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BAT OCCURRENCE RELATIVE TO SILVICULTURAL TREATMENTS INTENDED TO  
YIELD DESIRED FOREST CONDITIONS FOR PRIORITY WILDLIFE

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## EXECUTIVE SUMMARY

In September, 2012, the U.S. Fish and Wildlife Service and Stephen F. Austin State University entered into a grant agreement to examine bat occurrence at public conservation areas in the lower Mississippi Alluvial Valley (MAV), particularly as it related to silvicultural treatments intended to yield desired forest conditions (DFCs) for priority wildlife. These silvicultural treatments in bottomland hardwood forests have been advocated by managers of public conservation lands within the MAV to improve wildlife habitat by achieving forest structure described as desired forest conditions. Positive temporal responses to these treatments, which include group selection cuts, patch clearcuts, and variable-retention thinnings, have been observed for some forest-dependent bird species (e.g., Kentucky Warbler [*Oporornis formosus*] and Swainson's warbler [*Limnothlypis swainsonii*]). These practices also appear to benefit species of concern such as Louisiana black bears (*Ursus americanus luteolus*) and game species like white-tailed deer (*Odocoileus virginianus*) and eastern wild turkeys (*Meleagris gallopavo*). Although the aforementioned desired forest conditions for wildlife have also been espoused as beneficial for bats (*Chiroptera*), responses of bat species to these specific silvicultural treatments and resultant forest conditions were largely unknown.

Bats represent a diverse and important group of forest-dependent mammals. Furthermore, there are long-term concerns about declines in abundance of many bat species due to a variety of factors including habitat loss and degradation, disease, and energy development. Furthermore, many public conservation lands in the MAV did not have baseline occurrence data for bats or their nocturnal insect prey. Thus, we initiated this project to meet several objectives, including:

- (1) Collect baseline inventory data for bat species occurrence within hardwood forests on National Wildlife Refuges and other public conservation lands in the Mississippi Alluvial Valley.
- (2) Collect baseline inventory data for nocturnal flying insects within hardwood forests on National Wildlife Refuges and other public conservation lands in the Mississippi Alluvial Valley.
- (3) Quantify the relationships between bat species occurrence, indices of bat abundance and nocturnal insect abundance, and forest stand conditions, particularly related to silvicultural treatments prescribed and implemented to promote Desired Forest Conditions within bottomland hardwood forests.
- (4) Evaluate the temporal change in bat species occurrence, indices of bat abundance and nocturnal insect abundance, and forest stand conditions relative to the duration (years) since silvicultural treatment.

To address these objectives, we identified 64 bottomland hardwood stands on 15 public conservation lands (federal national wildlife refuges or state wildlife management areas) within the MAV in Arkansas, Louisiana, and Mississippi that had been treated within the past 12 years to achieve DFCs. Each treated stand was paired with an untreated reference stand that was nearby and similar in composition. We surveyed these stands between April and August in 2013 and 2014. Each stand was surveyed for bat occurrence using stationary acoustic monitors for 6 continuous nights at 2 locations. We also used blacklight traps to sample night-flying insects and quantified various vegetation structural characteristics (e.g., basal area, stem density, canopy coverage, snag density, woody debris density) in 10 0.05 ha plots in each stand.

Over the two field seasons, we recorded nearly 1.5 million acoustic files that resulted in 47,295 bat call passes that could be identified to species. We also collected nearly 5 kg of nocturnal insects and quantified them by order. We surveyed vegetation structure on 1,536 plots in the 128 survey stands. Specific to the objectives identified above, we determined:

- (1) Seven bat species (evening bats [*Nycticeius humeralis*], tri-colored bats [*Perimyotis subflavus*], silver-haired bats [*Lasionycteris noctivagans*], hoary bats [*Lasiurus cinereus*], big brown bats [*Eptesicus fuscus*], Rafinesque's big-eared bats [*Corynorhinus rafinesquii*], and Mexican free-tailed bats [*Tadarida brasiliensis*]) and 2 species groups (eastern red/Seminole bat [*Lasiurus* spp.] and myotine bats [*Myotis* spp.]) occurred on the various study areas during these summers. We identified the most acoustic recordings as evening bats, followed by eastern red/Seminole bats, tri-colored bats, and myotine species. We rarely identified silver-haired bats, hoary bats, Rafinesque's big-eared bats, big brown bats, or Mexican-free tailed bats.
- (2) Coleoptera (beetles) were the most abundant order (94% of the total biomass) of night-flying insects on all areas, with macro-Coleoptera comprising 81% of Coleopteran biomass. Lepidoptera (moths) were 2.7% of the total biomass, with macro-Lepidoptera accounting for 68% of this biomass. Diptera comprised only 0.12% of the total biomass. The cumulative biomass for all other orders was 2.4% of the total biomass.
- (3) Although numbers of bat detections were similar between treatment and reference stands, generalized linear models showed a positive association between silvicultural treatment and bat detections for most species. Bat abundance response varied among species, but was generally positively associated with increased insect biomass, greater abundance of dead wood, greater tree diversity, increased basal area, and less vegetation clutter.

Similarly, silvicultural treatment and abundance of dead wood were the most important predictors for increased invertebrate biomass.

- (4) Years since treatment was not a significant predictor of bat or insect abundance, suggesting that, at least within the range of ages in this study, we did not observe an association with time since treatment. Our ability to detect this effect may have been limited by our preference for more recently treated stands (limiting the range of ages) and the extensive variation in treatment intensity across the various study areas.

Silvicultural treatments prescribed to enhance wildlife habitat in the Mississippi Alluvial Valley appear to benefit multiple bat species by promoting heterogeneous landscapes with a mosaic of vegetation characteristics, including dead wood, large diameter trees, and high tree species diversity and by increasing insect prey abundances. However, because reference stands with high basal area provided habitat for some priority bat species, habitat managers should provide a mosaic of stands with varied structural characteristics, including passively managed stands.



BAT COMMUNITY RESPONSE TO SILVICULTURAL TREATMENTS IN  
BOTTOMLAND HARDWOOD FORESTS MANAGED FOR WILDLIFE IN THE  
MISSISSIPPI ALLUVIAL VALLEY

By

LORRAINE PATRICIA KETZLER, Bachelor of Science

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## ABSTRACT

Silviculture in bottomland hardwood forests has been advocated by land managers of public conservation lands within the Mississippi Alluvial Valley to improve wildlife habitat. This stewardship often targets management to achieve forest structure described as desired forest conditions for wildlife. Although some songbirds respond positively to these management actions (e.g., selective timber harvests), little research has been directed at the effects on other species, including bats and their prey. Bats are important predators of nocturnal insects, thereby influencing trophic interactions within forests. Concerns about declines in abundance of many bat species prompted my examination of the effects of silvicultural treatments, implemented to promote wildlife habitat, on insect abundance and acoustic detection of bat species. I conducted vegetation surveys and sampled insect biomass within 64 treated and 64 reference stands, located on 15 public conservation areas in Arkansas, Louisiana, and Mississippi. I examined the influence of vegetation metrics and insect biomass on the detection of acoustic calls of bats in these same stands. Dead wood and silvicultural treatments were positively associated with greater biomass of most insect taxa, and with greater acoustic detection of most bat species. Generalist bat species had positive relationships with increased insect biomass and dead

wood density. Increased large tree basal area was an important structural characteristic for both common and rare bat species, yet detections of most bat species were negatively associated with increased vegetative clutter. Silvicultural treatments prescribed to enhance wildlife habitat in the Mississippi Alluvial Valley appear to benefit multiple bat species by promoting heterogeneous landscapes with a mosaic of vegetation characteristics, including dead wood, large diameter trees, and high tree species diversity and by increasing insect prey abundances. However, because reference stands with high basal area provide habitat for some priority bat species, habitat managers should provide a mosaic of stands with varied structural characteristics, including passively managed stands.

## PREFACE

The following chapters were formatted to facilitate future publication of results. Each chapter has been written as a stand-alone document. There will be some overlap in field method, however analytical techniques used were different for each chapter. Chapter 2 was formatted to meet the guidelines specified by the Southeastern Naturalist. Chapter 3 was formatted to meet the guidelines of The Wildlife Society for the Journal of Wildlife Management. The chapters are the responsibility of the author; however, in publication, each chapter will have more than one author.

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## CHAPTER 1

### INTRODUCTION

## INTRODUCTION

Bottomland hardwood forests are a characteristic forest community associated with floodplains of large riverine systems of the Atlantic and Gulf Coastal Plains of the southeastern United States. These forests are dominated by broad-leaved hardwood trees (with some notable exceptions, e.g., bald cypress [*Taxodium distichum*]) and are characterized by a high degree of structural complexity and tree species diversity. Small variations in micro-topography can have a marked influence on hydrology and soil characteristics, resulting in high floral and faunal species diversity in these systems (Hodges 1997, Kellison and Young 1997). Tree species composition reflects site hydrology: streambeds (black willow, *Salix nigra*), temporarily flooded soils (elms, *Ulmus spp.*, ashes, *Fraxinus spp.*, and sugarberry, *Celtis laevigata*), poorly drained sites (overcup oak, *Quercus lyrata* and water hickory, *Carya aquatica*), and nearly permanently flooded depressions (bald cypress, and tupelos, *Nyssa spp.*). All species may be present in some systems (Hodges 1997, Bennett 2013).

Due to historic anthropogenic activities such as land conversion for agriculture, intensive timber production, and reservoir construction, less than 50% of historic bottomland hardwood forest remains (Lower Mississippi Valley

Joint Venture 2007). Furthermore, flood control and other anthropogenic activities have altered the natural disturbance regime (Harris and Gosselink 1990, Kellison and Young 1997) which historically maintained the structural and compositional variations that characterize these forests (Hodges 1994, Kellison and Young 1997, King and Antrobus 2001, Twedt and Wilson 2007). Remaining tracts of bottomland hardwood forest are typically fragmented, widely dispersed, relatively even-aged, second-growth forests with homogenous, closed canopies (Rudis 1995, Twedt and Wilson 2007).

The Mississippi Alluvial Valley (MAV) is over 800 km long and varies in width from 32 to 128 km encompassing 10 million ha in 7 states (Reinecke et al. 1989). Historically, The MAV consisted almost entirely of bottomland hardwood forests, although by the 1980's less than 20% of the original forest remained (Lower Mississippi Valley Joint Venture 2007). Across the MAV, Wildlife Management Areas (WMAs) and National Wildlife Refuges (NWRs) have been established to conserve and manage habitat for wildlife, provide wildlife-associated recreational opportunities, and serve as research areas (Ensminger 1968, U.S. Fish and Wildlife Service 2006, Arkansas Game and Fish Commission 2014). These WMAs and NWRs in the MAV primarily conserve bottomland hardwood forest, reclaimed agricultural lands that have been reforested with bottomland hardwood species and moist soil management units (U.S. Fish and Wildlife Service 2009, Louisiana Department of Wildlife and

Fisheries 2014). Given the extent of these and other public lands across the MAV, opportunities exist for active forest management programs aimed at improving habitat for wildlife.

For example, recommendations proposed by the Lower Mississippi Valley Joint Venture (LMVJV) call for managing forests to achieve forest structure described as desired forest conditions (DFCs) for wildlife. Structural components such as canopy closure, basal area, and snag density are measured in ranges, and prescriptions for silvicultural treatments depend upon many factors: management needs, landscape characteristics, and stand conditions (Wilson et al. 2007). Since 2007, when the LMVJV released their management suggestions for implementing DFCs, such treatments have been widely implemented on NWRs, WMAs, and private properties in the MAV (Wilson 2012). National Wildlife Refuges have embraced DFCs in their Comprehensive Conservation Plans, with special emphasis on retaining large trees with cavities and creating patches of early successional habitat (U.S. Fish and Wildlife Service 2009a, 2012a).

