $17.83 \pm 10.92_A$ | $15.33 \pm 10.13_A$ | $16.33 \pm 5.70_A$ | $9.67 \pm 6.16_A$ | |

[a] Means in a row followed by the same uppercase letter not different ($P > 0.05$)

[b] Treatments: SpL = spring prescribed fire and low overstory thinning (woodland with a target residual basal area of 14 $m^2ha^{-1}$), SpH = spring prescribed fire and high overstory thinning (savanna with a target residual basal area of 7 $m^2ha^{-1}$), FaL = fall prescribed fire and low overstory thinning, FaH = fall prescribed fire and high overstory thinning.

Table 2.3: Effect of a treatment * sampling period interaction on nocturnal flying Hemiptera abundance in hardwood forest stands subject to prescribed fire and overstory thinning at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013−2014.

| Sampling | Hemiptera Abundance (no. of individuals)/Treatment ($\bar{x}$ ± SE)[a] | | | | | |
|---|---|---|---|---|---|---|
| Period | Control | SpL[b] | SpH[b] | FaL[b] | FaH[b] | *P* |
| May | $6.00 \pm 2.20_{ABC}$ | $30.75 \pm 12.67_{AC}$ | $16.25 \pm 15.92_{B}$ | $11.00 \pm 3.34_{ABC}$ | $22.75 \pm 10.71_{C}$ | 0.032 |
| June | $1.75 \pm 1.11_{A}$ | $2.75 \pm 1.18_{A}$ | $4.75 \pm 1.89_{AB}$ | $14.00 \pm 10.11_{AB}$ | $30.50 \pm 17.72_{B}$ | |
| July | $13.00 \pm 5.58_{A}$ | $1.50 \pm 0.96_{B}$ | $5.00 \pm 4.36_{AB}$ | $7.50 \pm 3.20_{AB}$ | $10.00 \pm 8.72_{AB}$ | |

[a] Means in a row followed by the same uppercase letter not different (*P* > 0.05)

[b] Treatments: SpL = spring prescribed fire and low overstory thinning (woodland with a target residual basal area of 14 $m^2ha^{-1}$), SpH = spring prescribed fire and high overstory thinning (savanna with a target residual basal area of 7 $m^2ha^{-1}$), FaL = fall prescribed fire and low overstory thinning, FaH = fall prescribed fire and high overstory thinning.

### Vegetation Characteristics

Live overstory basal area, understory density, and percent cover of litter and coarse woody debris, forbs, graminoids, woody vegetation, and other vegetation were affected by treatment alone (Table 2.4, Appendix Table A.4 and A.5). There was no difference in live overstory basal area among control, SpL and FaL stands. Live overstory basal area was lower in SpH and FaH stands than controls, but did not differ between these two treatments. Midstory density was affected by a treatment * year interaction (Table 2.5), in addition to treatment alone (Appendix Table A.4). In 2013, there was no difference in midstory density between control and FaL stands. However, midstory density was lower in SpL and SpH compared to control stands and greater in FaH compared to control stands. In 2014, midstory density was higher in SpL, SpH, FaL and FaH compared to control stands, but did not differ between these four treatments. Understory density was greater on SpL, SpH, FaL, and FaH compared to control stands, but did not differ between these 4 treatments. Percent cover of litter and coarse woody debris was lower in SpL, SpH, FaL, and FaH compared to control stands, with the greatest, but similar, reductions observed in SpH and FaH stands. There was no difference in percent cover of forbs among control, SpL, and FaL stands. Percent cover of forbs was greater on SpH, and FaH stands, but did not differ between these two treatments. A greater percent cover of graminoids was observed on SpL, SpH, FaL, and FaH stands than controls, with the greatest, but similar, increases observed in SpH and FaH stands. Percent cover of woody vegetation was also greater in SpL, SpH, FaL, and FaH stands, with the greatest, but similar, increases observed in SpL, SpH, and FaL stands. Percent cover of other vegetation was similar among control, SpL, and FaL stands. It was greater in SpL and FaL stands, but did not differ between these two treatments. Percent cover of rock and bare ground was not affected by prescribed fire and overstory thinning and did not differ among treatment and control stands ($P \geq 0.059$; Appendix Table A.4 and A.5).

## DISCUSSION

We found the effects of prescribed fire and overstory thinning treatments on abundance and biomass of insects to be negligible. Abundance of Other (Blattodea, Ephemeroptera, Hymenoptera, Neuroptera, Odonata, Orthoptera, Plecoptera, Trichoptera combined) was lower in FaH compared to control stands. Abundance of Hemiptera was also lower in FaH stands compared to controls during the first year of our study and fluctuated in SpL, SpH, and FaH stands compared to controls during some sample periods. However, treatments had no effect on Coleoptera, Diptera, or Lepidoptera, despite changes in vegetation community composition and structure (lower overstory basal area and greater understory density and percent cover of litter and coarse woody debris, forbs, graminoids and woody vegetation in certain treatment stands compared to controls), which might be expected to alter the availability of insect food and cover resources and, in turn, insect carrying capacity (Herman et al. 1998, Strauss and Zangeri 2001, Armitage and Ober 2012).

Table 2.4: Effect of treatment on vegetation characteristics in hardwood forest subject to prescribed fire and overstory thinning at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013−2014.

| Vegetation | Vegetation Characteristic/Treatment ($\bar{x}$ ± SE)[b] | | | | | |
|---|---|---|---|---|---|---|
| Characteristic[a] | Control | SpL[c] | SpH[c] | FaL[c] | FaH[c] | *P* |
| Basal Area | 20.57 ± 1.87$_{A}$ | 13.71 ± 0.87$_{Ac}$ | 5.88 ± 2.41$_{B}$ | 12.49 ± 2.02$_{AC}$ | 8.70 ± 1.79$_{Bc}$ | 0.009 |
| Understory | 3.43 ± 0.98$_{A}$ | 7.50 ± 0.70$_{B}$ | 9.79 ± 2.12$_{B}$ | 8.12 ± 1.46$_{B}$ | 8.76 ± 0.98$_{B}$ | 0.037 |
| Litter/CWD | 59.26 ± 2.41$_{A}$ | 16.48 ± 2.29$_{B}$ | 6.17 ± 2.31$_{C}$ | 14.76 ± 1.82$_{B}$ | 7.68 ± 1.09$_{C}$ | ≤ 0.001 |
| Forb | 2.07 ± 0.83$_{A}$ | 2.68 ± 1.03$_{A}$ | 8.44 ± 1.23$_{B}$ | 3.54 ± 1.17$_{A}$ | 8.30 ± 0.98$_{B}$ | 0.004 |
| Graminoid | 0.65 ± 0.24$_{A}$ | 12.40 ± 1.03$_{B}$ | 19.13 ± 2.81$_{C}$ | 9.84 ± 2.81$_{B}$ | 22.07 ± 1.18$_{C}$ | ≤ 0.001 |
| Woody | 36.21 ± 1.27$_{A}$ | 63.51 ± 3.13$_{BC}$ | 61.63 ± 2.22$_{C}$ | 66.71 ± 3.23$_{B}$ | 56.63 ± 1.15$_{D}$ | ≤ 0.001 |
| Other | 1.15 ± 0.54$_{A}$ | 1.86 ± 0.74A$_{B}$ | 1.46 ± 0.72$_{A}$ | 1.20 ±0.11$_{A}$ | 3.37 ± 0.26$_{B}$ | 0.038 |

[a] Vegetation Characteristics: Basal Area = live overstory basal area (m$^2$ha$^{-1}$), Understory = understory density (stems/m$^2$) Litter/CWD = percent cover of litter and course woody debris (%), Forb = Percent cover of forbs (%), Graminoid = percent cover of graminoids (%), Woody = percent cover of woody vegetation (trees, shrubs, and woody vines; %), Other = percent cover of other vegetation (moss, lichen, fungus, fern).

[b] Means in a row followed by the same uppercase letter not different ($P > 0.05$)

[c] Treatments: SpL = spring prescribed fire and low overstory thinning (woodland with a target residual basal area of 14 m$^2$ha$^{-1}$), SpH = spring prescribed fire and high overstory thinning (savanna with a target residual basal area of 7 m$^2$ha$^{-1}$), FaL = fall prescribed fire and low overstory thinning, FaH = fall prescribed fire and high overstory thinning.

Table 2.5: Effect of a treatment * year interaction on midstory density over two years in hardwood forest stands subject to prescribed fire and overstory thinning at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013−2014.

| | Midstory Density (stems/m$^2$)/Treatment ($\bar{x}$ ± SE)[b] | | | | | |
|---|---|---|---|---|---|---|
| Year | Control | SpL[c] | SpH[c] | FaL[c] | FaH[c] | *P* |
| 2013 | $6.70 \pm 1.37_{A}$ | $4.16 \pm 0.78_{B}$ | $3.60 \pm 0.98_{BC}$ | $4.13 \pm 0.95_{AB}$ | $10.35 \pm 0.39_{C}$ | ≤ 0.001 |
| 2014 | $8.09 \pm 0.98_{A}$ | $9.65 \pm 0.07_{BC}$ | $24.60 \pm 0.10_{B}$ | $13.25 \pm 1.42_{BC}$ | $15.21 \pm 1.18_{C}$ | |

[b] Means in a row followed by the same uppercase letter not different (*P* > 0.05)

[c] Treatments: SpL = spring prescribed fire and low overstory thinning (woodland with a target residual basal area of 14 m$^2$ha$^{-1}$), SpH = spring prescribed fire and high overstory thinning (savanna with a target residual basal area of 7 m$^2$ha$^{-1}$), FaL = fall prescribed fire and low overstory thinning, FaH = fall prescribed fire and high overstory thinning.

Few studies have examined the combined effect of prescribed fire and overstory thinning on insects, although a considerable number have investigated the effects of these and similar treatments alone. A limited number of these studies had results similar to ours. Armitage and Ober (2012) found few differences in abundance or biomass of most insect orders in prescribed fire treated longleaf pine (*Pinus palustris*) stands of different fire frequency, with the exception of Lepidoptera, which had a lower biomass on sites subject to frequent fire. Similarly, Grindal and Brigham (1998) found insect availability was not affected by tree removal, being similar in 0.5 ha, 1.0 ha, and 1.5 ha cut blocks (areas where trees have been harvested) to un-cut blocks. However, research showing a response of insects to prescribed fire and overstory thinning or similar treatments is more common, even though the degree and duration of the response tends to vary considerably depending on the insect order and study. Many insect orders decline immediately after prescribed fires, with the magnitude of the decline closely related to the intensity of the fire and the proximity of insects to the flame (Swengel 2001). Siemann et al (1997) found flying insects declined in oak savanna areas the first year post-fire but increased in following years. Similarly, a study conducted in Florida flatwoods compared dormant and growing season prescribed fires and their effects on insect abundance, familial richness, and total familial richness and found that growing and dormant season fire caused a decline in total familial richness and relative abundance, but that these declines were relatively brief. This is in contrast to Lacki et al. (2009) who had a 34% increase in flying insects during the first year post-burn in Kentucky hardwood forest stands. Similarly Nagel (1973) and Hansen (1986) found prescribed fire had an effect on flying insect in grasslands, with recently burned areas having greater abundance than unburned areas. Burns were conducted in our treatment stands the fall and spring prior to the commencement of our study. However, despite the timing of prescribed fire implementation, night flying insect abundance and biomass still did not appear to be affected.

With regard to overstory thinning and similar treatments, most studies, unlike ours, found insects responded to treatment implementation. Burford et al. (1999) reported there was lower insect availability, particularly of Lepidopterans, in cleared areas with no trees compared to that of moderately mature (30-59 years old) or mature (>60 years old) stands. In a study conducted in Kentucky hardwood forest, Lepidopteran abundance was also found to be higher in control stands than those treated with seed tree, single-tree, or shelterwood cuts. However, Coleoptera and Diptera abundance were greater in stands where the seed tree method had been implemented than controls (Lacki et al. 2007).

Although in our study insect abundance and biomass did not appear to be influenced by prescribed fire and overstory thinning treatments, we recommend caution in assuming these treatments do not affect the availability of night flying insect prey important in the diet of bats. We recommend further data collection be conducted at additional study areas over a prolonged period before management recommendations are made. Until then we suggest treatments be applied in a mosaic across the landscape, leaving untreated areas adjacent to treated areas to ensure a diversity of insect prey sources are maintained.