In 2012, about 16% of the forest on White River NWR was considered within desired forest conditions, and forest management plans proposed that 40% of the refuge should be managed according to DFCs to sustain native wildlife and migratory bird biological needs (U.S. Fish and Wildlife Service 2012a). Due to the increasing application of DFC treatments, Mississippi State

University hosted the Bottomland Hardwood Management Symposium, to discuss silvicultural effects of DFCs in bottomland hardwoods, gaps in knowledge, and future research needs. Although impacts of DFCs on some taxa (primarily passerine birds) are well-studied, potential impacts on other forest-dwelling wildlife are poorly understood. In particular, bottomland hardwood forests support a rich and diverse bat community, including some species of conservation concern (e.g., Rafinesque's big-eared bat [*Corynorhinus rafinesquii*]). As a result, bat biologists have reached out to conservation organizations, proposing assistance with developing DFC guidelines for bottomland forests (Gulf Coastal Plains Ozarks Land Conservation Cooperative 2012). At bat conservation meetings, DFCs have been an important topic for discussion (Southeastern Bat Diversity Network 2012, Mississippi Bat Working Group 2014).

Microchiropteran bats are important predators that influence trophic linkages by preying on nocturnal insects (Altringham 1996, Dodd et al. 2012a). These bats are among the most endangered taxonomic groups worldwide (Arita 1993, Ceballos and Brown 1995, Mickelburgh et al. 2002, Weller et al. 2008), with several species listed as endangered or threatened (Miller et al. 2003, Avina et al. 2007). Bat population declines have been attributed to disease, habitat loss, pollution, and other anthropogenic causes (Agosta 2002, Blehert et al. 2009). Since bats with white-nose syndrome were first diagnosed in the

northeastern U.S., the disease has been linked to mortality of >6 million bats in North America (Knudsen et al. 2013). With the spread of white-nose syndrome, strategies for assessing bat populations before they become exposed, investigating other causes of decline, and improving habitat management to promote populations are becoming increasingly important (U.S. Fish and Wildlife Service 2011).

The habitat needs of forest-dwelling bats are complex (Trousdale 2011, Johnson and Lacki 2013); they often use different nocturnal and diurnal resources associated with varying roost availability, prey abundance, and prey distribution (Barclay and Kurta 2007, Hayes and Loeb 2007, Lacki et al. 2007). As a result, several studies have examined the effects of forest management on bat abundance, roost site availability, and foraging activity (Menzel et al. 2002, Hayes and Loeb 2007, Dodd et al. 2012*b*, Johnson and Lacki 2013). Selective harvest affects species assemblages and spatial activity patterns of bats differently than clearcutting (Perdue and Steventon 1996). Some species benefit from uncluttered foraging space in open-canopy forests (Barclay 1999, Patriquin and Barclay 2003, Menzel et al. 2005), whereas other species avoid such open conditions (Trousdale 2011). Lower-intensity harvests such as group or single-tree selection may result in only a moderate change in abundance of mature forest-associated species, yet providing habitat for early successional species (Annand and Thompson 1997, Moorman and Guynn 2001, Guenette and Villard



2005, Vanderwel et al. 2007, Twedt and Somershoe 2010). Consequently, mimicking natural disturbance processes within otherwise homogenous, closed-canopy forests maintains habitat for species requiring mature closed-canopy forest while concurrently encouraging colonization by early and mid-successional forest species (Ziehmer 1993, Beese and Bryant 1999, Rodewald and Yahner 2000, Twedt and Wilson 2007, Norris et al. 2009, Twedt and Somershoe 2010).

Management strategies that affect removal of structural clutter by thinning may increase bat use of mid-successional stands (Humes et al. 1999). Small partial cuts are well suited for bottomland hardwood forests, as these forests are naturally adapted to small-scale disturbances (Hamilton et al. 2005). Moreover, bat activity is higher in small openings and gaps within forests than in intact forests (Law and Chidel 2002, Tibbels and Kurta 2003), including bottomland hardwood forests (Menzel et al. 2002). Menzel et al. (2002) found that activity was highest along the edge between gaps and the forest interior, indicating that foraging and feeding activity can increase in forests below the canopy when access is available.

Species of concern such as the southeastern myotis (*Myotis austroriparius*) and Rafinesque's big-eared bat roost in large, hollow trees within forest stands that have high basal area and high canopy closure (Gooding and Langford 2004, Trousdale and Beckett 2005, Lucas 2009). These species may be negatively impacted by removal of hollow trees or by changes in vegetative

structure associated with post-harvest open canopy conditions (Trousdale 2011). Increased light in the understory could stimulate dense regeneration, which may negatively affect flight and foraging patterns of bats (Florence 1996, Adams et al. 2009, Dodd et al. 2012*b*). Conversely, some bat species may benefit from uncluttered foraging space in open-canopy forests and increased prey availability associated with vegetative regeneration and herbaceous growth (Barclay 1999, Patriquin and Barclay 2003, Menzel et al. 2005). The response of bats to silvicultural treatments within bottomland hardwood forests will likely be complex and vary among species that occur in the region.

Promotion of DFCs has occurred concurrently with the stated need for surveys to document wildlife responses to DFC treatments (U.S. Fish and Wildlife Service 2009*b*). Research to date indicates that silvicultural treatments to promote DFCs for wildlife are beneficial to a variety of songbirds (Twedt and Wilson 2007, Norris et al. 2009, Twedt and Somershoe 2010). Although some Comprehensive Conservation Plans specifically state the need for surveys aimed at Rafinesque's big-eared bats and the southeastern myotis (U.S. Fish and Wildlife Service 2009*b*, 2012*a*), a review of Comprehensive Conservation Plans in 2013 indicated that few NWRs listed bats as present on Refuges, and even fewer had undertaken surveys to assess populations (Dixon et al. 2013).

To increase this paucity of baseline data, Dixon et al. (2013) recommended conducting acoustic surveys because of their ability to collect

information passively at unmanned stations thereby reducing personnel requirements. To meet the need for baseline data, the US Fish and Wildlife Service's Southeast Region Inventory and Monitoring Branch joined a cooperative project to survey bat species occupancy acoustically using mobile transects (U.S. Fish and Wildlife Service 2012*b*). These surveys ranged over 42 NWRs and 3 Ecological Services Field Offices in 13 states (U.S. Fish and Wildlife Service 2012*b*), and provided much-needed information on species occupancy and distribution. Monitoring occupancy can indicate which species are most affected by white-nose syndrome as it spreads (Ford et al. 2011, Rodhouse et al. 2012), or anthropogenic changes made to the landscape (Yates and Muzika 2006).

Although valuable information was collected by these surveys, they are conducted along continuous routes, such as roadways, and therefore cannot provide detailed information about how DFCs affect bats because they do not enter the interior of DFC stands (U.S. Fish and Wildlife Service 2012*b*, 2012*c*). Bottomland bats continue to be under-studied and the impacts of DFCs on non-avian wildlife in bottomland hardwood forests continued to be poorly understood.

To assess how silvicultural treatments affect forest structural characteristics, insect abundance, and bat activity, I measured vegetation structural parameters within reference and treatment stands to quantify differences between them. I surveyed for bat prey abundances using blacklight

bucket traps to collect samples that were identified to order and weighed for biomass. Prey abundances could be influenced by structural changes in vegetation caused by DFCs (Chapter 2), and, in turn, influence bat activity in treated units. I used stationary passive acoustic recording devices to survey bat activity in reference stands and in treated stands on WMAs and NWRs across the MAV (Chapter 3). I identified bat species (or species groups) within the stands based on recorded detection of their acoustic signals. These recordings provided an index of bat species activity within treated and reference stands. Understanding how structural changes can impact prey is an important component for understanding how structural changes may impact bats. An improved understanding of how silvicultural treatments influence bat activity in bottomland hardwood forests will assist forest managers to promote management of multiple species, including bats, within the ecosystem.

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## CHAPTER 2

### INSECT AVAILABILITY IN BOTTOMLAND HARDWOOD FORESTS MANAGED FOR WILDLIFE IN THE MISSISSIPPI ALLUVIAL VALLEY

## ABSTRACT

Silviculture to promote wildlife habitat has been advocated for management of bottomland hardwood forests on public conservation lands within the Mississippi Alluvial Valley and involves managing forests to achieve forest structure described as desired forest conditions for wildlife. Although some songbirds respond positively to these management actions (e.g., selective timber harvests), little research has been directed at the effects on other species, including bats and their prey. Bats are important predators of nocturnal insects, thereby influencing trophic interactions within forests. To better understand how silviculture influences prey availability for bats, I conducted vegetation surveys and sampled insect biomass within silviculturally treated bottomland hardwood forest stands. I used passive blacklight traps to capture nocturnal flying insects in 128 treated and reference stands, located on 15 public conservation areas in Arkansas, Louisiana, and Mississippi. Dead wood and silvicultural treatments were positively associated with greater biomass of macro-Lepidoptera, macro-Coleoptera, and all taxa combined, although biomass of micro-Lepidoptera was negatively associated with silvicultural treatment. Understanding what factors influence prey availability within forested landscapes may influence prescribed

silvicultural management for species of conservation concern, such as Rafinesque's big-eared bat, northern long-eared bat, and Indiana bat.

## INTRODUCTION

Insects are important in maintaining the health and diversity of forest ecosystems (Andrewartha and Birch 1984) through pollination and defoliation (Janzen 1987), as well as by converting plant biomass into recyclable material and influencing nutrient cycling processes (Gist and Risley 1982, Gorham et al. 2002, Hamilton 1982, Porter et al. 1999). Although many studies have focused on silvicultural practices to reduce the impacts of insect pests (Behre et al. 1936, Belanger et al. 1993, Berryman 1986), less attention has been given to understanding how management actions affect forest insect communities (Burford et al. 1999, Ober and Hayes 2008, Sutton and Collins 1991).

Insect abundances are affected by vegetation characteristics such as structural complexity (Araujo et al. 2006, Gorham et al. 2002), species richness (Haddad et al. 2001, Knops et al. 1999), and composition (Mattson and Scriber 1987, Schowalter et al. 1986). Generally, greater densities of woody and herbaceous vegetation support greater numbers of insects (Gorham et al. 2002, Grindal 1996, Kalcounis and Brigham 1995). However, silvicultural methods and intensities used to promote woody and herbaceous growth have different effects, depending upon focal insect taxa (Burford et al. 1999, Intachat et al. 1997, Summerville et al. 2004). For example, Burford et al. (1999) found that in eastern

Kentucky different moth families (e.g., Yponomeutidae, Limacodidae, Pyralidae, Geometridae, Notodontidae, and Arctiidae) preferred different timber age classes. Summerville and Crist (2003) found that although there was no difference in moth species richness or abundance between managed and wilderness stands in southern Ohio, the community composition was influenced by management of the surrounding landscape.

Studies of silvicultural impacts on insects mainly emphasize the importance of diurnal pollinators or plant species used by these pollinators (Proctor et al. 2012, Wiegmann and Waller 2006). However, there are also many beneficial nocturnal insects, including predators of pest insects (Frank and Slosser 1996) and nocturnal pollinators (Bawa 1990).