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# CHAPTER III

## RESPONSE OF BATS TO PRESCRIBED FIRE AND OVERSTORY THINNING IN A HARDWOOD FOREST ON THE CUMBERLAND PLATEAU

This chapter is slightly modified from a paper that is being prepared for submission and potential publication:

Cox, M.R., E.V. Willcox, P.D. Keyser, and A.L. Vander Yacht,  Response of Bats to Prescribed Fire and Overstory Thinning in a Hardwood Forest on the Cumberland Plateau

My consistent use of “we” throughout this chapter is in reference to my co-authors and myself. I was the primary contributor to this work, which involved the following tasks: (1) development of project design and all data collection, (2) acoustic and statistical analyses, (3) gathering and interpretation of the relevant literature, and (4) all writing.

## ABSTRACT

Across the Southeastern U.S., including the Cumberland Plateau of Tennessee, prescribed fire and overstory thinning are being used to restore areas of closed-canopy hardwood forest to open woodland and savanna. These treatments can alter habitat conditions for bats. Many bat species utilize hardwood forests for foraging, particularly during the pre/post-hibernation and maternity periods. Unfortunately, knowledge is limited on the effects prescribed fire and overstory thinning have on bats which hinders the implementation of these treatments to benefit species in conservation need. We used acoustic recording of bat echolocation call sequences to examine bat activity (relative use of an area for foraging) in upland hardwood forest stands subject to 4 prescribed fire and overstory thinning treatments (spring fire with high [SpH] and low [SpL] overstory thinning, and fall fire with high [FaH] and low [FaL]) overstory thinning, as well as untreated controls. When possible, we classified recorded echolocation call sequences to species using automated identification software (Sonobat 3.1.4, SonoBat Inc., Arcata, California). To minimize errors in species classification of recorded bat call sequences, we combined similar species in groups based on call characteristics prior to conducting analyses. We found total bat activity ($P \leq 0.001$), as well as LBNH (eastern red bat [*Lasiurus borealis*] and evening bat [*Nycticeius humeralis*]; *P* = 0.001), EFLN (big brown bat [*Eptesicus fuscus*] and silver-haired bat [*Lasionycteris noctivagans*]; *P* ≤ 0.001), PESU (tricolored bat [*Perimyotis subflavus*]; *P* = 0.001), and LACI (hoary bat [*Lasiurus cinereus*]; *P* = 0.005) activity was generally greater in SpH and FaH stands. Activity of these bat species was influenced by live overstory basal area and was lower in Control, SpL and FaL stands where basal area was higher (*P* ≤ 0.001). Our results suggest these treatments reduce clutter (physical obstructions to flight and foraging including foliage, branches, and stems), leading to improved foraging conditions for bats, particularly larger bodied species with lower call frequencies that are adapted to fly and forage in open conditions. This provides support for continued use of prescribed fire and overstory thinning and restoration of closed canopy hardwood forest to woodland and savanna as a strategy to enhance habitat for forest bats.

## INTRODUCTION

In recent years, land managers have begun to increase their use of prescribed fire and overstory thinning in hardwood forests across the Southeastern U.S., including the Cumberland Plateau of Tennessee, in an attempt to restore and maintain the open woodland and savanna conditions that existed before the era of fire suppression (Delecourt and Delecourt 1998, Brose et al. 2001, Brose et al. 2012). The use of these practices across the region can modify habitat conditions for numerous bat species (Boyles and Aubrey 2006). Understanding bat responses to such habitat modifications is critical given the unprecedented conservation crisis and population declines many species are facing as a result of multiple threats. Over the past decade, the spread of wind energy installations (i.e., wind turbines) in the U.S. has caused increased mortality of migratory tree-roosting bats (e.g., eastern red bat [*Lasiurus borealis*], hoary bat [*Lasiurus cinereus*], and silver-haired bat [*Lasionycteris noctivagans*]), all of which roost and forage in hardwood forest systems and can be influenced by management and restoration activities (Cryan and Veilleux 2007, Cryan and Barclay 2009, Lacki at al. 2007). More recently, White-nose Syndrome (WNS), a disease caused by the fungus *Pseudogymnoascus destructans,* has caused catastrophic population declines in numerous cave-hibernating bat species across the Eastern U.S., threatening once abundant populations with regional extirpation (Frick et al. 2010, Turner et al. 2011, Langwig et al. 2012). The disease currently infects 7 bat species, 4 of which belong to the genus *Myotis* and are federally listed or being considered for listing (gray bat [*Myotis grisescens*], Indiana bat [*M. sodalis*], northern long-eared bat [*M. septentrionalis*], and little brown bat [*M. lucifugus*]; United States Fish and Wildlife Service 2015). All of these species use Southeastern hardwood forest systems for roosting and foraging, particularly during the pre- and post-hibernation and maternity periods (i.e., spring, summer, and early fall; Barclay and Kurta 2007, Lacki et al. 2007). This is an important time in the life-history of cave-hibernating bats because of the energetics associated with reproduction and entering and recovering from hibernation, especially if affected by WNS. Therefore, managing hardwood forests in proximity to hibernacula to provide high quality habitat during this period may be critical for population persistence and species recovery (Johnson et al. 2010).

Few studies have examined the effect of prescribed fire or silvicultural practices on bats in upland hardwood forest systems of the Southeastern U.S. Those studies that have been conducted focus on response of a single bat species to treatments rather than the bat community as a whole (Menzel et al. 2002, Owen et al. 2003, Lacki et al. 2009). No studies have been conducted examining the combined effect of prescribed fire and overstory thinning. Studies that have been conducted examining bat response to prescribed fire and silvicultral practices in other North American forest systems suggest prescribed fire and overstory thinning may affect bat activity (relative use of an area for foraging) through changes in forest structure and availability of nocturnal flying insect prey (Grindal and Brigham 1998 and 1999, Loeb and Waldrop 2008, Titchenell et al. 2011, Armitage and Ober 2012). Changes in forest structure alter the degree of clutter (physical obstructions including foliage, branches, and stems, that impede flight and limit prey detection by reflecting echolocation calls) with which bats must contend (Lacki et al. 2007). Morphological variations in body size and wing shape, particularly wing loading (mass of the bat divided by its total wing area; WL) and aspect ratio (length of the wing squared divided by its surface area; AR), along with differences in echolocation call frequency and structure determine whether bats can fly and capture prey in clutter and, in turn, their habitat use and activity in a forest stand (Alrdridge and Rautenbach 1987, Norberg and Rayner 1987). However, while bats may use a forest stand for foraging based on their adaptations to that environment, the availability of nocturnal insect prey also likely plays an important role in determining use, and in turn, activity in an area (Fenton 1990, Brigham et al. 1997, Jacobs 1999, Lacki et al. 2007, Erickson and West 2003).

In light of the threats and population losses currently faced by bats in the Southeastern U.S., the effects prescribed fire and overstory thinning have on bat activity in upland hardwood forest systems warrants further investigation. Land managers need to understand how these practices affect bats in order to better manage populations and communities, in conjunction with oak savanna restoration efforts and other forest management objectives. We experimentally assessed how bats, forest clutter, and availability of nocturnal flying insect prey respond to prescribed fire and overstory thinning treatments. The objectives of our study were to 1) compare bat activity among 4 prescribed fire and overstory thinning treatments and untreated controls in upland hardwood forests of Tennessee's Cumberland Plateau and 2) determine the relative contributions of forest clutter and availability of nocturnal flying insect prey in explaining any observed changes in bat activity following prescribed fire and overstory thinning treatments.

## METHODS

### Study Area

We conducted our research at Catoosa Wildlife Management Area (CWMA), managed by the Tennessee Wildlife Resources Agency (TWRA), which encompasses 32,374 ha in Cumberland, Morgan, and Fentress Counties, TN, within the Cumberland Plateau and Mountainous physiographic province (DeSelm 1994). It is comprised of oak-hickory dominated upland hardwood and pine-hardwood stands, approximately 80−100 years old. Prior to a pine bark beetle (*Dendroctonus frontalis*) outbreak in 1999−2000, short-leaf pine (*Pinus echinata*) was a major overstory component. Salvage cutting of short-leaf pine damaged or killed during the outbreak began in 2002. Shortly after, TWRA initiated an oak savanna restoration project involving prescribed fire and overstory thinning. Restoration activities began on our study area in 2008. At the initiation of this restoration, the overstory was comprised primarily of red maple (*Acer rubrum*; 2.89 $m^2ha^{-1}$), white oak (*Quercus alba*; 2.85 $m^2ha^{-1}$) sourwood (*Oxydendrum arboreum*; 1.86 $m^2ha^{-1}$), hickory (*Carya spp*; 1.13 $m^2ha^{-1}$), scarlet oak (*Q. coccinea*; 0.99 $m^2ha^{-1}$), blackgum (*Nyssa sylvatica*; 0.83 $m^2ha^{-1}$), and post oak (*Quercus stellata*; 0.83 $m^2ha^{-1}$). The midstory layer was dominated by blackgum, downy serviceberry (*Amelanchier arborea*), red maple, sourwood, and sassafras (*Sassafras albidum*). Groundcover consisted of a mixture of native grasses, forbs, legumes, and woody plant regeneration. At the start of the study, mean canopy cover within treatment stands was 85% and mean live overstory basal area was 18 $m^2ha^{-1}$ (Vander Yacht 2013). Elevations within the study area range from 437−521 m above sea-level, slopes from 1−60%, and average stand aspects from 131−267°. The average annual precipitation in the area is 153 cm and the average annual temperature 12 °C (National Oceanic and Atmospheric Administration 2013).

### Experimental Design

During spring of 2008, we delineated 10 20-ha study stands at CWMA. These stands were configured to minimize topographic variation and maximize core area. Using a completely randomized design with two replicates, we assigned one of 4 prescribed fire and overstory thinning treatments to 8 stands: spring prescribed fire and low overstory thinning (woodland with a target residual basal area of 14 $m^2ha^{-1}$; SpL), spring prescribed fire and high overstory thinning (savanna with a target residual basal area of 7 $m^2ha^{-1}$; SpH), fall prescribed fire and low overstory thinning (FaL), and fall prescribed fire and high overstory thinning (FaH). The remaining two stands were left as untreated controls. Commercial loggers completed overstory thinning in June 2008. We conducted prescribed fires 11 October, 2010 and 15 October, 2012 for the fall treatments and 22 March, 2011 and 20 March, 2013 for the spring treatments.

## Bat Activity

To examine the effect of prescribed fire and overstory thinning on bat activity, we conducted bat echolocation call monitoring (Hayes 2000) in all study stands 3 times each summer (May−July) for 2 years (2013−2014). In each study stand, we used Pettersson D500x (Pettersson Elektronik AB, Sweden) bat detectors to passively detect, record, and store full-spectrum bat echolocation call sequences (bat passes; Ahlén and Baagøe 1999, Fenton 2000). We deployed bat detectors in a waterproof housing at the center of each study stand. We secured detector microphones at a 45° angle, approximately 3m above the ground to monitor bat activity below the canopy (Armitage and Ober 2012). We programmed each detector to start recording 30 minutes prior to sunset and to stop recording 30 minutes after sunrise. We collected call recordings in 5 study stands (1 detector/treatment type) for 7 consecutive nights (Hayes 1997). At the end of the 7 nights, we relocated detectors to the remaining 5 study stands and collected call recordings for a further 7 nights. We repeated this process over an additional 2 monitoring periods each summer. We conducted all monitoring in accordance with the guidelines approved by the American Society of Mammalogists (Sikes et al. 2011).

We stored digitally recorded bat passes on compact flash cards inside detectors, downloading them to a computer once per week. Bat passes from a given 7-day sampling period were uploaded to SonoBat D500x file attributer 2.3 (SonoBat Inc., Arcata, California) and batch-processed through scrubbing to remove noise interference using default settings. We analyzed bat passes that remained post-scrubbing using SonoBat 3.1.4 Kentucky-Tennessee (SonoBat Inc., Arcata, California) default settings. Following visual verification, we accepted species identification with a decision threshold of ≥90%.

Even using full-spectrum echolocation call sequences and automated and visual identification, differentiating among species' calls can be difficult due to the quality of recordings, which is affected by the degree of forest clutter at sampling locations, the direction the bat is pointing relative to the microphone when it emits a call, the angle and direction of the detector microphone, call attenuation, and Doppler shift (Betts 1998, Loeb and Waldrop 2008). Also, there are a number of species in the Southeastern U.S. that share similar call characteristics, which can frequently lead to misclassification. One way to minimize errors in species classification of recorded bat passes is to combine similar species into groups (Yates and Muzika 2006, Titchenell et al 2011). Species with similar call structure and frequency were combined into three groups (Table 3.1; Betts 1998, Loeb and O'Keefe 2006, Yates and Muzika 2006, Titchnell et al. 2011), MYOT = members of the genus *Myotis*, including eastern small-footed bat (*Myotis leibii*), gray bat, little brown bat, Indiana bat, and northern long-eared bat; LBNH = eastern red bat and evening bat (*Nycticeius humeralis*), and EFLN = big brown bat (*Eptesicus fuscus*) and silver-haired bat. We assigned tricolored bats (*Perimyotis subflavus*) to their own group, PESU, as although they can have similar call structure and frequency to some of the *Myotis*, call frequency is typically slightly lower and duration a little longer (Lausen 2012). Because of their unique call characteristics, we assigned Rafinesque's big-eared bat (*Corynorhinus rafinesquii*), CORA, and hoary bat, LACI, to their own groups. We examined wing morphology of bat species assigned to each group based on published average WLs and ARs (Norberg and Rayner 1987). We categorized bats with high WL/AR values as those with a AR and WL ≥1 SE above the mean for bats found in the region. Low WL/AR bats had a AR and WL ≥1 SE below the mean (WL$\bar{X}$ = 6.464 ± 0.216 *SE*; AR$\bar{X}$ = 8.907 ± 0.86 *SE*). Moderate ML/AR bats were those whose comparative AR and WL fell within 1 SE of the mean (Armitage and Ober 2012). Bats grouped based on similar call structures and frequencies generally also shared similar WL/AR values (Table 3.1).

### Forest Clutter

Quantitative measurements of individual overstory and midstory forest variables have been found to be an effective measure of clutter. Therefore, to assess clutter we measured live overstory basal area and midstory density in each study stand during the summer (May−July) for 2 years (2013−2014; O'Keefe et al. 2014). We only sampled the core (50m buffer) of each 20 ha stand to reduce the bias associated with edge effects. We measured clutter variables at up to 15 randomly located sampling points per study stand. Each sampling plot ran perpendicular to the slope.

***Live overstory basal area***: To determine live overstory basal area ($m^2ha^{-1}$), we measured dbh of all live overstory trees with a dbh ≥12.7 cm within an 11.3 m radius

Table 3.1: Bat groupings, based on call frequency and wing morphology, used in a study examining bat response to prescribed fire and overstory thinning in hardwood forest stands conducted at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013−2014.

| Species Group[a] | Bat Species | Call Frequency | WL/AR Values[b] |
|---|---|---|---|
| MYOT | Eastern small-footed (*Myotis leibii*) | High | Low |
| | Gray (*M. grisescens*) | High | Moderate |
| | Indiana (*M. sodalis)* | High | Low |
| | Little brown (*M. lucifugus*) | High | Low |
| | Northern-long eared (*M. septentrionalis*) | High | Low |
| LBNH | Eastern red (*Lasiurus borealis*) | High | High |
| | Evening (*Nycticeius humeralis*) | High | High |
| EFLN | Big brown (*Eptesicus fuscus*) | Low | High |
| | Silver-haired (*Lasionycteris noctivagans*) | Low | Moderate |
| PESU | Tricolored (*Perimyotis subflavus*) | High | Low |
| CORA | Rafinesque's big-eared (*Corynorhinus rafinesquii*) | Low | Low |
| LACI | Hoary bat (*L. cinereus)* | Low | High |

[a] Species with similar call frequencies grouped together

[b] Wing loading and aspect ratio values

subplot centered on each sampling point (Figure 3.1).

***<u>Midstory stem density</u>*****:** To assess midstory stem density (stems/$m^2$), we counted all tree saplings, shrubs, woody vines, and semi-woody plants >1.4 m tall and with a diameter at breast height (dbh) <12.7 cm within 7 3-m radius subplots around each sampling point. The first of these subplots was centered on the sampling point. Two subplots were located on either side of the sampling point at 12.5 m intervals and parallel to the slope. Two additional subplots were located perpendicular to the slope, 12.5 m from the sampling point (one up-slope and one down-slope; Figure 3.1).

### Nocturnal Insect Prey Availability

We sampled availability of nocturnal insect prey in all study stands 3 times each summer (May−July) for 2 years (2013−2014) using Universal Black Light Traps (BioQuip Products Inc., Rancho Dominquez, California; Spalding 2004) powered by rechargeable 12 volt batteries. We deployed light traps at the center of each study stand, suspended 3 m above the ground (Armitage and Ober 2012). We deployed light traps every other night from sunset to sunrise over a 7 day period in 5 study stands (1 detector in each treatment type collecting 4 insect sub-samples/7 night sample period). These study stands were different than those being monitored for bat echolocation calls (a study stand was not simultaneously sampled for insects and monitored for echolocation calls). At the end of the 7 nights, we relocated light traps to the remaining 5 study stands and collected insects every other night for 7 additional nights. We repeated this process over 2 additional sampling periods each summer.

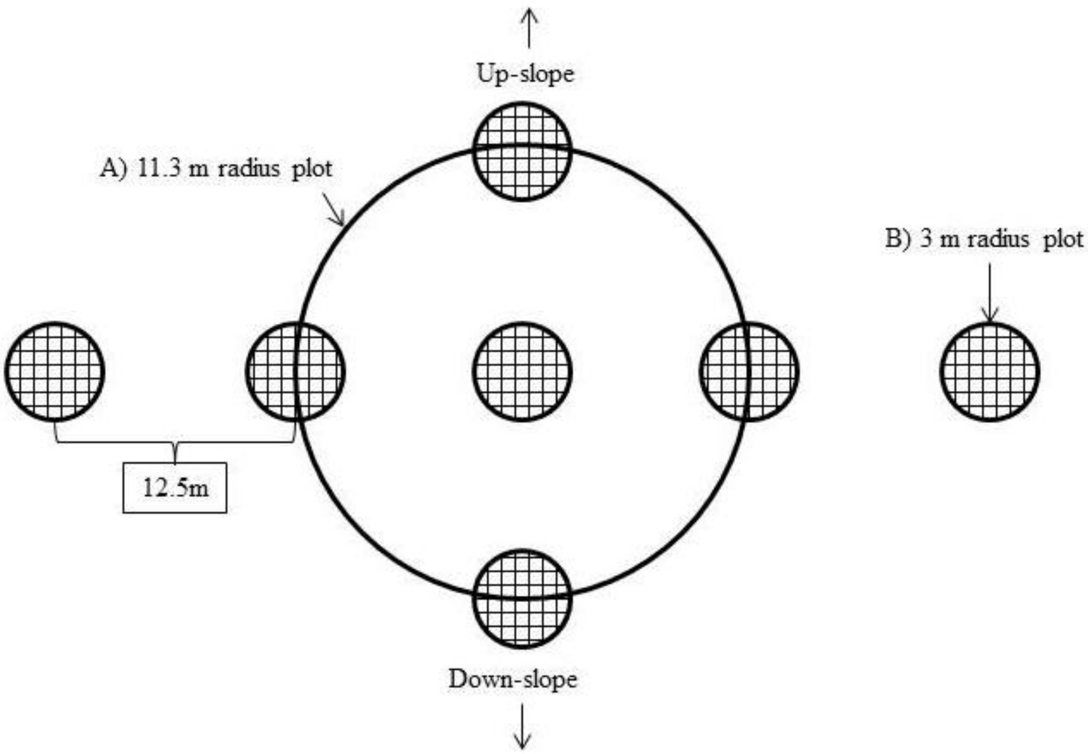

Figure 3.1: Sampling layout for assessing forest clutter in hardwood forest stands used to examine bat response to prescribed fire and overstory thinning at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013−2014. A) 11.3 m radius plot used to measure live overstory tree basal area (stems >12.7 cm dbh; $m^2ha^-1$), and B) 3 m radius plot used to assess midstory stem density (stems >1.4 m tall and <12.7 cm dbh; stems/$m^2$).

We used Nuvan Prostrip© (Amvac Chemical Corp., Los Angeles, California) kill strips to euthanize all insects captured in light traps and collected insect samples after each trap night. After collection, we placed insects in a container of 70% isopropyl alcohol until they could be sorted to order, counted, and body length of each measured (mm) from the anterior of the head to the posterior of the last abdominal segment using a dissecting microscope. From body length measurements, we estimated biomass (g) of insects collected using order specific length-mass equations derived from other studies conducted in the United States (Sample et al. 1993, Benke et al. 1999, Sabo et al. 2002, and Ober and Hayes 2008).

### Data Analysis

We used repeated measures mixed model regressions with sample period and year as repeated measures to compare bat activity and availability of insect prey among our 4 prescribed fire and overstory thinning treatments and untreated controls. The same procedure was used to compare clutter among treatments and controls but, as these clutter variables were measured just once each summer, only year was used as a repeated measure. We interpreted either a significant treatment effect, treatment * year interaction effect, or treatment * sampling period interaction effect as evidence of a bat activity, clutter, or insect prey availability response to treatment. We report but did not examine treatment * year * sampling period interaction effects due to difficulties in interpretation.  We performed post hoc tests using a Fisher's LSD comparison procedure. We rank-transformed all data prior to analyses to meet normality and homogeneity of variance assumptions (Conover 1998, Zar 1999, SYSTAT 2007). We concluded statistical significance for all tests at $P \leq 0.05$ (Zar 1999). Analyses were performed using SYSTAT 13 (Systat Software Inc., San Jose, CA).

To examine the relative contributions of clutter and availability of nocturnal insect prey in explaining observed changes in bat activity in treatment stands, we performed a multiple linear regression using an information theoretic framework (Burnham and Anderson 2002). Fifteen candidate models were developed that included the predictor variables live overstory basal area ($m^2ha^{-1}$), midstory density (stems/$m^2$), insect biomass (g), and distance to water (m). Distance to water is thought to be important to bats in selecting roosting locations and many bat species forage in proximity to water (Gellman and Zielinksi 1996, Ormsbee and McComb 1998, Rainho 2011). We determined this predictor variable from satellite imagery using ArcGIS 10.2.2 (ESRI, Redlands, CA). Based on the literature, prior knowledge, and our own field experiences, we determined any of our predictor variables, alone or in combination, could influence bat activity. Therefore, we examined all possible variable combinations during our analyses. We used Akaike's Information Criteria corrected for small sample sizes ($AIC_c$) to rank models and determine variable importance. For each model, we calculated $\Delta AIC_c$, the difference between the model with the lowest $AIC_c$ and the $AIC_c$ for the *i*th model, and $w_{i,}$ the Akaike's weight. We considered models with a $\Delta AIC_c \leq 2$ supported (Burnham and Anderson 2010). When multiple models were supported, we used model averaging to increase precision of inference. We considered variables within models with 95% confidence intervals that overlapped 0 to have a weak effect on the dependent variable and to be uninformative (Payton et al. 2003). For brevity and clarity we only present results for supported models. All multiple linear regression and AIC analyses were performed using packages bbmle and AICcmodavg in R (R 3.0.2; R Development Core Team).

## RESULTS

### Bat Activity

We monitored bat activity within our 10 study stands for 210 nights (21 nights/stand) from May−July 2013 and 2014 for a total of approximately 4920 monitoring hours (12 hours/night). Over two summers, we recorded 17,460 bat passes, of which we identified 62.74% (n = 10,955) as belonging to one of our 6 species groups (MYOT, LBNH, EFLN, PESU, CORA, and LACI; Table 3.1). EFLN constituted 62.48% (n = 6,845) of identified passes, LBNH 15.82% (n = 1,733), PESU 11.76% (n = 1,288), MYOT 4.74% (n = 519), LACI 4.78% (n = 524), and CORA 0.42% (n = 46).