Insects provide a major source of food for many wildlife species (Gorham et al. 2002, Pierson 1998, Rader 1999, Sjöberg and Dannell 1982, Wigley and Lancia 1998), including nocturnal predators (Jones and Rydell 2003, Whitaker and Maser 1976). Specifically, insect-eating bats are important predators, capable of consuming large quantities of insects every night (Altringham 1996, Dodd et al. 2012a, Kunz et al. 1995). The availability of insect prey for bats is often unknown (Dodd et al. 2012a, Whitaker 1994). Studies that have focused on the diet of bats (Agosta 2002, Belwood and Fenton 1976, Black 1974) found bats consumed large quantities of moths, beetles, and flies (Clare et al. 2009, Hamilton and Barclay 1998). However, bias towards particular insect taxa was

dependent upon bat species morphology, sympatric species, habitat conditions, and survey methodology (Dodd et al. 2012a, Fenton 1990, Freeman 1981, Lee and McCracken 2004, Menzel et al. 2002). Generally bats with larger body size and lower echolocation call frequencies forage in less cluttered environments and may consume larger prey (Aldridge and Rautenbach 1987, Findley 1976, Norberg and Rayner 1987).

Silvicultural practices, such as selective harvest, directly impact bat populations within forest stands by changing foraging and roosting habitats (Krusic and Neefus 1996; Menzel et al. 2002, 2005; Perdue and Steventon 1996; Titchenell et al. 2011). Given impacts of forest management on wildlife, silvicultural treatments prescribed to enhance wildlife habitat, called wildlife-forestry, have been advocated for management of bottomland hardwood forests on public conservation lands within the Mississippi Alluvial Valley (Twedt and Somershoe 2010, Wilson et al. 2007a). The Lower Mississippi Valley Joint Venture recommended managing forests to achieve a forest structure that is conducive for wildlife. Structural components such as canopy closure, basal area, and tree species richness can be managed through varying silvicultural prescriptions to promote desired forest conditions for wildlife. Previous research has indicated that silvicultural treatments undertaken to enhance habitat for wildlife are beneficial to songbirds (Twedt and Somershoe 2010, Twedt and Wilson 2007), but little research has been directed at the effect of these



treatments on other species, particularly nocturnal insects and their predators. In this study, I compared insect biomass in several orders between stands subjected to silvicultural treatments and reference forest stands. Furthermore, I examined the influence of various forest structural and environmental variables on insect biomass to identify those factors that are most important for determining insect abundance in these habitats.

## FIELD-SITE DESCRIPTION

I surveyed 128 bottomland hardwood forest stands on 15 public conservation lands managed by state and federal wildlife agencies (Wildlife Management Areas, WMA or U.S. Fish and Wildlife Service National Wildlife Refuge, NWR) within the Mississippi Alluvial Valley during April to August, 2013, and May to August, 2014. Surveyed locations were in Arkansas (Cache River NWR, Dagmar WMA, White River NWR), Louisiana (Bayou Cocodrie NWR, Big Lake WMA, Boeuf WMA, Dewey Wills WMA, Red River WMA, Russell Sage WMA, Three Rivers WMA, Tensas NWR), and Mississippi (Morgan Brake NWR, O'Keefe WMA, Panther Swamp NWR, Yazoo NWR; Fig. 2.1). Surveyed stands (i.e., finite forest areas subjected to a common silvicultural prescription) were mature bottomland hardwood forests. For each WMA and NWR, managers identified stands that were silviculturally treated to enhance wildlife habitat within the past 12 years. Because the predominant effects of silvicultural treatments on birds diminished after circa 12 years (Twedt and Somershoe 2010, Twedt and Wilson 2007), I restricted selection of treated stands to  $\leq 12$  years post-treatment.

Silvicultural treatments included group selection, small patch cuts, and individual tree selection that were applied individually or in combination. Based on availability, I randomly selected up to 3 treated stands at each WMA or NWR.

I concurrently selected a similar number (up to 3) of adjacent reference stands at each location. Reference stands were chosen to be proximate to treated stands, of similar area, with similar hydrology and vegetative species composition, but without silvicultural disturbance for >12 years (with preference given to older stands). Of 128 total stands, 46 stands were resurveyed in 2014, while 62 stands were surveyed once in either 2013 or 2014. Area of stands was  $168 \pm 151$  ha, ranging from 9.3 ha to > 600 ha with 37 stands < 100 ha, 72 stands between 100 ha and 300 ha, 9 stands between 300 and 600 ha, and 2 stands > 600 ha.

## METHODS

### Field methods 2013-2014

*Insect surveys.* Blacklight traps are a standard technique for sampling nocturnal flying insect assemblages (Covell 2005; Dodd et al. 2008, 2012a). I surveyed nocturnal flying insects using 10-W blacklight bucket traps (Universal Light Trap, BioQuip Products, Gardena, CA, US) powered by 12 V gel-cell batteries. I placed HERCON<sup>®</sup> Vaportape II insecticide-treated plastic strips (Hercon Environmental, Emigsville, PA, US) inside the traps, and lifted traps 1.5-2.5 m above the ground. Traps were active from 21:00 to 06:45 h (ca. dusk to dawn), and were either manually activated (in 2013) or automatically activated with digital timers (in 2014). I surveyed each stand for 4 nights, placing traps at one location within each stand for two nights, and then moving the trap to a second location within the same stand for the remaining two nights. I collected samples each following day and froze them for lab analysis. All traps were located >50 m from the edge of the stand (Dodd et al. 2008, 2012a) in order to reduce edge effects.

*Vegetation surveys.* I surveyed forest vegetation 10 within circular, 0.05 ha (12.62 m radius) plots that were located at 100 m intervals along two 400 m transects per treatment and reference stand based on surveys used for habitat

assessments in the Mississippi Alluvial Valley (Wilson et al. 2007b). I started transects at least 50 m from the edge of the stand at a pre-determined, randomly selected access point and traversed the transect on a randomly selected azimuth, with the restriction that the transect would not exit the stand (Fig. 2.2). If barriers were encountered (i.e., oxbow lakes), the observer altered the azimuth of the route but continued the survey transect. For all trees >20 cm diameter at breast height (dbh) within each plot, I measured dbh to calculate basal area of large trees. I identified each tree to species, and classified tree condition as 1 = no crown die-off, 2 = lower crown die-off, 3 = < 1/3 top crown die-off, 4 = > 1/3 top crown die-off, 5 = recently dead with twigs, 6 = dead with large limbs, 7 = dead with only bole, and 8 = dead downed wood (Wilson et al. 2007b). I estimated mean percent canopy closure using a spherical densiometer at 4 points in the cardinal directions along the edge of the circular plot boundary (Twedt and Somershoe 2010). I measured vegetative clutter of small trees by counting stems of woody vegetation <20 cm dbh within a 4 m radius nested sub-plot (Martin et al. 1997). All vegetation characteristics were averaged across all plots within each treatment or reference stand.

*Weather parameters.* Although my focus was on silvicultural impacts, weather is an important regulator of insect populations (Gandhi et al. 2007, Kingslover 1989). Therefore, I included weather measurements to account for their confounding effects. Weather measurements were accessed through the

Remote Automated Weather Stations, USA Climate Archive (Western Regional Climate Center) for the stations nearest each surveyed location (average distance to station 82 km). I calculated the following weather variables overnight from 21:00 – 07:00 h: mean nightly temperature (°C), relative humidity (mean percent), total precipitation (mm), and mean nightly wind speed (m/s). I also calculated moon illumination as the percent illumination of the moon's face from space for each survey night based on Kiffney et al. (2003) as calculated using the U.S. Naval Observatory's fraction of the moon illuminated calendar ([aa.usno.navy.mil/data/docs/moonfraction.php](http://aa.usno.navy.mil/data/docs/moonfraction.php)). This variable essentially reflects moon phase without incorporating cloud cover.

### Data analysis

I analyzed insect biomass from one randomly selected sample night at each treatment and reference stand. Total arthropod biomass was determined after air-drying samples overnight, to the nearest 0.01 g. I did not include samples that weighed <0.01 g. In addition to total biomass, I also measured biomass for Lepidoptera, Coleoptera, and Diptera because these insect orders are frequent prey for bats (Carter et al. 2004, Claire et al. 2009, Feldhamer et al. 2009, Hamilton and Barclay 1998). Because some bat species forage preferentially on larger or smaller insects (Dodd et al. 2008, 2011, 2012b), I divided Lepidoptera based on wingspan into micro-Lepidoptera (<20 mm) or macro-Lepidoptera (≥20

mm). Similarly, I used body length to distinguish between micro-Coleoptera (<10 mm) and macro-Coleoptera ( $\geq 10$  mm). All other orders were combined as other biomass (i.e., total biomass-Diptera-Coleoptera-Lepidoptera = other biomass).

I performed randomized block analyses of variance (ANOVA) on raw data in SAS (v.9.2, SAS Institute, Inc., Cary, NC; Environmental Systems Research Institute, Inc., Redlands, CA) using PROC GLM to identify the treatment effect of insect biomass and forest structural characteristics while accounting for location effect (Dellasala et al. 1996, Zar 2010). I blocked locations to reduce the variability inherent in sampling many locations across a broad geographic area (Zar 2010). I did not differentiate treatment stands by silvicultural intensity, but assumed vegetative measurements sufficiently characterized treatment intensity.

I used principal component analysis (PCA) using PROC FACTOR to derive uncorrelated vegetation and weather variables based on measured values (Jamison et al. 2002, Thompson et al. 2013). I transformed vegetation ( $\sin\sqrt{x}$  or  $\sqrt{x}$ ), weather ( $\ln[x]$  or  $\ln[x+1]$ ), and insect biomass ( $\ln[x+1]$ ) variables to improve normality (Zar 2010). Because I surveyed locations sequentially (i.e., non-concurrently), I added survey date to the vegetation and weather variables in PCA. This variable incorporated both location and chronological information and reduced the confounding effect of surveying over a large regional area (Summerville and Crist 2003). I rotated the components using the varimax score method (Manly 1986) and I used factor loadings to identify relationships between

original variables and principal components (Jamison et al. 2002). I used Cook's distance with PROC REG to identify and remove 9 influential outliers that indicated deviance in conditions from all other observations (Gehrt and Chelsvig 2003, Hutcheson and Sofroniou 1999; Zuur et al. 2007, 2010).

I used PROC GLMSELECT to generate 95 candidate regression models for each insect taxon (using biomass by taxon as the response variable). I included silvicultural treatment as a categorical (binary) indicator of stand structure (i.e., treatment = 1, reference = 0), age of the treatment (number of years since treated) as a within treatment variable, and principal components in all possible subsets, including a null model (intercept-only) and a treatment-only model. I used Akaike's Information Criterion for small sample sizes ( $AIC_c$ ) to calculate  $\Delta AIC_c$  and model weights ( $w_i$ ) for each candidate model. I considered models competitive at  $\Delta AIC_c \leq 2.0$  to have support as predictors of insect biomass (Burnham and Anderson 2002, Ober and Hayes 2008, Thompson et al. 2013). I calculated the summed weights of these supported models with shared predictors as evidence supporting the relative strength of each predictor (Johnson and Omland 2003, Wagenmakers and Farrell 2004).



## RESULTS

### Vegetation and weather

I quantified forest structural characteristics on 1,536 plots from 15 April to 12 August, 2013, and 1 May to 15 August, 2014. The average age of treatment stands was  $5.1 \pm 4.0$  years. Treated stands were similar to reference stands for canopy closure, stem density of small trees, dead downed wood density, and tree species richness (Table 2.1). Treated stands had lower large tree basal area ( $27.2 \text{ m}^2$  per ha compared to  $33.85 \text{ m}^2$  per ha;  $F_{1,111} = 12.5$ ;  $P = 0.0006$ ) and more snags (13 per ha compared to 10 per ha;  $F_{1,111} = 4.4$ ;  $P = 0.04$ ).