Total bat activity (identified and unidentified bat passes) and activity of LBNH, EFLN, PESU, and LACI were affected by treatment alone (Table 3.2). There was no difference in total bat activity between control and SpL stands. However, total bat activity was greater in SpH, FaL, and FaH compared to control stands. The greatest increase occurred in SpH stands, where total bat activity differed from that seen in FaL and FaH stands. Similarly, there was no difference in EFLN activity between control and SpL stands. However, activity of this species group was also greater in SpH, FaL, and FaH than control stands. Again, the greatest increase occurred in SpH stands, where EFLN activity differed from that seen in FaL and FaH stands. For LBNH and PESU, activity in Control, SpL, and FaL stands was similar. LBNH activity was greater in SpH and FaH stands compared to control stands. The greatest increase in activity occurred in SpH stands where LBNH activity differed from that seen in FaH stands. PESU

Table 3.2: Effect of treatment on bat activity in hardwood forest stands subject to prescribed fire and overstory thinning at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013−2014.

| Species | Mean Bat Passes (no. of passes)/Treatmen ($\bar{x}$ ± SE)[b] | | | | | |
|---|---|---|---|---|---|---|
| Groups[a] | Control | SpL[c] | SpH[c] | FaL[c] | FaH[c] | *P* |
| Total | 99.17 ± 26.96$_{\mathrm{A}}$ | 127.42 ± 49.35$_{\mathrm{AC}}$ | 651.92 ± 97.15$_{\mathrm{B}}$ | 293.50 ± 101.93$_{\mathrm{CD}}$ | 283.00 ± 33.22$_{\mathrm{D}}$ | ≤ 0.001 |
| LBNH | 7.17 ± 3.93$_{\mathrm{A}}$ | 13.50 ± 7.94$_{\mathrm{A}}$ | 59.67 ± 15.47$_{\mathrm{B}}$ | 33.30 ± 18.90$_{\mathrm{AC}}$ | 30.75 ± 7.84$_{\mathrm{BC}}$ | 0.001 |
| EFLN | 12.20 ± 5.60$_{\mathrm{A}}$ | 29.50 ± 8.92$_{\mathrm{AC}}$ | 355.75 ± 60.03$_{\mathrm{B}}$ | 56.53 ± 17.58$_{\mathrm{C}}$ | 115.67 ± 29.04$_{\mathrm{D}}$ | ≤ 0.001 |
| PESU | 10.25 ± 6.98$_{\mathrm{A}}$ | 15.58 ± 8.48$_{\mathrm{A}}$ | 32.75 ± 10.49$_{\mathrm{B}}$ | 24.75 ± 19.38$_{\mathrm{A}}$ | 24.00 ± 4.61$_{\mathrm{B}}$ | 0.001 |
| LACI | 4.58 ± 1.91$_{\mathrm{AC}}$ | 2.67 ± 1.15$_{\mathrm{A}}$ | 13.75 ± 3.84$_{\mathrm{BD}}$ | 14.92 ± 7.53$_{\mathrm{CD}}$ | 7.75 ± 2.13$_{\mathrm{C}}$ | 0.005 |

[a] Species groups: Total = all bats (identified and unidentified); LBNH = eastern red bat (*Lasiurus borealis*) and evening bat (*Nycticeius humeralis*); EFLN = big brown bat (*Eptesicus fuscus*) and silver-haired bat (*Lasionycteris noctivagans*); PESU = tricolored bat (*Perimyotis subflavus*), LACI = hoary bat (*Lasiurus cinereus*)

[b] Means in a row followed by the same uppercase letter not different ($P > 0.05$)

[c] Treatments: SpL = spring prescribed fire and low overstory thinning (woodland with a target residual basal area of 14 $m^2ha^{-1}$), SpH = spring prescribed fire and high overstory thinning (savanna with a target residual basal area of 7 $m^2ha^{-1}$), FaL = fall prescribed fire and low overstory thinning, FaH = fall prescribed fire and high overstory thinning.

activity was also greater in SpH and FaH compared to control stands, but did not differ between these two treatments. LACI activity was similar in Control, SpL, FaL, and FaH stands but greater in SpH compared to control stands. MYOT and CORA activity were unaffected by prescribed fire and overstory thinning and did not differ among treatment and control stands ($P \geq 0.067$; Appendix A.6, A.7, A.8).

### Forest Clutter

Live overstory basal area was affected by treatment alone (Table 3.3). There was no difference in live overstory basal area among control, SpL and FaL stands. Overstory basal area was lower in SpH and FaH stands, but did not differ between these two treatments. Midstory density was affected by a treatment * year interaction (Table 3.4), in addition to treatment alone (Appendix Table A.4). In 2013, there was no difference in midstory density between control and FaL stands. However, midstory density was lower in SpL and SpH compared to control stands and greater in FaH compared to control stands. In 2014, midstory density was higher in SpL, SpH, FaL and FaH compared to control stands, but did not differ between these four treatments.

### Nocturnal Flying Insect Availability

We collected nocturnal flying insects within our 10 study stands for 120 nights from May−July 2013 and 2014 (12 nights/stand/year), for a total of 2,880 collection hours (i.e., 12 hours/night) over 2 years. Overall, we captured a total of 40,220 insects with a biomass of 242.95 g. Of this total, 130 g (53.50%) were collected in 2013 and 113 g

Table 3.3: Effect of treatment on live overstory basal area in hardwood forest stands subject to prescribed fire and overstory thinning at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013−2014.

| Live Overstory Basal Area ($m^2ha^{-1}$)/Treatment ($\bar{x}$ ± SE)[a] | | | | | |
|---|---|---|---|---|---|
| Control | SpL[b] | SpH[b] | FaL[b] | FaH[b] | *P* |
| 20.57 ± $1.87_{A}$ | 13.71 ± $0.87_{AC}$ | 5.88 ± $2.41_{B}$ | 12.49 ± $2.02_{AC}$ | 8.70 ± $1.79_{BC}$ | 0.009 |

[a] Means in a row followed by the same uppercase letter not different ($P > 0.05$)

[b] Treatments: SpL = spring prescribed fire and low overstory thinning (woodland with a target residual basal area of 14 $m^2ha^{-1}$), SpH = spring prescribed fire and high overstory thinning (savanna with a target residual basal area of 7 $m^2ha^{-1}$), FaL = fall prescribed fire and low overstory thinning, FaH = fall prescribed fire and high overstory thinning.

Table 3.4: Effect of a treatment * year interaction on midstory density in hardwood forest stands subject to prescribed fire and overstory thinning at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013−2014.

| | Midstory Density (stems/m$^2$)/Treatment ($\bar{x}$ ± SE)[b] | | | | | |
|---|---|---|---|---|---|---|
| Year | Control | SpL[c] | SpH[c] | FaL[c] | FaH[c] | *P* |
| 2013 | $6.70 \pm 1.37_{A}$ | $4.16 \pm 0.78_{B}$ | $3.60 \pm 0.98_{BC}$ | $4.13 \pm 0.95_{AB}$ | $10.35 \pm 0.39_{C}$ | ≤ 0.001 |
| 2014 | $8.09 \pm 0.98_{A}$ | $9.65 \pm 0.07_{BC}$ | $24.60 \pm 0.10_{B}$ | $13.25 \pm 1.42_{BC}$ | $15.21 \pm 1.18_{C}$ | |

[b] Means in a row followed by the same uppercase letter not different (*P* > 0.05)

[c] Treatments: SpL = spring prescribed fire and low overstory thinning (woodland with a target residual basal area of 14 m$^2$ha$^{-1}$), SpH = spring prescribed fire and high overstory thinning (savanna with a target residual basal area of 7 m$^2$ha$^{-1}$), FaL = fall prescribed fire and low overstory thinning, FaH = fall prescribed fire and high overstory thinning.

(46.50%) in 2014. Insect biomass was not affected by prescribed fire and overstory thinning and did not differ among treatment and control stands ($P \geq 0.478$).

### Effects of Clutter and Nocturnal Flying Insect Availability on Bat Activity

Two models were the best predictors of total bat activity. These models contained the variables live overstory basal area and insect biomass. These same two models were also the best predictors of EFLN activity (Table 3.5). Total bat activity and EFLN activity were both inversely related with live overstory basal area. Insect biomass had a weak effect on total bat activity and EFLN activity (Table 3.6). Three models, containing the variables live overstory basal area, insect biomass, and distance to water, were the best predictors of LBNH activity (Table 3.5). LBNH activity was also inversely related to live overstory basal area. Insect biomass and distance to water had a weak effect on LBNH activity (Table 3.6). Two models were the best predictor of PESU activity, and contained the variables live overstory basal area, midstory density, and insect biomass (Table 3.5). PESU activity was inversely related to both live overstory basal area and midstory density. Insect biomass had a weak effect on PESU activity. Five models, including the null, were the best predictors of LACI activity. These models contained the variables live overstory basal area, midstory density, and insect biomass (Table 3.5). All of these variables had a weak effect on LACI activity (Table 3.6; All models shown in Appendix Table A.9).

Table 3.5: Supported models of variables affecting bat activity in hardwood forest stands subject to prescribed fire and overstory thinning at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013−2014.

| Species Group[a] | Model[b] | *K* | AICc | ΔAICc | $w_i$ |
|---|---|---|---|---|---|
| Total | BA | *2* | 851.20 | 0.00 | 0.31 |
| | BA + IB | *3* | 851.35 | 0.15 | 0.29 |
| LBNH | BA | 2 | 625.78 | 0.00 | 0.24 |
| | BA + IB | 3 | 626.15 | 0.38 | 0.20 |
| | BA + DW | 3 | 627.47 | 1.69 | 0.10 |
| EFLN | BA | 2 | 764.95 | 0.00 | 0.37 |
| | BA + IB | 3 | 765.61 | 0.66 | 0.26 |
| PESU | BA + MD | 3 | 608.15 | 0.00 | 0.34 |
| | BA + MD + IB | 4 | 610.15 | 1.99 | 0.13 |
| LACI | MD + IB | 3 | 491.11 | 0.00 | 0.18 |
| | MD | 2 | 491.73 | 0.62 | 0.13 |
| | BA + IB | 3 | 492.36 | 1.25 | 0.10 |
| | BA | 2 | 492.42 | 1.31 | 0.09 |
| | IB | 2 | 492.58 | 1.47 | 0.09 |
| | Null | 1 | 493.01 | 1.90 | 0.07 |

[a] Species groups: Total = all bats (identified and unidentified); LBNH = eastern red bat (*Lasiurus borealis*) and evening bat (*Nycticeius humeralis*); EFLN = big brown bat (*Eptesicus fuscus*) and silver-haired bat (*Lasionycteris noctivagans*); PESU = tricolored bat (*Perimyotis subflavus*), LACI = hoary bat (*Lasiurus cinereus*)

[b] Variables: BA = live overstory basal area ($m^2ha^{-1}$); MD = midstory density (stems/$m^2$), IB = insect biomass (g); DW = distance to water (m)

Table 3.6: Coefficients from supported models of variables affecting bat activity in hardwood forest stands subject to prescribed fire and overstory thinning at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013−2014.

| | | | | 95% CI | |
|---|---|---|---|---|---|
| Species Group[a] | Variable[b] | *B* | SE | Lower | Upper |
| Total | BA | -20.65 | 6.09 | -32.59 | -8.71 |
| | IB | -13.20 | 9.17 | -31.17 | 4.76 |
| LBNH | BA | -2.29 | 0.99 | -4.24 | -0.34 |
| | IB | -1.91 | 1.40 | -4.66 | 0.84 |
| | DW | -0.04 | 0.05 | -0.15 | 0.06 |
| EFLN | BA | -2.19 | 0.93 | -4.02 | -0.36 |
| | IB | -1.91 | 1.40 | -4.66 | 0.83 |
| PESU | BA | -2.42 | 1.09 | -4.55 | -0.28 |
| | MD | -2.64 | 1.00 | -4.59 | -0.69 |
| | IB | 0.73 | 1.22 | -1.66 | 3.13 |
| LACI | BA | -0.49 | 0.31 | -1.09 | 0.11 |
| | MD | 0.53 | 0.28 | -0.02 | 1.07 |
| | IB | -0.74 | 0.46 | -1.64 | 0.16 |

[a] Species groups: Total = all bats (identified and unidentified); LBNH = eastern red bat (*Lasiurus borealis*) and evening bat (*Nycticeius humeralis*); EFLN = big brown bat (*Eptesicus fuscus*) and silver-haired bat (*Lasionycteris noctivagans*); PESU = tricolored bat (*Perimyotis subflavus*), LACI = hoary bat (*Lasiurus cinereus*)

[b] Variables: BA = live overstory basal area ($m^2ha^{-1}$), MD = midstory density (stems/$m^2$), IB = insect biomass (g), DW = distance to water (m)

# DISCUSSION

The results of our study suggest that prescribed fire and overstory thinning treatments may increase the use of previously closed-canopy hardwood forest stands by foraging bats. We found total bat activity within control stands to be relatively low; comprising only 6.8% of the activity recorded across all study stands. This is comparable to other studies that have found low levels of bat activity in closed canopy forest (Grindal and Brigham 1998, Humes et al. 1999, Erickson and West 2003, Menzel et al. 2005; Loeb and Waldrop 2008, Titchenell et al. 2011). However, total bat activity was greater in stands that had been subject to prescribed fire, particularly during the spring and high levels of overstory thinning, representing 64% of the activity recorded across all stands. Activity of LBNH, EFLN, PESU and LACI was greater in these same stands. It is likely greater activity was a result of these stands being selected by bats as foraging areas (Titchenell et al. 2011).

Our results are comparable to those of other studies examining bat response to prescribed fire and overstory thinning or similar silvicultural treatments, although most of these studies have been conducted in pine forests. Bat activity was higher in recently burned Florida longleaf pine-wiregrass stands and was positively associated with height of canopy closure, suggesting benefits to certain species of reduced clutter (Armitage and Ober 2012). Humes et al. (1999) found bat activity was higher in thinned Douglas fir (*Pseudotsuga menziesii*) stands than un-thinned stands of the same age. They concluded that the structural changes resulting from thinning may benefit bats by creating a habitat structure they are able to use more effectively. Loeb and Waldrop (2008) also found that total bat activity was higher in thinned southern pine stands than in control stands, but stands that were burned and thinned didn't vary from that of controls. Consistent with our results, Ford et al. (2006) found red bats, tri-colored bats, and big brown bats were detected more often in open habitats than in closed forest in the coastal plain of South Carolina. These same species were detected more in forests with less dense vegetation in South Carolina (Loeb and O'Keefe 2006). However, there are exceptions. Thinning of red pine (*Pinus resinosa*) stands in Michigan did not lead to an increase in their use by bats, despite significant changes in their structural complexity. Even after thinning, red pine plantations may be too structurally complex for use by foraging bats (Tibbels and Kurta 2003). Another study, conducted in boreal forest, also found thinning had minimal effect on habitat use by bats. However, this study did emphasize the practice may have different effects on different species that may be obscured if the community is studied as a single entity (Patriquin and Barclay 2003), something we potentially avoided by studying individual species or groups of species with similar call characteristics and wing morphology.

We suggested fire and overstory thinning treatments might affect bat activity through changes in forest clutter. Live overstory basal area, a variable that has been shown to provide an effective quantitative measure of clutter (O'Keefe 2014), was lower in stands that were subject to prescribed fire and high levels of overstory thinning, the same stands that had the greatest activity of LBNH, EFLN, PESU and LACI. This indicated increases in bat activity in SpH and FaH stands may be a result of reduced clutter. This was supported by our findings, which showed total bat activity and activity of LBNH, EFLN, PESU and LACI are inversely related with live overstory basal area.

A bat’s ability to maneuver in clutter and capture insect prey depends on a number of factors including body size and wing morphology, particularly wing aspect ratio (AR; length of the wing squared divided by its surface area) and wing loading (WL; mass of the bat divided by its total wing area). Larger-bodied bat species with high WLs or ARs tend to be less maneuverable and more adapted to flight in more open, less cluttered areas (Findley and Black 1983, Aldridge and Rautenbach 1987, Crome and Richards 1988; Kalcounis et al. 1999, Kingston et al. 2000, Lee and McCracken 2004). A bat’s capacity to maneuver in and capture insect prey in clutter also depends on its echolocation call capabilities. The structure of search-phase calls emitted by bats when looking for prey, are related to habitat and foraging strategy (Schnitzler and Kalko 1998). Species with broadband calls of high frequency are better suited to foraging in more cluttered forest locations (Simmons and Stein 1980). In contrast, species with narrowband calls of low frequency are more suited to open locations (Neuweiler 1983). This is consistent with our observations. Groups (EFLN, LBNH, and LACI) containing bats with moderate to low frequency calls and/or moderate to high WL/AR values exhibited greater activity in stands with less clutter than in more cluttered control stands, likely due to the increased efficiency of flight during foraging and easier prey capture. A study in Kentucky hardwood forest found a shift in the foraging ranges of larger-bodied bats with high ARs and WLs towards burned areas with less clutter (Lacki et al. 2009b). These species also had low frequency calls. In Florida longleaf pine stands, small-bodied bat species with low ARs and WLs replaced large-bodied, less maneuverable species below the canopy at sites with >8-year burn frequencies due to increased midstory growth and clutter (Armitage and Ober 2012). We might have expected to see lower activity of MYOT in stands treated with prescribed fire and overstory thinning compared to controls based upon wing morphology (low AR/WLs) and echolocation call characteristics (high frequency calls; Lacki et al. 2007) but we found no support for this. This may have been because sample size was too small or, alternatively, as proposed by Titchnell et al. (2011), because myotine species may be better able to exploit forest habitat regardless of clutter and therefore forage in areas that are most profitable.

We also proposed prescribed fire and overstory thinning treatments might affect bat activity through changes in availability of nocturnal flying insect prey (Grindal and Brigham 1998 and 1999, Loeb and Waldrop 2008, Titchenell et al. 2011, Armitage and Ober 2012). All bats inhabiting North American forests are insectivorous and rely on insects as a prey base (Lacki et al. 2007). Although specializations have been reported, most species consume insects from multiple orders, their diet varying by geographic location, time of night, season, and year, presumably as a result of shifts in the availability of insects of different types (Whitaker 1972, Whitaker and Clem 1992, Kurta and Whitaker 1998, Murray and Kurta 2002, Lee and McCracken 2001). However, we found no difference in nocturnal flying insect abundance or biomass among treatment and control stands, and our results indicate insect availability was not driving the changes in bat activity we observed.

Most studies indicate a response of insects to prescribed fire and overstory thinning or similar treatments, although results are highly variable (Nagel 1973, Hansen 1986, Siemann et al. 1997, Swengel 2001, Lacki et al. 2009). However, only a few studies, like ours, found no response of abundance and biomass of insects to treatments. Armitage and Ober (2012) found few differences in abundance or biomass of most insect orders in prescribed fire treated longleaf pine stands of different fire frequency, with the exception of Lepidoptera, which had a lower biomass on sites subject to frequent fire. Similarly, Grindal and Brigham (1998) found insect availability was not affected by tree removal, being similar in 0.5 ha, 1.0 ha, and 1.5 ha cut blocks (areas where trees have been harvested) to uncut blocks.

One of the most important assumptions of our study is that the number of echolocation calls recorded in a stand provides a good indication of bat activity and use in that stand. This should hold true if we successfully avoided variation among detectors, as well as temporal variation (Hayes 2000, Loeb and Waldrop 2008, Titchenell et al. 2011). We minimized these sources of variation by programming our detectors with the same settings and sampling in replicate areas for multiple nights, several times over the course of each summer. Other studies suggest variation in detectability of bats among habitats due to forest structure (i.e., clutter) is minimal (Patriquin et al. 2003, Yates and Muzika 2006, Obrist et al. 2011, Titchenell et al. 2011) and we believe this to be the case for our study. Of the bat passes we recorded, we were able to identify >60% to species. This is high compared to some other studies (Loeb and Waldrop 2008, Titchenell et al. 2011, O'Keefe et al. 2014) and may be a result of using full spectrum rather than zero-crossing recording methods. Full spectrum recordings provide complete time-frequency data, including minimum frequencies, call duration, slope of call, and harmonics (Ahlén and Baagøe 1999). In addition, full spectrum recordings provide amplitude components such as frequency of maximum amplitude and relative energy among calls and harmonics. Measurement of these parameters may allow better species identification than zero-crossing recording methods (Fenton 2000, Fenton et al. 2001). However, even though during analysis we were able to identify a large proportion of recordings to species, we decided to group species based on call frequency and wing morphology. If we had used a less conservative approach we may have identified more calls, but at the cost of some misclassification, which may have influenced our results and management recommendations.

## CONCLUSIONS

Our results indicate the use of prescribed fire and overstory thinning treatments to restore and maintain woodlands and savanna in the Southeastern U.S. has minimal negative effects on bats and benefits a number of species. These treatments can reduce clutter in hardwood forest stands leading to improved foraging conditions for bats, particularly species with lower call frequencies or high AR/WL ratios. This provides support for continued restoration of closed canopy hardwood forest to more open woodland and savanna. We recognize that our study was only conducted for two years and that foraging conditions are likely to change over time depending on the frequency of prescribed fire application. Therefore, long-term research that focuses on forest structure and clutter must be implemented in stands that have been subject to overstory thinning and are being burned under varying fire frequencies to aid forest managers in making sound management decisions regarding bat management and conservation.

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# CHAPTER IV

# CONCLUSIONS

# CHAPTER II: THE EFFECTS OF PRESCRIBED FIRE AND OVERSTORY THINNING OF HARDWOOD FORESTS IN THE CUMBERLAND PLATEAU ON NOCTURNAL FLYING INSECTS IMPORTANT IN THE DIET OF BATS

- We observed localized reductions in nocturnal flying insect abundance, typically following times of no precipitation lasting several days/ weeks.
- We also observed localized increases in certain orders of insects, typically aquatic insects, such as Trichoptera, Ephemeroptera, and Plecoptera, but only for brief periods, usually one night during certain times of the summer. Perhaps the increases came during insect emergence from the nearby Obed River or from the ponds that are scattered throughout our research area.
- Prescribed fire and overstory thinning treatments generally did not to affect insects during this study.
- We would recommend that if future research is conducted on the effects of prescribed fire and/or overstory thinning, that nocturnal flying insects should be collected for two weeks prior to the prescribed fire and/or overstory thinning treatment and for two weeks post treatment. In addition, we recommend attempting to identify insects to family or species.

- Although, prescribed fire and overstory thinning treatments in our study don’t appear to influence nocturnal flying insect availability. We still recommend that these treatments be applied in a mosaic across the landscape leaving untreated areas to promote a diversity of insect prey for bats.

## CHAPTER III: RESPONSE OF BATS TO PRESCRIBED FIRE AND OVERSTORY THINNING IN A HARDWOOD FOREST ON THE CUMBERLAND PLATEAU

- Prescribed fire and overstory thinning treatments benefit bats with high wing-loading/ aspect ratios, such as *E. fuscus, N. humeralis, L. cinereus, L. borealis, and L. noctivagans*, by creating a more open foraging area that they are better adapted for flying. They also seem to benefit *P. subflavus* which is a bat species with a low wing-loading/ aspect ratio.
- Of the six species listed above, two have tested positive for *P. destructans* (*L. noctivagans* and *L. borealis*) and two have been confirmed to have WNS (*E. fuscus* and *P. subflavus*). It would be beneficial to continue this research to see if there activity in the more open stands with lower basal area changes over time, so we can better understand the mechanism driving their activity in these areas.
- We did observe a decline in *Myotis spp.* and *P. subflavus* acoustic activity in all stands from summer 2013-2014. *Myotis spp.* declined 70.29% and *P. subflavus* declined 73.23%. We do not know what caused the declines. They could have been a result of WNS or other environmental factors, but further research is needed.
- Increased acoustic activity of species unaffected by WNS was driven by *L. cinereus*, which is a regional endemic and maybe filling the niche once occupied by species that are being affected by WNS.
- According to our predictive model, live overstory basal area accounted for 31% of the AIC weight for total bat activity. It would be helpful if future research could include other clutter variables, such as canopy crown volume, to see what accounts for the remaining 69%.

- If this project continues it would be beneficial to include locations of potential roost trees and try to capture bats, via mist-netting, in each stand, so we can verify the species being recorded and what the roost tree availability is in the research area.

# APPENDICES

Table A.1: Effect of treatment on nocturnal flying insect abundance and biomass in hardwood forest stands subject to prescribed fire and overstory thinning treatments at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013−2014.

| Insect Order[a] | Nocturnal Flying Insect Abundance (no. of individuals) and Biomass (g) /Treatment ($\bar{x}$ ± SE)[b] | | | | | |
|---|---|---|---|---|---|---|
| | Control | SpL[c] | SpH[c] | FaL[c] | FaH[c] | *P* |
| Abundance | | | | | | |
| Total | 576.92 ± 109.26 | 569.25 ± 230.21 | 522.08 ± 129.56 | 673.58 ± 170.53 | 1009.83 ± 235.76 | 0.399 |
| Coleoptera | 302.25 ± 94.30 | 197.75 ± 83.95 | 328.58 ± 93.55 | 400.17 ± 148.05 | 547.58 ± 133.36 | 0.220 |
| Diptera | 77.58 ± 29.01 | 47.00 ± 17.67 | 45.75 ± 12.76 | 59.92 ± 13.88 | 76.42 ± 17.57 | 0.451 |
| Lepidoptera | 175.00 ± 41.41 | 305.08 ± 135.30 | 135.92 ± 45.30 | 193.33 ± 49.42 | 355.00 ± 131.89 | 0.729 |
| Hemiptera | 6.92 ± 2.31 | 11.67 ± 5.60 | 8.67 ± 5.26 | 10.83 ± 3.45 | 21.08 ± 7.24 | 0.138 |
| Biomass | | | | | | |
| Total | 60.78 ± 14.02 | 30.20 ± 7.15 | 39.03 ± 14.96 | 40.77 ± 9.21 | 31.68 ± 9.57 | 0.478 |
| Coleoptera | 16.68 ± 4.60 | 10.89 ± 2.98 | 17.03 ± 4.77 | 19.42 ± 4.41 | 14.67 ± 3.95 | 0.812 |
| Diptera | 0.25 ± 0.08 | 0.49 ± 0.21 | 0.42 ± 0.18 | 0.54 ± 0.15 | 0.48 ± 0.22 | 0.614 |
| Lepidoptera | 42.51 ± 10.86 | 17.57 ± 5.89 | 18.83 ± 10.10 | 19.29 ± 4.57 | 15.02 ± 5.63 | 0.212 |
| Hemiptera | 0.16 ± 0.09 | 0.29 ± 0.14 | 0.62 ± 0.02 | 0.61 ± 0.28 | 0.32 ± 0.12 | 0.895 |

[a] Insect Orders: Total = abundance for all orders combined (no. of individuals or g)

[b] Means in a row followed by the same uppercase letter not different (*P* > 0.05)

[c] Treatments: SpL = spring prescribed fire and low overstory thinning (woodland with target residual basal area of 14 $m^2ha^{-1}$), SpH = spring prescribed fire and high overstory thinning (savanna with target residual basal area of 7 $m^2ha^{-1}$), FaL = fall prescribed fire and low overstory thinning, FaH = fall prescribed fire and high overstory thinning.