Principal components analysis summarizing vegetation, weather, and date variables resulted in five principal components (Table 2.2). I interpreted principal components as representing increased dead downed wood and snags from large trees (PC1); increased large tree basal area and tree species richness (PC2); increased wind and decreased relative humidity (PC3); combined survey date and increased stem density of small trees as a result of decreased canopy closure (PC4); and increased precipitation and moon illumination (PC5; Table 3). These five principal components explained 68% of the cumulative variance (Table 2.2).

Temperature was not a strong variable for any component. Principal component 2 was likely an index of gap recovery post-disturbance as gap

dynamics promote species diversity and tree growth (Runkle 1982). Principal component 4 could also represent early gap-phase regeneration when young stems have access to increased resources such as light (Brokaw 1985, Swanson et al. 2011).

### Insect biomass

From 128 stand-night samples surveyed from 15 April to 12 August, 2013, and 1 May to 15 August, 2014, I weighed 4,925 g of insect biomass (mean = 41.14 g, range 0 – 346.13 g). Coleoptera (beetles) were the most abundant order (94% of the total biomass) with macro-Coleoptera comprising 81% of Coleopteran biomass. Lepidoptera (moths) were 2.7% of the total biomass, with macro-Lepidoptera accounting for 68% of this biomass. Diptera comprised only 0.12% of the total biomass. The cumulative biomass for all other orders was 2.4% of the total biomass. Mean insect biomass was similar between treatment and reference stands for total biomass ( $F_{1,111} = 0.4$ ;  $P = 0.6$ ), macro-Lepidoptera ( $F_{1,111} = 1.3$ ;  $P = 0.27$ ), macro-Coleoptera ( $F_{1,111} = 0.1$ ;  $P = 0.8$ ), micro-Coleoptera ( $F_{1,111} = 1.2$ ;  $P = 0.29$ ), Diptera ( $F_{1,111} = 0.5$ ;  $P = 0.5$ ), and other orders ( $F_{1,111} = 0.9$ ;  $P = 0.34$ ; Table 2.4). Biomass of micro-Lepidoptera was lower ( $F_{1,111} = 4.6$ ;  $P = 0.04$ ) in treated stands than in reference stands, but these small insects accounted for <1% of total biomass.

### Influence of vegetation and weather on insect biomass

Models with support ( $\Delta AIC_c \leq 2$ ) for predicting insect biomass varied among taxa and size classes but included only treatment and the first principal component (PC1) as predictors (Table 2.5). The null model was the most supported model for Diptera. Although most vegetation measurements (Table 2.1) and most insect taxa (Table 2.4) did not differ between treated and reference stands, treatment had support as a predictor variable for all taxa comparisons, except Lepidoptera (Table 2.5). Treatment was positively related to biomass for other insect orders, and in addition to PC1, was positively related to total biomass and biomass of macro-Coleoptera. Treatment had the greatest predictor weight for Diptera (Table 2.6), suggesting that there were likely unmeasured effects associated with treatment that influence Diptera.

Models incorporating PC1 were supported for all taxa except Diptera (Table 2.5). Dead wood had a positive effect on biomass when considered alone and when associated with treatment for total biomass, macro-Lepidoptera, macro-Coleoptera, and other orders. However, for smaller size class micro-Lepidoptera and micro-Coleoptera, dead wood was negatively associated with biomass. Models with PC1 had greatest model weight for all taxa except Diptera (Table 2.6). Large tree basal area was a stronger predictor of Dipteran biomass than were other principal components (Table 2.6), but it was not strong enough to be included in supported models (i.e.,  $\Delta AIC < 2.0$ ) for any taxon.

## DISCUSSION

Although vegetation variables appeared to be similar between treatment and reference stands (Table 2.1), principal components derived from measured forest variables were useful for predicting insect biomass in bottomland hardwood forests within the Mississippi Alluvial Valley (Table 2.5). I found dead wood (snags and woody debris of large trees) to be the most influential predictor of insect biomass for all taxa except Diptera. The presence and abundance of dead wood, particularly in treated stands, were positively related to large size class insect biomass but negatively associated with smaller size class insect biomass. The relationship between wood-boring beetles and dead wood is well known (Buse et al. 2009, New 2010, Siitonen 2001). Dead wood provides important shelter, foraging and reproductive habitat for many beetle genera (Stockland et al. 2012, Ulyshen et al. 2004). Dead wood also provides resources for moth genera that consume wood, fungal spores, mycelium, and other animals living in dead wood (Stockland et al. 2012).

Other forest structural characteristics and microclimate conditions have been found to influence insect taxa in forests (Dodd et al. 2008, 2012b; Furniss and Carolin 1977; Newell and King 2009), though I did not find them to be strong predictors in my study. The similarity in variables between treatment and

reference stands suggests that silvicultural treatments to enhance habitat for wildlife were implemented with less intensity than most commercial timber harvests or that sufficient time since treatment elapsed for tree growth to compensate for treatment. I attempted to capture this time effect by using age of treatment as a within treatment effect, but did not find this variable to be a strong predictor. For each WMA and NWR, unique silvicultural treatments were prescribed based on forest conditions and management priorities of agencies and foresters (Mississippi Forestry Commission 2008; USFWS 2006, 2009). Large variation in treatment intensity among treated stands likely reduced the effects of vegetative variables and age of treatment on insect abundance in my models. That I did not detect a difference in tree species richness is likely directly attributable to the recommendations given by Wilson et al. (2007a) to promote desired forest conditions.

In bottomland hardwood forests, precipitation is not typically a limiting factor as a result of the topography and geography of these areas (Taylor et al. 1990). My field seasons were within the average rainfall estimates for the region (State of the Climate, National Centers for Environmental Information, [ncdc.noaa.gov](https://www.ncep.noaa.gov)). Likely the abundance of standing water within study stands maintained humidity in the microclimate and decreased the immediate impact of precipitation and other weather variables. Also, because I collected climatic data from stations at a distance from my research locations, weather parameters probably reflected

regional weather patterns for the sample days rather than microscale weather conditions at the sample points. Moonlight seems to have had little influence on insect abundance in this ecosystem.

Silvicultural prescriptions have historically been implemented to reduce the effects of specific insect pest species (Amman and Logan 1998, Berryman 1986), but I observed positive responses in insect abundance associated with silvicultural treatments. Although my model associations were not strong, they indicated that even weakly associated parameters may impact different insect taxa and size classes within forested ecosystems. Other vegetation variables, such as herbaceous plant structure and composition may be important in structuring arthropod communities. These factors likely contributed to the influence of treatment for prediction of insect abundance despite lack of clear differences between treated and reference stands for many of the vegetation characteristics I measured.

Silvicultural manipulations can positively influence bat prey by promoting higher abundance of specific insect taxa. If increasing foraging opportunities for insectivorous bats is a management objective, silvicultural treatments promoting wildlife habitat, particularly dead wood, are likely beneficial for providing higher insect abundances. Snags are sometimes the result of tree-damage that occurred accidentally or deliberately during silvicultural disturbance (Guldin et al. 2007, Krusac and Mighton 2002). Silvicultural practices that promote increased

snag availability may be useful within stands that are lacking snags as an available resource. However, longer-term studies may be needed to fully describe the influence of silvicultural treatments and dead wood retention on insect abundance.

Particular attention should be applied to important taxa, such as moths. In treated stands, the reduction in abundance of small size class insects may affect bat community composition. Generally, smaller bats are expected to forage on smaller and softer prey (Norberg and Rayner 1987) because bats with elongate skulls and narrow jaws are not expected to have the bite force necessary for consuming larger, harder-bodied prey (Freeman 1984). Tri-colored bats and the southeastern myotis generally fit this expectation, preferring prey such as caddisflies (Trichoptera; Feldhamer et al. 2009). These two bat species could be impacted by a reduction in small prey abundance.

I caution against large-scale habitat conversion focused on one taxonomic group such as bats. As well, I remind readers that my study occurred over two years, a relative snapshot in the development of forest structural characteristics. Wildlife that depend upon these stands are in a constant state of flux, and as conditions change over time, the wildlife within these stands will change accordingly. I also propose that dietary preferences of bats in the southeastern US be studied in greater detail, to determine if bats in this region are indeed preferentially selecting specific taxa as prey items. The recommendations for

desired forest conditions for wildlife in the Mississippi Alluvial Valley promote dead wood retention (Wilson et al. 2007a) and I feel that this management strategy promotes food resources used by other animals, specifically bats. Silvicultural treatments to promote desired forest conditions are likely to increase bat use of treated bottomland hardwood forest stands in the MAV as a reflection of increases in prey availability.



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Fig. 2.1. Map of locations surveyed 2013-2014 in the Mississippi Alluvial Valley. Arkansas Wildlife Management areas are colored yellow. Mississippi Wildlife Management Areas are colored green. Louisiana Wildlife Management Areas are colored purple. Three Rivers WMA and Red River WMA are labeled as Yancey WMA. National Wildlife Refuges are colored blue.

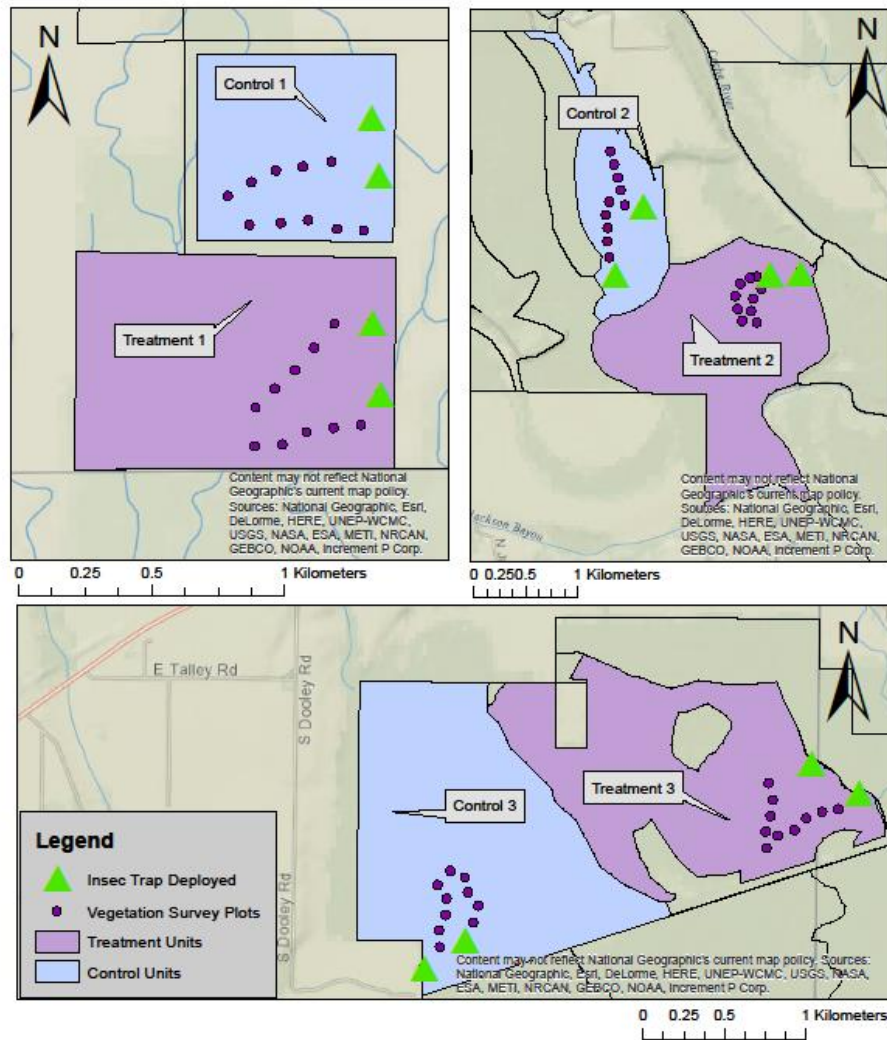


Fig. 2.2. Insect abundance survey locations and vegetation survey plots are depicted within the 2014 field season's treatment and reference stands at Cache River National Wildlife Refuge, Arkansas.