Table A.2: Effect of a treatment * year interaction on nocturnal flying insect abundance and biomass in hardwood forests stands subject to prescribed burning and overstory thinning over 2 years at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013−2014.

| | | Nocturnal Flying Insect Abundance (no. of individuals) and Biomass (g)/Treatment (x̄ ± SE)[b] | | | | | |
|---|---|---|---|---|---|---|---|
| Insect Orders[a] | Year | Control | SpL[c] | SpH[c] | FaL[c] | FaH[c] | *P* |
| Abundance | | | | | | | |
| Total | 2013 | 451.17 ± 63.44 | 519.83 ± 342.10 | 495.83 ± 172.24 | 485.83 ± 149.42 | 1098.83 ± 367.41 | 0.901 |
| | 2014 | 702.67 ± 205.36 | 618.67 ± 339.37 | 548.33 ± 209.57 | 861.33 ± 302.53 | 920.83 ± 326.19 | |
| Coleoptera | 2013 | 149.50 ± 33.21 | 183.67 ± 92.68 | 284.83 ± 92.09 | 151.33 ± 35.32 | 511.17 ± 130.00 | 0.411 |
| | 2014 | 455.00 ± 169.38 | 211.83 ± 149.46 | 372.33 ± 171.07 | 649.00 ± 265.38 | 584.00 ± 246.63 | |
| Diptera | 2013 | 111.83 ± 54.27 | 55.00 ± 35.53 | 52.83 ± 18.75 | 74.83 ± 24.51 | 70.83 ± 19.58 | 0.812 |
| | 2014 | 43.33 ± 16.95 | 39.00 ± 9.23 | 38.67 ± 18.56 | 45.00 ± 12.57 | 82.00 ± 31.03 | |
| Lepidoptera | 2013 | 161.67 ± 42.58 | 266.17 ± 216.81 | 154.67 ± 82.66 | 246.83 ± 89.37 | 472.83 ± 229.60 | 0.538 |
| | 2014 | 188.33 ± 75.24 | 344.00 ± 181.46 | 117.17 ± 45.36 | 139.83 ± 40.18 | 237.17 ± 135.15 | |
| Other | 2013 | 23.00 ± 7.17 | 9.50 ± 3.90 | 1.50 ± 0.50 | 7.50 ± 3.71 | 11.50 ± 2.88 | 0.103 |
| | 2014 | 7.33 ± 2.29 | 6.00 ± 4.27 | 4.83 ± 2.71 | 11.17 ± 4.15 | 8.00 ± 4.22 | |
| Biomass | | | | | | | |
| Total | 2013 | 57.71 ± 15.09 | 35.60 ± 12.68 | 19.10 ± 39.37 | 40.17 ± 11.04 | 23.44 ± 12.76 | 0.687 |
| | 2014 | 63.84 ± 25.18 | 24.80 ± 7.24 | 58.96 ± 28.46 | 41.37 ± 15.84 | 39.92 ± 14.58 | |
| Coleoptera | 2013 | 11.68 ± 3.20 | 10.21 ± 5.18 | 10.23 ± 3.13 | 19.32 ± 6.39 | 11.11 ± 5.61 | 0.920 |
| | 2014 | 21.68 ± 8.54 | 11.57 ± 3.51 | 23.83 ± 8.49 | 19.53 ± 6.69 | 18.22 ± 5.68 | |
| Diptera | 2013 | 0.15 ± 0.06 | 0.65 ± 0.39 | 0.50 ± 0.34 | 0.39 ± 13.41 | 0.25 ± 0.15 | 0.972 |
| | 2014 | 0.35 ± 15.23 | 0.32 ± 0.16 | 0.33 ± 0.15 | 0.70 ± 27.34 | 0.71 ± 0.40 | |
| Lepidoptera | 2013 | 45.24 ± 14.92 | 23.18 ± 10.83 | 6.67 ± 2.03 | 18.90 ± 4.17 | 10.09 ± 5.78 | 0.524 |
| | 2014 | 39.78 ± 17.12 | 11.97 ± 4.81 | 30.98 ± 19.63 | 19.67 ± 8.62 | 19.95 ± 9.83 | |
| Other | 2013 | 0.56 ± 0.32 | 1.17 ± 0.56 | 1.30 ± 0.35 | 0.94 ± 0.32 | 1.55 ± 1.26 | 0.642 |
| | 2014 | 1.80 ± 78.26 | 0.75 0.27 | 2.97 ± 1.36 | 0.87 ± 0.37 | 0.84 ± 0.41 | |

[a] Insect Orders: Total = abundance for all orders combined (no. of individuals or g)

[b] Means in a row not different (*P* > 0.05)

[c] Treatments: SpL = spring prescribed fire and low overstory thinning (woodland with target residual basal area of 14 $m^2ha^{-1}$), SpH = spring prescribed fire and high overstory thinning (savanna with target residual basal area of 7 $m^2ha^{-1}$), FaL = fall prescribed fire and low overstory thinning, FaH = fall prescribed fire and high overstory thinning.

Table A.3: Effect of a treatment * sample period on nocturnal flying insect abundance and biomass in hardwood forests stands subject to prescribed burning and overstory thinning over 2 years at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013-2014.

| Insect Order[a] | Sampling Period | Nocturnal Flying Insect Abundance (no. of individuals) and Biomass (g)/Treatment ($\bar{x}$ ± SE)[b] | | | | | *P* |
|---|---|---|---|---|---|---|---|
| | | Control | SpL[c] | SpH[c] | FaL[c] | FaH[c] | |
| Abundance | | | | | | | |
| Total | May | 728.50 ± 257.57 | 819.25 ± 495.46 | 630.75 ± 290.55 | 593.75 ±183.48 | 1426.25 ± 518.58 | 0.687 |
| | June | 283.25 ± 81.44 | 732.75 ± 495.00 | 529.50 ± 203.70 | 800.75 ± 463.94 | 1042.00 ± 409.75 | |
| | July | 719.00 ± 123.29 | 155.75 ± 75.54 | 406.00 ± 224.27 | 626.25 ± 250.43 | 561.25 ± 222.17 | |
| Coleoptera | May | 429.00 ± 257.02 | 351.25 ± 204.27 | 500.75 ± 239.27 | 191.25 ± 36.68 | 831.50 ± 317.51 | 0.710 |
| | June | 120.75 ± 47.81 | 187.75 ± 141.55 | 241.50 ± 89.19 | 612.75 ± 376.27 | 483.25 ± 185.04 | |
| | July | 357.00 ± 110.17 | 54.25 ± 31.68 | 243.50 ± 127.47 | 396.50 ± 261.83 | 328.00 ± 127.51 | |
| Diptera | May | 58.50 ± 24.62 | 42.25 ± 11.38 | 40.00 ± 30.05 | 80.50 ± 32.15 | 60.00 ± 15.07 | 0.675 |
| | June | 35.25 ± 10.87 | 75.50 ± 52.28 | 53.25 ± 10.33 | 41.25 ± 22.55 | 116.25 ± 44.05 | |
| | July | 139.00 ± 80.96 | 23.25 ± 10.16 | 44.00 ± 27.39 | 58.00 ± 17.82 | 53.00 ± 20.67 | |
| Lepidoptera | May | 222.75 ± 103.01 | 377.25 ± 286.37 | 72.25 ± 46.68 | 300.50 ± 117.85 | 497.75 ± 346.82 | 0.539 |
| | June | 117.25 ± 57.59 | 462.25 ± 299.49 | 227.00 ± 109.28 | 121.25 ± 62.55 | 401.75 ± 198.87 | |
| | July | 185.00 ± 55.03 | 75.75 ± 46.35 | 108.50 ± 63.92 | 158.25 ± 55.63 | 165.50 ± 109.59 | |
| Other | May | 12.25 ± 5.78 | 17.75 ± 5.45 | 1.50 ± 0.87 | 10.50 ± 4.81 | 14.25 ± 6.22 | 0.091 |
| | June | 8.25 ± 3.35 | 4.50 ± 1.94 | 3.00 ± 0.41 | 11.50 ± 6.55 | 10.25 ± 3.10 | |
| | July | 25.00 ± 10.37 | 1.00 ± 1.00 | 5.00 ± 4.34 | 6.00 ± 3.03 | 4.75 ± 2.21 | |
| Biomass | | | | | | | |
| Total | May | 80.48 ± 14.29 | 39.16 ± 18.66 | 31.56 ± 13.95 | 45.57 ± 19.51 | 34.35 ± 11.51 | 0.786 |
| | June | 73.61 ± 37.26 | 31.67 ± 11.42 | 14.49 ± 4.75 | 37.11 ± 14.95 | 47.87 ± 25.29 | |
| | July | 28.24 ± 5.78 | 19.76 ± 4.50 | 71.04 ± 41.02 | 39.62 ± 17.76 | 12.83 ± 5.16 | |
| Coleoptera | May | 14.20 ± 1.45 | 62.52 ± 24.86 | 11.18 ± 3.94 | 22.06 ± 7,51 | 19.37 ± 5.30 | 0.760 |
| | June | 20.02 ± 14.00 | 16.52 ± 7.86 | 10.96 ± 4.14 | 16.94 ± 6.85 | 18.02 ± 9.33 | |
| | July | 15.82 ± 5.38 | 9.91 ± 3.52 | 28.96 ± 12.12 | 19.28 ± 10.31 | 6.60 ± 4.87 | |
| Diptera | May | 0.29 ± 0.07 | 0.91 ± 0.55 | 0.74 ± 0.47 | 0.36 ± 0.25 | 0.32 ± 0.19 | 0.560 |
| | June | 0.31 ± 0.23 | 0.38 ± 24.26 | 0.06 ± 0.04 | 0.61 ± 0.37 | 0.73 ± 0.63 | |
| | July | 0.14 ± 0.12 | 0.17 ± 0.08 | 0.45 ± 0.21 | 0.65 ± 0.20 | 0.39 ± 0.22 | |
| Lepidoptera | May | 63.92 ± 14.80 | 30.71 ± 16.55 | 17.13 ± 8.26 | 21.13 ± 11.30 | 13.23 ± 6.31 | 0.412 |
| | June | 52.77 ± 23.20 | 13.57 ± 3.13 | 2.43 ± 1.06 | 18.66 ± 7.52 | 26.47 ± 15.15 | |
| | July | 10.83 ± 4.14 | 8.44 ± 2.77 | 36.91 ± 29.19 | 18.07 ± 6.59 | 5.37 ± 1.95 | |

Table A.3 Cont.: Effect of a treatment * sample period on nocturnal flying insect abundance and biomass in hardwood forests stands subject to prescribed burning and overstory thinning over 2 years at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013-2014.

| | Sampling | Nocturnal Flying Insect Biomass (g)/Treatment ($\bar{x}$ ± SE)[b] | | | | | |
|---|---|---|---|---|---|---|---|
| Insect Order[a] | Period | Control | SpL[c] | SpH[c] | FaL[c] | FaH[c] | *P* |
| Other | May | 1.95 ± 1.12 | 10.13 ± 9.02 | 1.74 ± 1.19 | 1.12 ± 0.49 | 1.10 ± 0.56 | 0.349 |
| | June | 0.21 ± 0.19 | 0.96 ± 0.35 | 0.96 ± 0.54 | 0.62 ± 0.38 | 2.21 ± 1.87 | |
| | July | 1.38 ± 0.61 | 0.89 ± 0.27 | 3.71 ± 1.61 | 0.97 ± 0.43 | 0.28 ± 0.23 | |

[a] Insect Orders: Total = abundance for all orders combined (no. of individuals or g)

[b] Means in a row not different (*P* > 0.05)

[c] Treatments: SpL = spring prescribed fire and low overstory thinning (woodland with target residual basal area of 14 $m^2ha^{-1}$), SpH = spring prescribed fire and high overstory thinning (savanna with target residual basal area of 7 $m^2ha^{-1}$), FaL = fall prescribed fire and low overstory thinning, FaH = fall prescribed fire and high overstory thinning.