Table 2.1. Comparison of mean ( $\bar{x}$ ), minimum, and maximum values for forest structural characteristics measured in silviculturally treated and reference stands at 15 study areas in the Mississippi Alluvial Valley 2013-2014.

Parameter	Treatment			Reference			ANOVA Statistics	
	$\bar{x}$	Min	Max	$\bar{x}$	Min	Max	F*	P-value**
Canopy Closure (%)	79	76	89	79	76	86	2.9	0.09
Basal Area (m <sup>2</sup> /ha)	27.22	5	71	33.85	14	81	12.5	0.0006
Stem Density (#/ha)	3746	200	14100	3803	133	11483	0.05	0.8
Snag Density (#/ha)	13	2	60	10	0	45	4.4	0.04
Dead Downed Wood Density (#/ha)	9	0	37	10	0	33	0.7	0.40
Tree Species Richness	10	3	18	10	5	18	3.5	0.07

\* F-statistics calculated with numerator degrees of freedom = 1, denominator degrees of freedom = 111.

\*\* P-value presents the difference between treatment and reference stand means performed using a randomized block analysis of variance.

Table 2.2. Comparison of mean ( $\bar{x}$ ), minimum, and maximum values for insect biomass (non-transformed) in the Mississippi Alluvial Valley, 2013-2014. Number of traps = 128. Biomass weighed to the nearest 0.01g, biomass <0.01g not considered. Other orders = Total Biomass – Lepidoptera, Coleoptera, and Diptera.

Insect Taxa	Treatment			Reference			ANOVA Statistics	
	$\bar{x}$	Min	Max	$\bar{x}$	Min	Max	F*	P-value**
Total Biomass	41.14	0	346.13	35.51	0	160.35	0.4	0.6
Macro-Lepidoptera	0.59	0	5.53	0.82	0	6.5	1.3	0.27
Micro-Lepidoptera	0.24	0	1.64	0.43	0	2.58	4.6	0.04
Macro-Coleoptera	30.58	0	209.67	28.72	0	135.65	0.1	0.77
Micro-Coleoptera	8.91	0	239.5	4.72	0	54.5	1.2	0.29
Diptera	0.05	0	1.22	0.38	0	0.44	0.5	0.50
Other	0.8	0.02	3.85	1.1	0.23	20.01	0.9	0.34

\* F-statistics calculated with numerator degrees of freedom = 1, denominator degrees of freedom = 111.

\*\* P-value presents the difference between treatment and reference stand means performed using a randomized block analysis of variance.

Table 2.3. Factor loadings rotated using the varimax score to identify relationships between original structural characteristics measured and principal components in silviculturally treated and reference stands at 15 study areas in the Mississippi Alluvial Valley 2014-2015. Eigenvalues and cumulative variance included.

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Day	0.10	0.07	0.12	-0.68	0.23
Basal Area	0.24	0.74	-0.23	-0.22	-0.19
Canopy Closure	-0.43	-0.47	-0.07	-0.51	-0.05
Stem Density	0.01	-0.12	-0.05	0.72	0.11
Snag Density	0.82	-0.04	-0.14	-0.13	0.05
Down Wood Density	0.79	0.15	0.13	0.12	-0.05
Tree Species Richness	-0.18	0.85	-0.03	-0.00	0.19
Moon Illumination	0.07	0.12	0.24	-0.02	0.65
Wind Speed	-0.19	-0.03	0.87	-0.00	0.31
Air Temperature	-0.52	0.32	0.32	0.42	0.06
Relative Humidity	-0.14	0.04	-0.79	0.22	0.42
Precipitation	-0.06	-0.08	-0.18	-0.04	0.78
Eigenvalue	2.085	1.784	1.674	1.427	1.235
Cumulative Variance	0.174	0.322	0.462	0.581	0.684

Table 2.4.  $\Delta AIC_c$  values for top models that predict insect biomass collected in blacklight bucket traps across the Mississippi Alluvial Valley, 2013-2014. Model with  $\Delta AIC_c = 0.00$  is selected best model. Models with  $\Delta AIC_c \leq 2.00$  considered competitive.  $AIC_c$  weights ( $w_i$ ) represent the relative likelihood of each model. Parameter estimates presented for top models. Second-best models ( $AIC > 2.0$ ) presented for comparison with top models.

Taxon Models	$AIC_c$	$\Delta AIC_c$	$w_i$	Parameter Estimate
Total Biomass				
pc1 <sup>a</sup> + treatment <sup>b</sup>	109.2	0	0.9	42.5
pc1	113.7	4.5	0.1	-2.4
Macro-Lepidoptera				
pc1	-153.4	0	0.8	2.2
pc1 + treatment	-151.1	2.3	0.2	-57.6
Micro-Lepidoptera				
pc1	-373.0	0	0.8	-7.2
pc1 + treatment	-370.8	2.2	0.3	72.3
Macro-Coleoptera				
pc1 + treatment	144.3	0	0.9	41.7
pc1	147.9	3.6	0.1	-3.2
Micro-Coleoptera				
pc1 + treatment	28.5	0	0.6	-152.5
pc1	28.9	0.5	0.4	13.8
pc1 + age(treatment) <sup>c</sup>	55.5	27.0	7.6e-7	-165.5
Diptera				
Null	-554.8	0	0.6	-7.1
treatment	-553.6	0.6	0.4	-10.2
pc2	-547.4	7.4	0.0	4.4
Other Orders				
pc1	-154.2	0	0.7	23.2
treatment	-152.5	1.7	0.3	86.5
pc1 + age(treatment)	-118.4	35.8	1.2e-8	108.8

<sup>a</sup> pc1 (principal component 1) is interpreted as the positive correlation with snags and dead downed wood.

<sup>b</sup> treatment = silvicultural treatment as a categorical (binary) indicator of stand structure (i.e., treatment = 1, reference = 0).

<sup>c</sup> age(treatment) = treatment age as a within treatment factor.

Table 2.5. Akaike weights ( $w_i$ ) summed for models with each parameter, and evidence ratios ( $w_1/w_2$ ) presented as the relative evidence to favor one parameter over another for predicting insect biomass in the Mississippi Alluvial Valley 2013-2014.

Taxon Parameters	$\Sigma w_i$	$\Sigma w_1/\Sigma w_2$
Total Biomass		
pc1 <sup>a</sup>	1.000	1.106
treat	0.904	
pc2 <sup>b</sup>	2.907e-4	
age(treatment)	4.174e-6	
pc3	8.949e-17	
pc4	1.375e-24	
pc5	2.908e-70	
Macro-Lepidoptera		
pc1	1.000	4.115
treat	0.243	
age(treatment)	2.231e-6	
pc2	3.771e-7	
pc3	2.344e-19	
pc4	2.997e-48	
pc5	8.705e-94	
Micro-Lepidoptera		
pc1	1.000	4.032
treat	0.248	
pc2	9.152e-8	
age(treatment)	2.489e-8	
pc3	5.261e-22	
pc4	2.432e-52	
pc5	3.890e-99	
Macro-Coleoptera		
pc1	1.000	1.164
treat	0.859	
age(treatment)	9.575e-7	
pc3	1.432e-16	
pc4	1.507e-26	
pc5	1.144e-71	
pc2	4.650e-188	
Micro-Coleoptera		
pc1	1.000	1.799
treat	0.556	
age(treatment)	7.616e-7	
pc2	1.373e-7	
pc3	1.206e-20	
pc4	1.411e-40	
pc5	6.032e-72	

Diptera		
treat	0.354	19.667
pc2	0.018	
pc1	0.005	
age(treatment)	4.445e-6	
pc3	7.640e-8	
pc5	9.610e-66	
pc4	3.070e-115	
Other Orders		
pc1	1.000	3.290
treat	0.304	
age(treatment)	1.200e-8	
pc2	1.198e-8	
pc3	2.072e-21	
pc4	4.084e-46	
pc5	1.249e-88	

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<sup>a</sup> Highest parameter  $w_i = w_1$

<sup>b</sup> Second-highest parameter  $w_i = w_2$



## CHAPTER 3

# BAT COMMUNITY RESPONSE TO SILVICULTURAL TREATMENTS IN BOTTOMLAND HARDWOOD FORESTS MANAGED FOR WILDLIFE IN THE MISSISSIPPI ALLUVIAL VALLEY

## ABSTRACT

Silvicultural treatments (e.g., selective timber harvests) that are prescribed to promote wildlife habitat target creation of forests with physical structure described as desired forest conditions for wildlife. Such treatments have been advocated for management of bottomland hardwood forests on public conservation lands within the Mississippi Alluvial Valley. Although some songbirds respond positively to these management actions, little research has been directed at the effects on other species, including bats and their prey. Bats influence trophic interactions in forests by consuming large numbers of insects. Forest structure may affect bat use of bottomland forests due to differences in foraging space or roost sites. In light of growing concerns about declines in abundance of many bat species, I examined the effects of silvicultural treatments implemented to promote wildlife habitat on bat species activity. I conducted vegetation surveys and sampled insect biomass within 64 treated and 64 reference stands, that were distributed among 15 wildlife conservation areas in Arkansas, Louisiana, and Mississippi, USA. I examined the influence of vegetation metrics and insect biomass on the acoustic detections of bats during passive nocturnal surveys in these same stands. Detections of bat activity were similar between silviculturally treated stands and reference stands, indicating that

management of these locations is providing habitat for generalist bat species as well as forest interior species. Generalist bat species (e.g., evening bats, eastern red bats, Seminole bats, and big brown bats) were positively associated with increased insect biomass. Evening bats, eastern red bats and Seminole bats were also positively related to the amount of dead wood within a stand. Increased large tree basal area was positively associated with detection of big brown bats and bottomland specialists (Rafinesque's big-eared bats and myotis bats) as well as tri-colored bats. Conversely, acoustic detection of bats was negatively associated with stands with increased vegetative density (i.e., clutter). Managers that implement silvicultural treatments to improve desired forest conditions for wildlife can provide habitat for both generalist and forest interior bat species by providing heterogeneous forest structure that includes dead wood, high basal area of large trees, high tree species diversity, and gaps that are thinned to allow unimpeded flight by bats.

## INTRODUCTION

Bats are among the most endangered taxonomic groups worldwide (Arita 1993, Ceballos and Brown 1995, Mickelburgh et al. 2002, Weller et al. 2008), with several species listed as endangered or threatened (Miller et al. 2003, Avina et al. 2007). Long-lived animals with low fecundity, such as bats, are especially sensitive to environmental changes (Tuttle and Stevenson 1982, Bright and Morris 1996). Their habitat needs are complex (Trousdale 2011, Johnson and Lacki 2013); bats often use different forest areas according to nocturnal and diurnal requirements such as roost availability, prey abundance, and prey distribution (Barclay and Kurta 2007, Hayes and Loeb 2007, Lacki et al. 2007). Consequently, several studies have examined the effects of forest management on bat abundance, roost site availability and foraging activity (Menzel et al. 2002, Hayes and Loeb 2007, Dodd et al. 2012b, Johnson and Lacki 2013).