Table A.4: Effect of treatment on vegetation characteristics/clutter in hardwood forest stands subject to prescribed fire and overstory thinning at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013−2014.

| Vegetation Characteristic [a] | Vegetation Characteristic and Clutter/Treatment ($\bar{x}$ ± SE) | | | | | |
|---|---|---|---|---|---|---|
| | Control | SpL[b] | SpH[b] | FaL[b] | FaH[b] | *P* |
| Midstory [c] | $7.39 \pm 0.828_{A}$ | $6.91 \pm 0.91_{A}$ | $14.10 \pm 3.20_{B}$ | $8.69 \pm 1.60_{AB}$ | $12.78 \pm 0.94_{B}$ | 0.148 |
| Rock/Bare[d] | 0.67 ± 0.13 | 3.08 ± 1.75 | 3.16 ± 1.42 | 3.96 ± 2.04 | 1.95 ± 0.69 | 0.102 |

[a] Vegetation Characteristics: Midstory = midstory density (stems/$m^2$), Rock/Bare = percent cover of rock or bare ground (%)

[b] Treatments: SpL = spring prescribed fire and low overstory thinning (woodland with target residual basal area of 14 $m^2 ha^{-1}$), SpH = spring prescribed fire and high overstory thinning (savanna with target residual basal area of 7 $m^2 ha^{-1}$), FaL = fall prescribed fire and low overstory thinning, FaH = fall prescribed fire and high overstory thinning.

[c] Means in row followed by the same uppercase letter not different ($P > 0.05$).

[d] Means in row not different ($P > 0.05$).

Table A.5: Effect of a treatment * year interaction on vegetation characteristics/clutter in hardwood forest stands subject to prescribed fire and overstory thinning at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013−2014.

| Vegetation | | Vegetation Characteristic and Clutter/Treatment ($\bar{x}$ ± SE) | | | | | |
|---|---|---|---|---|---|---|---|
| Characteristic [a] | Year | Control | SpL [b] | SpH [b] | FaL [b] | FaH [b] | P |
| Basal Area | 2013 | 19.26 ± 1.74 | 14.19 ± 0.76 | 9.38 ± 1.40 | 12.88 ± 12.9 | 10.21 ± 1.58 | 0.689 |
| | 2014 | 21.89 ± 0.67 | 13.22 ± 0.49 | 2.38 ± 0.37 | 12.11 ± 1.78 | 7.20 ± 0.66 | |
| Understory | 2013 | 4.45 ± 1.88 | 6.37 ± 0.44 | 7.68 ± 4.17 | 6.68 ± 0.09 | 9.64 ± 1.87 | 0.449 |
| | 2014 | 2.41 ± 0.43 | 8.63 ± 0.42 | 11.92 ± 0.81 | 9.57 ± 2.93 | 7.87 ± 0.85 | |
| Rock/Bare | 2013 | 0.88 ± 0.11 | 6.06 ± 0.64 | 5.60 ± 0.56 | 7.20 ± 1.94 | 3.13 ± 0.15 | 0.059 |
| | 2014 | 0.46 ± 0.06 | 0.09 ± 0.09 | 0.72 ± 0.17 | 0.71 ± 0.32 | 0.77 ± 0.29 | |
| Litter/CWD | 2013 | 56.48 ± 1.48 | 20.29 ± 0.18 | 9.98 ± 1.33 | 15.92 ± 2.36 | 9.50 ± 0.65 | 0.191 |
| | 2014 | 62.03 ± 4.16 | 12.67 ± 1.50 | 2.36 ± 1.12 | 13.58 ± 3.42 | 5.86 ± 0.32 | |
| Forb | 2013 | 2.90 ± 1.33 | 1.24 ± 0.06 | 9.21 ± 1.77 | 2.84 ± 0.13 | 7.98 ± 0.59 | 0.310 |
| | 2014 | 1.25 ± 0.99 | 4.11 ± 1.50 | 7.77 ± 2.17 | 4.24 ± 2.69 | 8.63 ± 2.27 | |
| Graminoid | 2013 | 0.77 ± 0.38 | 11.01 ± 0.23 | 15.75 ± 3.27 | 9.33 ± 0.60 | 21.28 ± 0.61 | 0.673 |
| | 2014 | 0.52 ± 0.40 | 13.79 ± 1.56 | 22.51 ± 3.73 | 10.35 ± 6.82 | 22.86 ± 2.59 | |
| Woody | 2013 | 37.13 ± 0.98 | 60.24 ± 0.38 | 58.88 ± 0.64 | 63.60 ± 3.41 | 54.80 ± 0.80 | 0.172 |
| | 2014 | 35.29 ± 2.64 | 66.78 ± 6.13 | 64.40 ± 3.73 | 69.82 ± 5.62 | 58.47 ± 0.77 | |
| Other | 2013 | 1.84 ± 0.86 | 1.15 ± 0.15 | 0.58 ± 0.25 | 1.10 ± 0.16 | 3.13 ± 0.40 | 0.124 |
| | 2014 | 0.46 ± 0.20 | 2.57 ± 1.50 | 2.33 ± 1.21 | 1.30 ± 0.15 | 3.41 ± 0.47 | |

[a] Vegetation Characteristic: Basal Area = live overstory basal area ($m^2ha^{-1}$), Understory = understory density (stems/$m^2$), Rock/Bare = percent cover of rock and bare ground (%), Litter/CWD = percent cover of litter and course woody debris (%), Forb = Percent cover of forbs (%), Graminoid = percent cover of graminoids (%), Woody = percent cover of woody vegetation (trees, shrubs, and woody vines; %), Other = percent cover of other vegetation (moss, lichen, fern, fungus).

[b] Means in a row not different ($P > 0.05$)

[c] Treatments: SpL = spring prescribed fire and low overstory thinning (woodland with target residual basal area of 14 $m^2ha^{-1}$), SpH = spring prescribed fire and high overstory thinning (savanna with target residual basal area of 7 $m^2ha^{-1}$), FaL = fall prescribed fire and low overstory thinning, FaH = fall prescribed fire and high overstory thinning.

Table A.6: Effect of treatment on bat activity in hardwood forest stands subject to prescribed fire and overstory thinning at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013−2014.

| Species Groups[a] | Mean Bat Passes (no. of passes)/Treatment ($\bar{x}$ ± SE) [b] | | | | | |
|---|---|---|---|---|---|---|
| | Control | SpL[c] | SpH[c] | FaL[c] | FaH[c] | *P* |
| MYOT | 15.17 ± 6.85 | 9.25 ± 2.72 | 7.08 ± 5.66 | 6.58 ± 1.55 | 5.17 ± 1.26 | 0.067 |
| CORA | 1.00 ± 0.84 | 1.00 ± 0.44 | 0.67 ± 0.58 | 0.50 ± 0.20 | 0.67 ± 0.38 | 0.724 |

[a] Species groups: MYOT = all *Myotis* spp.; CORA = Rafinesque's big-eared bat (*Corynorhinus rafinesquii*)

[b] Means in a row not different (*P* > 0.05)

[c] Treatments: SpL = spring prescribed fire and low overstory thinning (woodland with target residual basal area of 14 $m^2ha^{-1}$), SpH = spring prescribed fire and high overstory thinning (savanna with target residual basal area of 7 $m^2ha^{-1}$), FaL = fall prescribed fire and low overstory thinning, FaH = fall prescribed fire and high overstory thinning.

Table A.7: Effect of a treatment * year interaction on bat activity in hardwood forests stands subject to prescribed burning and overstory thinning over 2 years at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013−2014.

| Species | | Mean Bat Passes (no. of passes)/Treatment (x̄ ± SE)[b] | | | | | |
|---|---|---|---|---|---|---|---|
| Groups[a] | Year | Control | SpL[c] | SpH[c] | FaL[c] | FaH[c] | *P* |
| TOTAL | 1 | 169.67 ± 33.94 | 179.00 ± 93.05 | 570.83 ± 113.35 | 258.67 ± 93.90 | 364.00 ± 43.85 | 0.416 |
| | 2 | 28.67 ± 7.58 | 75.83 ± 31.50 | 733.00 ± 161.39 | 328.33 ± 190.81 | 202.00 ± 17.60 | |
| MYOT | 1 | 29.67 ± 11.06 | 13.17 ± 11.20 | 10.00 ± 4.31 | 5.83 ± 2.02 | 8.00 ± 1.71 | 0.121 |
| | 2 | 0.67 ± 0.49 | 1.00 ± 0.82 | 8.50 ± 3.72 | 4.50 ± 1.65 | 5.17 ± 2.63 | |
| LBNH | 1 | 7.50 ± 6.35 | 18.83 ± 15.85 | 53.17 ± 25.75 | 22.17 ± 10.63 | 41.67 ± 12.69 | 0.771 |
| | 2 | 6.83 ± 5.25 | 8.17 ± 3.83 | 66.17 ± 19.31 | 44.50 ± 37.55 | 19.83 ± 7.86 | |
| EFLN | 1 | 21.83 ± 10.16 | 26.00 ± 10.23 | 298.00 ± 64.64 | 78.33 ± 32.04 | 156.00 ± 53.91 | 0.430 |
| | 2 | 4.00 ± 0.93 | 33.00 ± 15.50 | 413.50 ± 101.71 | 34.83 ± 11.95 | 75.33 ± 12.37 | |
| PESU | 1 | 18.50 ± 13.61 | 26.67 ± 16.05 | 48.00 ± 18.62 | 45.33 ± 38.49 | 30.83 ± 5.49 | 0.999 |
| | 2 | 2.00 ± 1.29 | 4.50 ± 3.07 | 17.50 ± 6.64 | 4.17 ± 1.33 | 17.17 ± 6.70 | |
| CORA | 1 | 2.00 ± 1.63 | 1.33 ± 1.15 | 1.00 ± 0.68 | 1.00 ± 0.68 | 0.67 ± 0.33 | 0.795 |
| | 2 | 0.00 ± 0.00 | 0.00 ± 0.00 | 1.00 ± 0.63 | 0.33 ± 0.33 | 0.33 ± 0.21 | |
| LACI | 1 | 8.17 ± 3.16 | 4.33 ± 2.01 | 7.67 ± 2.04 | 10.50 ± 5.42 | 9.00 ± 2.99 | 0.084 |
| | 2 | 1.00 ± 1.00 | 1.00 ± 0.82 | 19.83 ± 6.79 | 19.33 ± 14.59 | 6.50 ± 3.21 | |

[a] Species groups: TOTAL = all bats (identified and unidentified); MYOT = all *Myotis* spp.; LBNH = eastern red bat (*Lasiurus borealis*) and evening bat (*Nycticeius humeralis*); EFLN = big brown bat (*Eptesicus fuscus*) and silver-haired bat (*Lasionycteris noctivagans*); PESU = tricolored bat (*Perimyotis subflavus*), CORA = Rafinesque's big-eared bat (*Corynorhinus rafinesquii*); LACI = hoary bat (*Lasiurus cinereus*).

[b] Means in a row not different ($P > 0.05$)

[c] Treatments: SpL = spring prescribed fire and low overstory thinning (woodland with target residual basal area of 14 $m^2ha^{-1}$), SpH = spring prescribed fire and high overstory thinning (savanna with target residual basal area of 7 $m^2ha^{-1}$), FaL = fall prescribed fire and low overstory thinning, FaH = fall prescribed fire and high overstory thinning.