Silvicultural practices within forest stands, such as selective harvest, directly impact bat populations by changing roosting and foraging habitats (Krusic and Neefus 1996; Menzel et al. 2002, 2005; Perdue and Steventon 1996; Titchenell et al. 2011). Generally, higher levels of bat activity were associated with low structural volume habitats (Patriquin and Barclay 2003, Menzel et al. 2005), although forest specific species (i.e., northern long-eared bats [*Myotis*

*septentrionalis*]) may avoid open areas (Patriquin et al. 2003). Bat morphology (body size and wing shape), as well as their echolocation call characteristics interact with the structural volume of vegetation within forests to influence selection of foraging habitats by bats (Findley 1976, Aldridge and Rautenbach 1987, Norberg and Rayner 1987, Fullard et al. 1991, Fenton 2001).

Stewards of publicly-managed wildlife conservation lands within the Mississippi Alluvial Valley have advocated silvicultural treatments for management of bottomland hardwood forests to enhance wildlife habitat (Twedt and Somershoe 2010, Wilson et al. 2007a). Managing forests to achieve forest structure described as desired forest conditions for wildlife promotes heterogeneous forests with varying structural components (Wilson et al. 2007a). Structurally heterogeneous forests are favored by many wildlife species (Tews et al. 2004, Twedt and Wilson 2007) because they provide multiple characteristics such as regenerating, mature, and senescent trees all of which provide wildlife habitat for reproductive purposes, foraging, and escape cover (Twedt and Wilson 2007, Greenberg et al. 2011). Silvicultural treatments undertaken to enhance habitat for wildlife (a.k.a., wildlife forestry) are beneficial to many species of songbirds (Twedt and Wilson 2007, Twedt and Somershoe 2010, Twedt 2012), but little research has been directed at the effect of these treatments on other species, including forest-dwelling bats.

Silvicultural actions that remove roost sites or that change forest structure may impact bats (Law 1996, Parker et al 1996, Patriquin and Barclay 2003, Loeb and Waldrop 2008, Adams et al. 2009). Bat species of concern, such as southeastern myotis (*Myotis austroriparius*) and Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) roost in large, hollow trees within bottomland hardwood forest stands that have high basal area and high canopy closure (Gooding and Langford 2004, Trousdale and Beckett 2005, Lucas 2009). Thus, these species may be negatively impacted by removal of large hollow trees or by lower basal area and canopy closure associated with post-harvest open canopy conditions (Trousdale 2011). Conversely, some other bat species may benefit from uncluttered foraging space in open-canopy forests and increased prey availability associated with vegetative regeneration and herbaceous growth (Barclay 1999, Patriquin and Barclay 2003, Menzel et al. 2005). However, bats exhibit fidelity to foraging grounds (Wai-Ping and Fenton 1989) and they may be slow to respond to newly created habitats (Patriquin et al. 2003).

In this study, I compared the relationship between forest structural characteristics, insect biomass, and bat activity in stands recently (<12 years) subjected to silvicultural treatments that were implemented to promote wildlife habitat, and in reference stands with similar characteristics but which had not been subjected to any silvicultural treatment for >12 years.

## STUDY AREA

I surveyed 64 silvicultural treated and 64 untreated reference bottomland hardwood forest stands on 15 wildlife conservation lands within the Mississippi Alluvial Valley managed by state wildlife agencies (Wildlife Management Areas [WMA]) or federal wildlife agencies (U.S. Fish and Wildlife Service National Wildlife Refuges [NWR]). These included three locations in Arkansas (Cache River NWR, Dagmar WMA, White River NWR), eight in Louisiana (Bayou Cocodrie NWR, Big Lake WMA, Boeuf WMA, Dewey Wills WMA, Red River WMA, Russell Sage WMA, Three Rivers WMA, Tensas NWR), and four in Mississippi (Morgan Brake NWR, O'Keefe WMA, Panther Swamp NWR, Yazoo NWR; Fig. 3.1). I surveyed locations starting from the southernmost to the northernmost location in order to minimize the seasonal impact on bat activity caused by temperate deciduous forest growth (Hayes 1997). Mature bottomland hardwood forest stands (i.e., finite forest areas subjected to a common silvicultural prescription) were surveyed during summer 2013 and 2014. Land managers on each NWR and WMA identified stands that had been silviculturally treated to enhance desired forest conditions for wildlife within the past 12 years. I restricted selection of treated stands to  $\leq 12$  years post-treatment because the

predominant effects of silvicultural treatments on birds diminish after circa 12 years (Twedt and Wilson 2007, Twedt and Somershoe 2010).

Subject to stand availability, I randomly selected up to 3 treated stands on each WMA and NWR. I concurrently selected a similar number of untreated reference stands that were proximate to the treated stands, of similar area, with similar hydrology and vegetative species composition, but without silvicultural disturbance for >12 years (with preference given to older stands). If multiple stands met those criteria, I preferentially selected stands with greater time since disturbance (i.e., older stands) as reference stands. Because silvicultural prescriptions associated with wildlife forestry focus on attainment of a desired physical structure within the forest stand, treatments are not uniform but may include group selection, small patch cuts, thinning of canopy or understory trees, and harvest of individual trees. Within a treated stand, these silvicultural treatments may be applied uniformly or in patches, and treatments may be applied individually or in combination. Of 128 total stands, 46 stands were resurveyed in 2014, while 62 stands were surveyed once in either 2013 or 2014. Area of surveyed stands was  $168 \pm 151$  ha, ranging from 9.3 ha to > 600 ha with 37 stands < 100 ha, 72 stands between 100 ha and 300 ha, and 9 stands between 300 and 600 ha, and 2 stands > 600 ha.



## METHODS

### Field methods

*Acoustic field surveys.*— Acoustic surveys can be used to elucidate bat range distribution, community structure, relative population size, temporal activity, and habitat use (Betts 1998). Acoustic surveys have advantages over capture of bats via harp-trapping or mist netting, and subsequently outfitting captured bats with radio transmitters to obtain location information. Specifically, acoustic surveys require fewer personnel, cost less to survey over long periods of time, and can more readily survey multiple habitats (Kunz and Brock 1975, Cross 1986, Thomas and West 1989, O'Farrell and Gannon 1999, Lumsden and Bennett 2005). Use of full-spectrum processing when analyzing acoustic recordings provides an additional advantage to acoustic surveying by creating a visual sonograph including harmonic, amplitude, and frequency information for bat species identification (Szewczak 2004).

The numbers of acoustic recordings collected and identified to species provide an index of species activity rather than a measure of absolute abundance because recordings can equally be produced by one or many bats (O'Donnell and Sedgely 1994). Therefore, to detect bat species and quantify activity during these acoustic surveys, I deployed two Pettersson D500x full-spectrum acoustic

monitoring devices (Pettersson Elektronik AB, Uppsala, Sweden) with external microphones, powered by 6-V rechargeable external gel-cell batteries within each surveyed stand for a maximum of 12 devices synchronously deployed within a WMA or NWR (Ahlén and Baagoe 1999, Ancillotto et al. 2014, Slough et al. 2014).

I programmed each device to passively monitor and record the acoustic signals emitted by bats from 20:00 h to 06:45 h (ca. dusk to dawn) for 6 continuous nights with settings tailored to the conditions encountered in the field (e.g., very low trigger sensitivity to reduce insect noise). I deployed devices >200 m apart and >50 m from the edge of the stand (Dodd et al. 2008, 2012b) within silviculturally induced canopy gaps or in natural treefall gaps when no treatment gap was apparent. Device locations were not selected randomly, but were chosen as observers within the stand encountered gaps that met the distance from edge and distance from second device requirements. I used extendable fiberglass and aluminum poles to extend microphones 7 m into canopy gaps to avoid ground-level sampling bias (Waters and Jones 1995, Adams et al. 2009). I positioned microphones at a 45 degree angle using PVC pipe, aimed at the center of the canopy gap to increase the likelihood of acoustic detections (Patriquin et al. 2003, Adams et al. 2009) and to reduce the confounding effects of sampling in different microhabitats within stands (Hayes 2000, Weller and Zabel 2002). I typically swapped batteries after 3 nights as-needed.

*Insect surveys.*— Blacklight traps are a standard technique for sampling nocturnal flying insect assemblages (Covell 2005; Dodd et al. 2008, 2012a). I surveyed nocturnal flying insects using 10-W blacklight bucket traps (Universal Light Trap, BioQuip Products, Gardena, CA, US) powered by 12-V gel-cell batteries. Inside traps, I placed HERCON<sup>®</sup> Vaportape II insecticide treated plastic strips (Hercon Environmental, Emigsville, PA, US). I lifted traps between 1.5 and 2.5 m above the ground (Dodd et al. 2008, 2012b) and traps were active from 21:00 to 06:45. Traps were manually activated during 2013 surveys but were automatically activated with digital timers during 2014. I surveyed insects within each stand during 4 nights: I placed each trap at one location within each stand for two nights, and then I moved the trap to a second location within the stand for the remaining two nights. I collected sampled insects from each bucket trap on the following day. I bagged, labeled, and froze each night's sample. I positioned traps >50 m from the edge of each stand (Dodd et al. 2008, 2012a) to reduce edge effects, and >50 m from acoustic recording devices to avoid interactions between traps and acoustic devices (Muirhead-Thomson 1991; Dodd et al. 2008, 2012b; Obrist et al. 2011).

*Vegetation surveys.*— I surveyed forest vegetation within 10 circular 0.05 ha (12.62 m radius) plots that were located at 100 m intervals along two 400 m transects within each surveyed stand. This vegetation survey system was based on surveys used for forest habitat assessments in the Mississippi Alluvial Valley

(Wilson et al. 2007b). I started vegetation survey transects  $\geq 50$  m from the edge of the stand at a pre-determined, randomly selected access point and traversed a randomly selected azimuth, with the restriction that the transect azimuth would not exit the stand (Fig. 3.2). If barriers were encountered along the transect (i.e., oxbow lakes), the observer altered the azimuth of the route traversed but continued the survey transect. For all trees  $> 20$  cm diameter at breast height (dbh) within each 0.05 ha plot, I measured dbh to calculate basal area of large trees ( $\text{m}^2/\text{ha}$ ). I identified each tree to species, and classified tree condition as 1 = no crown die-off, 2 = lower crown die-off, 3 =  $< 1/3$  top crown die-off, 4 =  $> 1/3$  top crown die-off, 5 = recently dead with twigs, 6 = dead with large limbs, 7 = dead with only bole, and 8 = dead downed wood (Wilson et al. 2007b). I estimated mean percent canopy closure using a spherical densiometer at 4 points in the cardinal directions along the edge of the circular plot boundary (Twedt and Somershoe 2010). I measured vegetative clutter of small trees by counting stems of woody vegetation  $< 20$  cm dbh within a 4 m radius nested sub-plot (Martin et al. 1997). All vegetation characteristics were averaged across all vegetation sample plots within each surveyed stand.

### Data Analysis

*Acoustic analysis and species identification.*— I used SonoBat™ version 3.1 Northeast and version 3.2 Kentucky-Tennessee (DND Design, Arcata, CA) to

identify collected acoustic recordings to bat species (Kalcounis-Ruppell et al. 2013), referred to as activity. I included recordings in the 5-20 kHz range as an additional optional setting because some bat species in this geographic range call within that frequency range (Lacki et al. 2007). I reduced the amount of extraneous (presumably non-bat call) acoustic recordings by subjecting all recordings to the SonoBat Batch Scrubber 5.2 program. Using medium settings within this “scrubbing” or “filtering” program, I retained all but poor quality acoustic recordings. Recordings that remained after scrubbing were first analyzed using automated identification software in SonoBat 3.1 or 3.2 at default settings. For final species assignment via manual examination, each recording that passed through the automated identification software needed to have a consensus species assignment (Kalcounis-Ruppell et al. 2013, Slough et al. 2014).

I used version 3.1 for the northeastern U.S. because 1) there is no SonoBat version specifically for the southeastern U.S. and 2) when I began surveys in 2013, version 3.2 was not available. When version 3.2 for Kentucky-Tennessee became available in 2014, I began using it because more of the non-myotine species in the Mississippi Alluvial Valley overlap with the species for which Kentucky-Tennessee is optimized. Mexican free-tailed bats (*Tadarida brasiliensis*) are present in the southeastern U.S., but are not included in any of

the eastern U.S. SonoBat packages, so I used SonoBat 3.0 for the western U.S. to identify calls for this species.

I grouped congeneric species when necessary due to similarity in acoustic signatures. Seminole bats (*Lasiurus seminolus*) and eastern red bats (*L. borealis*) were grouped because Seminole bats and eastern red bats are not readily distinguished based on acoustic recordings. Similarly, myotine bats (*Myotis* spp.) are likewise difficult to distinguish based on acoustic recordings. In particular, southeastern myotis, the presumed most abundant myotine bat in much of this study area, is not included in the identification algorithms for SonoBat (Morris et al. 2010).

Bats with similar foraging behavior often have similar calls (Siemers et al. 2001, Jones and Holderied 2007), call variants that overlap with other species (Thomas et al. 1987, Obrist 1995, Barclay 1999), and variation within species (Betts 1998). To reduce the risk of incorrect identifications, I manually examined each sonograph that was identified as a bat with a consensus species assignment. I compared each of these recorded files with reference file sonographs of known species that were provided in SonoBat (Szewczak 2004, Slough et al. 2014, White et al. 2014).

Some species, such as Rafinesque's big-eared bats have low intensity calls that are difficult to record through passive monitoring (Fenton 1982, Murray et al. 1999). I noted that few recordings met the consensus standard for this

species, so I manually examined any recording with a vote species assignment of Rafinesque's big-eared bat. All verified species identifications were tallied by night and stand. I created a unique alpha-numeric identifier (ID) to distinguish each stand by location and year.

I assessed the effect of silvicultural treatment on bat activity by species, using a randomized block analysis of variance (ANOVA) test using the R statistical platform (R Project for Statistical Computing release 3.1.2, [www.r-project.org](http://www.r-project.org), accessed 07 February 2015; Kalcounis et al. 1999; Zar 2010). I blocked locations by NWR or WMA to reduce the variability inherent in sampling many locations across a broad geographic area (Zar 2010). I did not differentiate treatments by silvicultural intensity, as I assumed vegetative measurements sufficiently characterized treatment and temporal variability within treated stands.

*Insect biomass and vegetation.*— I analyzed insect biomass from one randomly selected sample night from each surveyed stand. After air-drying thawed insect samples overnight, samples were identified to order, sized, and biomass was determined to the nearest 0.01 g. In addition to total biomass, I measured biomass for Lepidoptera, Coleoptera, and Diptera because these insect orders are frequent prey for bats (Hamilton and Barclay 1998, Carter et al. 2004, Claire et al. 2009, Feldhamer et al. 2009). Some bat species forage preferentially on larger or smaller insects (Dodd et al. 2008, 2011, 2012b), therefore I sub-divided Lepidopteran insects based on wingspan into micro-

Lepidoptera (<20 mm) or macro-Lepidoptera ( $\geq 20$  mm). Similarly, I sub-divided Coleopteran insects based on body length into micro-Coleoptera (<10 mm) and macro-Coleoptera ( $\geq 10$  mm; Dodd et al. 2008, 2011, 2012b). All other insect orders were combined as other insect biomass (i.e., total biomass-Diptera-Coleoptera-Lepidoptera = other insect biomass).

Similar to the ANOVA performed to identify treatment effect on bat activity, I performed a randomized block ANOVA on raw data to identify the treatment effect on insect biomass and forest structural characteristics while accounting for a location effect (Dellasala 1996, Zar 2010). Again, I did not differentiate treatment stands by silvicultural intensity.

*Identification of factors influencing bat activity.*— As an initial data reduction step, I used principal component analysis (PCA) in R to derive uncorrelated vegetation and insect biomass variables based on measured values (Jamison et al. 2002, Akutsu et al. 2007, Thompson et al. 2013). I transformed vegetation ( $\arcsin\sqrt{x}$  or  $\sqrt{x}$ ) and all insect biomass ( $\ln[x+1]$ ) measurements to improve normality (Zar 2010). I rotated the components using the varimax score method (Manly 1986, Reymont and Joreskog 1996) and I used factor loadings to identify relationships between original variables and principal components (Jamison et al. 2002).

I used generalized linear mixed models (GLMMs) with the log-link function (Ashrafi et al. 2013, Lourenço et al. 2013) to identify variables affecting bat



activity. For each bat species, GLMMs included the principal components representing vegetation and insect biomass variables. I included a binary (i.e., 1 = treatment, 0 = reference) categorical predictor for treatment effect with age of the treatment (i.e., number of years since treated) as a within-treatment variable. I also included the ID variable in GLMM models to describe the year, location, and stand from which each recording came. Because I surveyed each location for 6 nights, a repeated measure, I defined each night as a survey night, and nested survey night within ID to account for the confounding effects associated with repeated measures and multiple locations (Baayen et al. 2008, Bolker et al. 2009).

I used the R package glmmADMB (v.0.8.1, [www.r-project.org](http://www.r-project.org), accessed 11 March 2015) to fit a global model for each species because my response variables (i.e., the number of recordings for each species) had a zero-inflated, negative binomial error structure (Bolker et al. 2012, Fournier et al. 2012, Kalan et al. 2015, Kleinke and Reinecke 2015). I compared the variance parameterizations between the typical negative binomial variance (variance =  $\mu(1 + \mu/k)$ ), and the Quasi-Poisson variance (variance =  $\phi\mu$ ) for possible global models (Bolker et al. 2012, Lourenço et al. 2013), holding my random effects constant. I used the default Akaike's Information Criterion (AIC) to compare the global models and chose a variance structure based on which model had the lowest  $\Delta AIC$  (Bolker et al. 2012, Lourenço et al. 2013).

I used the R package MuMIn (v.1.12.1, [www.r-project.org](http://www.r-project.org), accessed 15 July 2015) to generate and analyze candidate models with all possible subsets of predictive variables from each species' global model (Bartoń 2015, Grueber et al. 2010, Kessler et al. 2011, Martin and Fahrig 2012). I included a null model (intercept-only), and held treatment age within treatment and survey night within ID constant across all models (Grueber et al. 2010). I used Akaike's Information Criterion for small sample sizes (AICc) values to calculate  $\Delta\text{AICc}$  and model weights ( $w_i$ ) for each candidate model. I considered models competitive with  $\Delta\text{AICc} \leq 2.0$  to have support as predictors of bat activity (Burnham and Anderson 2002, Ober and Hayes 2008, Martin and Fahrig 2012, Thompson et al. 2013). If only one model had  $\Delta\text{AICc} \leq 2.0$ , I selected it as the best fit model. For species with multiple competitive top models, I used the zero method of model averaging to rescale and calculate predictor estimates (Grueber et al. 2010, Nakagwa and Freckleton 2010). I calculated the summed predictor weights of supported models with shared predictors as evidence supporting the relative strength of each predictor (Johnson and Omland 2003, Wagenmakers and Farrell 2004, Meyer and Kalko 2008).

## RESULTS

### Bat Species Identification

I recorded 1,433,121 total acoustic files from 15 April to 12 August, 2013, and 1 May to 15 August, 2014. I used SonoBat Batch Scrubber 5.2 to filter and eliminate recordings that were deemed to be insects and bat calls that were faint, or lacked distinguishing characteristics necessary for bat species identification. After filtering, 47,295 recorded acoustic files (3%) were ascribed to 7 bat species (evening bats [*Nycticeius humeralis*], tri-colored bats [*Perimyotis subflavus*], silver-haired bats [*Lasionycteris noctivagans*], hoary bats [*Lasiurus cinereus*], big brown bats [*Eptesicus fuscus*], Rafinesque's big-eared bats, and Mexican free-tailed bats), or 2 bat species groups (eastern red bat - Seminole bat group, and myotine bat species group).

I identified most acoustic recordings as evening bats, followed by eastern red/Seminole bats, tri-colored bats, and myotine species (Table 3.1). I rarely identified silver-haired bats, hoary bats, Rafinesque's big-eared bats, big brown bats, or Mexican-free tailed bats. I detected more bat activity (i.e., more identifiable acoustic recordings) at locations in Mississippi (Fig. 3.3). Detection of bat activity was temporally quadratic: being lowest at the start of each survey

season (April-May), increasing through mid-season (June-July), then decreasing during late summer (August; Fig. 3.3).

Bat activity in treated and reference stands was similar for most locations (Fig. 3.4). Although the mean total bat recordings from treated stands were 59% of the total number of recordings identified to species, treated and reference stands were similar ( $F_{1,127} = 3.53$ ;  $P = 0.06$ ; Table 3.1). Mean bat activity per species was similar in treated and reference stands for all species ( $P > 0.05$ ).

#### Insect Order Biomass

From 128 stand-night samples collected from 15 April to 12 August, 2013, and 1 May to 15 August, 2014, I weighed 4,925g of insect biomass (mean = 41.14 g, range 0 – 346.13 g). Coleoptera were the most abundant order (94% of total biomass) with macro-Coleoptera comprising 81% of Coleopteran biomass. Lepidoptera were 2.7% of the total biomass, with macro-Lepidoptera accounting for 68% of this biomass. Diptera comprised only 0.12% of the total biomass. Cumulative biomass for all other orders was 2.4% of the total biomass. Mean insect biomass was similar between treatment and reference stands for total biomass ( $F_{1,111} = 0.4$ ;  $P = 0.60$ ), macro-Lepidoptera ( $F_{1,111} = 1.3$ ;  $P = 0.27$ ), macro-Coleoptera ( $F_{1,111} = 0.1$ ;  $P = 0.77$ ), micro-Coleoptera ( $F_{1,111} = 1.2$ ;  $P = 0.29$ ), Diptera ( $F_{1,111} = 0.5$ ;  $P = 0.50$ ), and other orders ( $F_{1,111} = 0.9$ ;  $P = 0.34$ ; Table

3.2). Micro-Lepidopteran biomass was lower ( $F_{1,111} = 4.6$ ;  $P = 0.04$ ) in treated stands but these small insects accounted for <1% of total biomass.

### Vegetation

I quantified forest structural characteristics on 1,536 sample plots in 128 surveyed stands from April to 15 April to 12 August, 2013, and 1 May to 15 August, 2014. For the 64 treated stands, the mean time since treatment was  $5.1 \pm 4.0$  years. Treated and reference stands were similar for canopy closure, stem density, dead downed wood density, and tree species richness (Table 3.3). However, compared to reference stands, treated stands had more snags (13 per ha compared to 10 per ha;  $F_{1,111} = 4.4$ ;  $P = 0.04$ ) and lower large tree basal area ( $27.2 \text{ m}^2$  per ha compared to  $33.85 \text{ m}^2$  per ha;  $F_{1,111} = 12.5$ ;  $P < 0.001$ ).