Table A.8: Effect of a treatment * sample period interaction on bat activity in hardwood forests stands subject to prescribed burning and overstory thinning over 2 years at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013-2014.

| Species | Sampling | Mean Bat Passes (no. of passes)/Treatment ($\bar{x}$ ± SE)[b] | | | | | |
|---|---|---|---|---|---|---|---|
| Groups[a] | Period | Control | SpL[c] | SpH[c] | FaL[c] | FaH[c] | *P* |
| TOTAL | May | 78.50 ± 35.45 | 125.75 ± 69.94 | 603.00 ± 126.723 | 297.00 ± 89.38 | 307.75 ± 67.12 | 0.948 |
| | June | 111.00 ± 59.67 | 193.00 ± 133.73 | 742.00 ± 241.32 | 216.75 ± 136.51 | 232.00 ± 33.83 | |
| | July | 108.00 ± 54.42 | 63.50 ± 34.86 | 610.75 ± 159.53 | 366.75 ± 289.65 | 309.25 ± 72.05 | |
| MYOT | May | 4.50 ± 4.50 | 1.25 ± 0.95 | 9.75 ± 4.13 | 5.50 ± 2.40 | 4.00 ± 1.47 | 0.565 |
| | June | 17.50 ± 14.55 | 18.75 ± 16.79 | 10.75 ± 6.76 | 7.50 ± 2.18 | 10.25 ± 3.22 | |
| | July | 23.50 ± 14.89 | 1.25 ± 1.25 | 7.25 ± 4.07 | 2.50 ± 1.66 | 5.50 ± 2.63 | |
| LBNH | May | 2.25 ± 1.03 | 27.25 ± 23.42 | 53.50 ± 15.66 | 80.00 ± 52.48 | 42.75 ± 20.22 | 0.856 |
| | June | 18.25 ± 10.323 | 9.25 ± 5.44 | 81.00 ± 35.13 | 16.00 ± 7.67 | 26.00 ± 10.95 | |
| | July | 1.00 ± 0.71 | 4.00 ± 4.00 | 44.50 ± 30.18 | 4.00 ± 2.74 | 23.50 ± 8.63 | |
| EFLN | May | 27.25 ± 14.99 | 27.5 ± 9.98 | 458.75 ± 47.09 | 94.25 ± 34.01 | 185.75 ± 79.12 | 0.483 |
| | June | 3.25 ± 1.60 | 37.75 ± 21.70 | 389.50 ± 139.54 | 56.75 ± 34.87 | 68.00 ± 16.57 | |
| | July | 8.25 ± 2.39 | 23.25 ± 16.35 | 219.00 ± 88.34 | 18.75 ± 8.59 | 93.25 ± 13.37 | |
| PESU | May | 1.00 ± 0.70 | 17.50 ± 17.50 | 38.75 ± 15.52 | 5.25 ± 1.38 | 10.50 ± 5.33 | 0.583 |
| | June | 24.25 ± 20.32 | 25.50 ± 19.96 | 39.00 ± 28.68 | 67.00 ± 56.85 | 30.00 ± 7.83 | |
| | July | 5.50 ± 4.56 | 3.75 ± 2.25 | 20.50 ± 8.43 | 2.00 ± 1.68 | 31.50 ± 7.27 | |
| CORA | May | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.25 ± 0.25 | 1.00 ± 1.00 | 0.50 ± 0.50 | 0.827 |
| | June | 0.50 ± 0.50 | 1.75 ± 1.75 | 2.00 ± 1.16 | 1.00 ± 0.58 | 0.25 ± 0.25 | |
| | July | 2.50 ± 2.50 | 0.25 ± 0.25 | 0.75 ± 0.48 | 0.00 ± 0.00 | 0.75 ± 0.25 | |
| LACI | May | 2.50 ± 1.44 | 5.75 ± 2.96 | 21.25 ± 9.23 | 17.75 ± 6.76 | 15.50 ± 3.59 | 0.372 |
| | June | 3.00 ± 1.29 | 1.50 ± 0.87 | 12.50 ± 5.50 | 2.50 ± 1.19 | 2.75 ± 1.03 | |
| | July | 8.25 ± 5.45 | 0.75 ± 0.48 | 7.50 ± 3.86 | 24.50 ± 2.21 | 5.00 ± 2.20 | |

[a] Species groups: TOTAL = all bats (identified and unidentified); MYOT = all *Myotis* spp.; LBNH = eastern red bat (*Lasiurus borealis*) and evening bat (*Nycticeius humeralis*); EFLN = big brown bat (*Eptesicus fuscus*) and silver-haired bat (*Lasionycteris noctivagans*); PESU = tricolored bat (*Perimyotis subflavus*), CORA = Rafinesque's big-eared bat (*Corynorhinus rafinesquii*); LACI = hoary bat (*Lasiurus cinereus*).

[b] Means in a row not different ($P > 0.05$)

[c] Treatments: SpL = spring prescribed fire and low overstory thinning (woodland with target residual basal area of 14 $m^2ha^{-1}$), SpH = spring prescribed fire and high overstory thinning (savanna with target residual basal area of 7 $m^2ha^{-1}$), FaL = fall prescribed fire and low overstory thinning, FaH =fall prescribed fire and high overstory thinning.

Table A.9: All models of variables affecting bat activity in hardwood forest stands subject to prescribed fire and overstory thinning treatments at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013−2014.

| Species Group[a] | Model[b] | *K* | AICc | ΔAICc | $w_i$ |
|---|---|---|---|---|---|
| TOTAL | BA | *2* | 851.20 | 0.00 | 0.31 |
| | BA + IB | *3* | 851.35 | 0.15 | 0.29 |
| | BA+DW | 3 | 853.35 | 2.16 | 0.11 |
| | BA+MD | 3 | 853.46 | 2.27 | 0.10 |
| | BA+MD+IB | 4 | 853.73 | 2.54 | 0.09 |
| | BA+MD+DW | 4 | 855.70 | 4.51 | 0.03 |
| | BA+MD+IB+DW | 5 | 856.05 | 4.85 | 0.03 |
| | MD+IB | 3 | 857.49 | 6.30 | 0.01 |
| | MD | 2 | 858.02 | 6.82 | 0.01 |
| | MD+IW+DW | 4 | 859.34 | 8.14 | 0.01 |
| | MD+DW | 3 | 859.64 | 8.44 | 0.00 |
| | IB | 2 | 859.82 | 8.62 | 0.00 |
| | IB+DW | 3 | 859.96 | 8.77 | 0.00 |
| | DW | 2 | 860.02 | 8.82 | 0.00 |
| | NULL | 1 | 860.11 | 8.92 | 0.00 |
| LBNH | BA | 2 | 625.78 | 0.00 | 0.24 |
| | BA + IB | 3 | 626.15 | 0.38 | 0.20 |
| | BA + DW | 3 | 627.47 | 1.69 | 0.10 |
| | BA+MD | 3 | 628.08 | 2.30 | 0.08 |
| | BA+MD+IB | 4 | 628.52 | 2.74 | 0.06 |
| | MD+IB | 3 | 628.72 | 2.94 | 0.06 |
| | MD | 2 | 628.87 | 3.09 | 0.05 |
| | IB | 2 | 629.18 | 3.40 | 0.04 |
| | NULL | 1 | 629.22 | 3.44 | 0.04 |
| | BA+MD+DW | 4 | 629.85 | 4.08 | 0.03 |
| | BA+MD+IB+DW | 5 | 630.34 | 4.56 | 0.02 |
| | DW | 2 | 630.96 | 5.18 | 0.02 |
| | IB+DW | 3 | 631.08 | 5.31 | 0.02 |

Table A.9: Continued

| Species Group[a] | Model[b] | *k* | AICc | ΔAICc | $w_i$ |
|---|---|---|---|---|---|
| LBNH | MD+IW+DW | 4 | 631.10 | 5.32 | 0.02 |
| | MD+DW | 3 | 631.15 | 5.38 | 0.02 |
| EFLN | BA | 2 | 764.95 | 0.00 | 0.37 |
| | BA + IB | 3 | 765.61 | 0.66 | 0.26 |
| | BA+DW | 3 | 767.25 | 2.30 | 0.12 |
| | BA+MD | 3 | 767.25 | 2.30 | 0.12 |
| | BA+MD+IB | 4 | 767.98 | 3.03 | 0.08 |
| | BA+MD+DW | 4 | 769.63 | 4.68 | 0.04 |
| | BA+MD+IB+DW | 5 | 770.45 | 5.50 | 0.023 |
| | MD+IB | 3 | 778.32 | 13.37 | 0.00 |
| | MD+DW | 3 | 778.43 | 13.48 | 0.00 |
| | MD | 2 | 778.50 | 13.54 | 0.00 |
| | MD+IW+DW | 4 | 778.55 | 13.60 | 0.00 |
| | DW | 2 | 781.70 | 16.75 | 0.00 |
| | IB+DW | 3 | 782.20 | 17.25 | 0.00 |
| | NULL | 1 | 785.64 | 20.68 | 0.00 |
| | IB | 2 | 785.89 | 20.94 | 0.00 |
| PESU | BA + MD | 3 | 608.15 | 0.00 | 0.34 |
| | BA + MD + IB | 4 | 610.15 | 1.99 | 0.13 |
| | MD | 2 | 610.79 | 2.64 | 0.09 |
| | NULL | 1 | 610.87 | 2.72 | 0.09 |
| | MD+DW | 3 | 612.18 | 4.02 | 0.045 |
| | BA+MD+IB+DW | 5 | 612.62 | 4.47 | 0.036 |
| | BA | 2 | 612.78 | 4.62 | 0.034 |
| | MD+IB | 3 | 612.98 | 4.83 | 0.03 |
| | IB | 2 | 613.00 | 4.84 | 0.03 |
| | DW | 2 | 613.00 | 4.85 | 0.03 |
| | MD+IW+DW | 4 | 614.40 | 6.25 | 0.01 |

Table A.9: Continued

| Species Group[a] | Model[b] | *k* | AICc | ΔAICc | $w_i$ |
|---|---|---|---|---|---|
| PESU | BA+IB | 3 | 614.96 | 6.80 | 0.01 |
| | BA+DW | 3 | 615.07 | 6.92 | 0.01 |
| | IB+DW | 3 | 615.20 | 7.04 | 0.01 |
| LACI | MD + IB | 3 | 491.11 | 0.00 | 0.18 |
| | MD | 2 | 491.73 | 0.62 | 0.13 |
| | BA + IB | 3 | 492.36 | 1.25 | 0.10 |
| | BA | 2 | 492.42 | 1.31 | 0.09 |
| | IB | 2 | 492.58 | 1.47 | 0.09 |
| | Null | 1 | 493.01 | 1.90 | 0.07 |
| | BA+MD+IB | 4 | 493.35 | 2.24 | 0.06 |
| | MD+IW+DW | 4 | 493.47 | 2.36 | 0.06 |
| | BA+MD | 3 | 493.70 | 2.59 | 0.05 |
| | MD+DW | 3 | 494.03 | 2.92 | 0.04 |
| | IB+DW | 3 | 494.53 | 3.42 | 0.03 |
| | BA+DW | 3 | 494.60 | 3.50 | 0.03 |
| | DW | 2 | 494.79 | 3.68 | 0.03 |
| | BA+MD+IB+DW | 5 | 495.69 | 4.58 | 0.02 |
| | BA+MD+DW | 4 | 495.97 | 4.86 | 0.02 |

[a] Species groups: TOTAL = all bats (identified and unidentified); LBNH = eastern red bat (*Lasiurus borealis*) and evening bat (*Nycticeius humeralis*); EFLN = big brown bat (*Eptesicus fuscus*) and silver-haired bat (*Lasionycteris noctivagans*); PESU = tricolored bat (*Perimyotis subflavus*), LACI = hoary bat (*Lasiurus cinereus*).

[b] Variables: BA = live overstory basal area ($m^2ha^{-1}$); MD = midstory density (stems/$m^2$), IB = insect biomass (g); DW = distance to water (m)

# VITA

Maxwell Cox was born in Baton Rouge, Louisiana. He graduated from Union County High School in 2004. He received an Associate in Applied Sciences with a concentration in Wildlife and Fisheries Management Technologies from Haywood Community College in 2008, and a B.S. in Wildlife and Fisheries Management from the University of Tennessee, Knoxville in 2013. Between graduating Haywood Community College and graduating from UTK, He worked various wildlife jobs throughout the South east with agencies such as the US Fish and Wildlife Service, National Park Service, USDA Forest Service, University of Tennessee, Knoxville and Kentucky Department of Fish and Wildlife Resources. After completing his B.S. Max began working towards a Master’s Degree in Wildlife and Fisheries Science under Dr. Emma Willcox, focusing on Bat Community Response to Prescribed Fire and Overstory Thinning within Hardwood Forests of the Southeastern U.S.