### Factors influencing bat activity

Principal components analysis summarizing vegetation, insect biomass, and date variables resulted in five principal components that explained 70% of the cumulative variance (Table 3.4). I interpreted each principal component based on the factor loadings associated with each principal component. The first principal component (PC1) represented increased insect biomass (especially Lepidoptera, Coleoptera, and other orders). The remaining principal components represented increased dead downed wood and snags from large trees (PC2); increased large tree basal area and tree species richness (PC3); survey date

(PC4); and increased stem density of small trees along with decreased canopy closure (PC5; Table 3.5). Principal components 3 and 5 are likely indexes of gap recovery post-disturbance as increased resources (i.e., light) promote species diversity and stem growth (Runkle 1982, Brokaw 1985, Swanson et al. 2011). Because total biomass and macro-Coleopteran biomass were highly correlated, total biomass was eliminated from the PCA. Dipteran biomass was low and weakly related to other factors.

The Quasi-Poisson variance best fit global models for evening bats, eastern red and Seminole bats, Rafinesque's big-eared bats, Mexican free-tailed bats and myotome bats. The negative binomial variance best fit global models for all other species. Models with support ( $\Delta AIC_c \leq 2$ ) for predicting the level of acoustic recording of bats varied among taxa (Table 3.6).

Insect biomass (PC1) and dead wood (PC2) were positively associated with evening bat activity. Conversely, increased stem density of small trees (PC5) was negatively associated with evening bat activity (Table 3.7). Similarly, acoustic detection of eastern red and Seminole bats, only one model was supported with  $\Delta AIC_c \leq 2$ . Eastern red and Seminole bats was positively associated with PC1 and PC2, and being negatively associated with PC5 (Table 3.6). For tri-colored bats, PC3 had the greatest model weight (Table 3.6). Survey date associated with the factor of treatment age within treatment also

received support (Table 3.7). These predictors were positively associated with tri-colored bat activity.

For silver-haired bats, dead wood (PC2) and large tree basal area (PC3) had high model weight (Table 3.7), both being negatively associated with silver-haired bat activity (Table 3.6). Hoary bats were similar, though in addition to PC2 and PC3, stem density of small trees (PC5) also had high model weight (Table 3.7). These predictors were all negatively associated with hoary bat activity (Table 3.6).

The global model for Rafinesque's big-eared bats failed to converge with all possible predictors, so I removed date (PC4) from the global model because I determined the other predictors to be of greater conservation concern. With PC4 removed, the global model for Rafinesque's big-eared bats converged. One model was supported with  $\Delta AIC_c \leq 2$  wherein PC2 and PC3 had high model weight (Table 3.7). Dead wood was negatively associated with Rafinesque's big-eared bat activity, but large tree basal area (PC3) was positively associated with activity of this bat species (Table 3.6).

Insect biomass (PC1), dead wood (PC2), large tree basal area (PC3), and date (PC4) had high model weight for big brown bats (Table 3.7). Acoustic recordings of big brown bats were positively associated with PC1 and PC3, whereas PC2 and PC4 were negatively associated with big brown bat activity (Table 3.6). The null model was the most supported model for Mexican free-

tailed bats. Stem density of small trees (PC5) had high model weight (Table 3.7), though it was negatively associated with activity (Table 3.6). For myotis species, PC3 and PC5 had high model weights (Table 3.7). Large tree basal area (PC3) was positively associated with activity, whereas stem density was negatively associated with activity (Table 3.6). I did not find survey night within ID to be an important predictor of bat activity for any particular species.



## DISCUSSION

Detection of acoustic recordings of bats was similar in stands silviculturally treated to enhance habitat for wildlife, and reference stands, though the proportion of acoustic recordings was higher in treated stands for most bat species. I assumed that increased numbers of recorded bat calls was proportional to bat activity. Similar activity for all bat species in treated stands compared to their activity in reference stands is a reflection of the silvicultural management implemented at each NWR and WMA to move forest structure towards a more desirable condition that is beneficial for wildlife, including bats.

Although species responded uniquely to changes in forest structure and insect biomasses that occurred post-treatment, there appeared to be a pattern among functionally similar bat groups regarding foraging habitat preferences. These species groups were: generalist foraging bats of openings and edges (evening bats, eastern red bats, Seminole bats), forest interior bat species (Rafinesque's big-eared bats, myotine bats, tri-colored bats), migratory bat species (silver-haired bats, hoary bats), true generalist bat species (big brown bats) and Mexican free-tailed bats.

Generalist foraging bat species of openings and edges responded favorably to insect abundance and dead wood while avoiding areas of high stem

density. Most insect-eating bats of the U.S. tend to be generalists in their foraging preferences (Anthony and Kunz 1977, Zinn and Humphrey 1981, Kalcounis-Rueppell et al. 2007, Feldhamer et al. 2009), taking beetles, moths, flies, and other insect orders (Carter et al. 2004, Feldhamer et al. 2009, Morris et al. 2010) based on bat species' morphology, sympatric species, habitat conditions, and survey methodology (Freeman 1981, Fenton 1990, Menzel et al. 2002, Lee and McCracken 2004, Dodd et al. 2012a). Species such as evening bats, eastern red bats, Seminole bats, and big brown bats likely benefit from increased insect biomass, regardless of stand type. These bat species were more active in both treated and reference stands when those stands had high insect abundance. Increased insect abundance was likely a result of increased dead wood density (see Chapter 2).

The association of bat activity with snag density in treated stands, and dead wood's importance in predictive models of most bat species, especially evening bats, indicate that treated stands can offer a resource that may be limited in reference stands. The relationship between dead wood and bat species is complex, but dead wood is generally presumed to be beneficial by providing roosting sites in the form of cavities (Tuttle 1976, Barclay and Brigham 1996), and improving foraging habitat by increasing insect abundance (see Chapter 2). Many studies of cavity roosting bats have concluded that retention and maintenance of potential roost trees, particularly snags, is important for bats

(Campbell et al. 1996, Jung et al. 1999, Gooding and Langford 2004). I did not evaluate snag quality for roosting, but dead wood may be an important indicator of habitat quality and prey availability in the MAV (Scott et al. 1977, Naiman et al. 2002). Eastern red and Seminole bats are foliage roosting species that were positively related to dead wood density, supporting the supposition that dead wood is also important for species that are not cavity-roosting bats.

Changes in vegetation structure that result in more open and uncluttered flying space seem to benefit bats by reducing clutter echoes, or the noise caused by reflected echolocations from multiple surfaces (Schnitzler and Kalko 2001), as well as by reducing flight hindrances and obstacles (Kalko and Schnitzler 1993). Therefore, bats tend to prefer to forage in habitats that provide easy maneuverability and prey capture (Aldridge and Rautenbach 1987, Fenton 1990, Brigham et al. 1997, Patriquin and Barclay 2003). I found that even species that are generally associated with cluttered environments may have clutter tolerance levels that can be exceeded. Eastern red bats, Seminole bats, and myotine bats appear to contradict the general assumption that small, highly maneuverable species are clutter-tolerant (Fenton 1990). My observations support those of other researchers that morphological adaptations may not be indicative of habitat preference (Broders et al. 2003, Patriquin and Barclay 2003).

Forest interior bat species were scarcer in the MAV than were generalist bat species. Structural differences in vegetation, particularly large tree basal

area, appeared to be an important predictor of forest interior bat species activity. Silvicultural treatment prescriptions often include basal area reduction to decrease resource competition and stimulate growth of desired tree species (Leak et al. 1987, Loftis 1990). However, Rafinesque's big-eared bat and myotine bat activity were positively related with increased large tree basal area and tree species richness, suggesting prescribed silvicultural treatments reduce habitat quality for these bats. These species tend to roost in large, living, hollow trees (Gooding and Langford 2004, Johnson and Lacki 2013). Rafinesque's big-eared bats have previously been found to prefer forests with high basal area (Gooding and Langford 2004). Both species tend to roost in large, living, hollow trees (Gooding and Langford 2004, Johnson and Lacki 2013). Typically, Rafinesque's big-eared bats forage near their day roosts, such that foraging habitat preference may be influenced by proximity to appropriate roost trees (Johnson and Lacki 2013). Similarly, myotine bats, were more commonly detected in stands with higher large tree basal area. Thus, conservation of unmanaged stands with high large tree basal area should remain a key strategy in the promotion of roosting and foraging habitat for these species. That I did not observe a difference in tree species richness between treated and reference stands is likely a result of the recommendations made by Wilson et al. (2007a) for promoting desired forest conditions for wildlife.

I grouped myotine bats due to difficulty in discriminating among their recorded calls. This grouping may have obscured species differences as individual species may react differently to forest structural characteristics. In general, northern long-eared bats (*Myotis septentrionalis*) avoid open areas (Loeb and O'Keefe 2006) whereas the clutter tolerance of southeastern myotis, presumably more the more common species in the MAV, is less well understood (Morris et al. 2010). Therefore, by grouping myotine species, I cannot determine which species influenced the negative relationship with high stem density.

Tri-colored bats and big brown bats were the only species with a relationship to survey date. That tri-colored bats showed a positive association with survey date when combined with age of treatment indicates that this species may have an affinity for stands of a certain age. This interaction merits further investigation.

Migratory species such as hoary bats and silver-haired bats may have activity related to factors that I did not measure. Presumably, their habitat preferences would be reflective of locations where they spend more of their time. I observed that both hoary bats and silver-haired bats had a negative association with dead wood and high large tree basal area. Hoary bats had an additional negative association with stem density. Hoary bats have relatively large body size and both of these species tend to forage using long-range prey detection acoustic signals (Barclay 1985, Barclay et al. 1999, Menzel et al. 2005). Mexican

free-tailed bats are fast-flyers with low maneuverability (Vaughan 1966, Long and Kamensky 1967, Iriarte-Díaz et al. 2002). Although detected in my study, Mexican free-tailed bats are more commonly found in western cave systems and near urban areas with manmade structures (Harvey et al. 2011). Bottomland hardwood forests may not provide habitat suitable for these large bodied or fast-flying species.

## MANAGEMENT IMPLICATIONS

Silvicultural treatments prescribed to enhance wildlife habitat in the Mississippi Alluvial Valley appear to benefit multiple bat species by promoting heterogeneous landscapes with a mosaic of vegetation characteristics and insect prey abundances. Promotion of habitat features including dead wood, large diameter trees, and high tree species diversity are priorities for desired forest conditions for wildlife as discussed in Wilson et al. (2007a). However, because reference stands with high large tree basal area provide habitat for some priority bat species, retaining high basal area forest stands within the landscape should also be a priority. To accommodate both disturbance-dependent and forest interior bat species, habitat managers should continue to promote a mosaic of forest structural characteristics, including passively managed (i.e., reference) stands. Silvicultural practices that retain or create dead wood, particularly snags, in stands lacking this resource could benefit multiple species, including evening bats, eastern red bats, and Seminole bats. Silvicultural prescriptions that include large canopy gaps provide uninhibited flight space for foraging bats. Thinning of dense regrowth within these gaps to reduce small diameter stem growth (i.e., clutter) will increase bat access for foraging in forests below the canopy. This study occurred over two years, a relative snapshot in the development of forest

structural characteristics, but I found little evidence that silvicultural activities proposed by the LMVJV for managing bottomland hardwood forests negatively impacted bat communities. These activities are likely to increase use of forest stands by bats, especially if retention of important habitat features like potential roost trees are considered in silvicultural prescriptions.



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Fig. 3.1. Map of locations surveyed 2013-2014 in the Mississippi Alluvial Valley. Arkansas Wildlife Management areas are colored yellow. Mississippi Wildlife Management Areas are colored green. Louisiana Wildlife Management Areas are colored purple. Red River WMA and Three Rivers WMA were renamed as Yancey WMA in 2014. National Wildlife Refuges are colored blue.

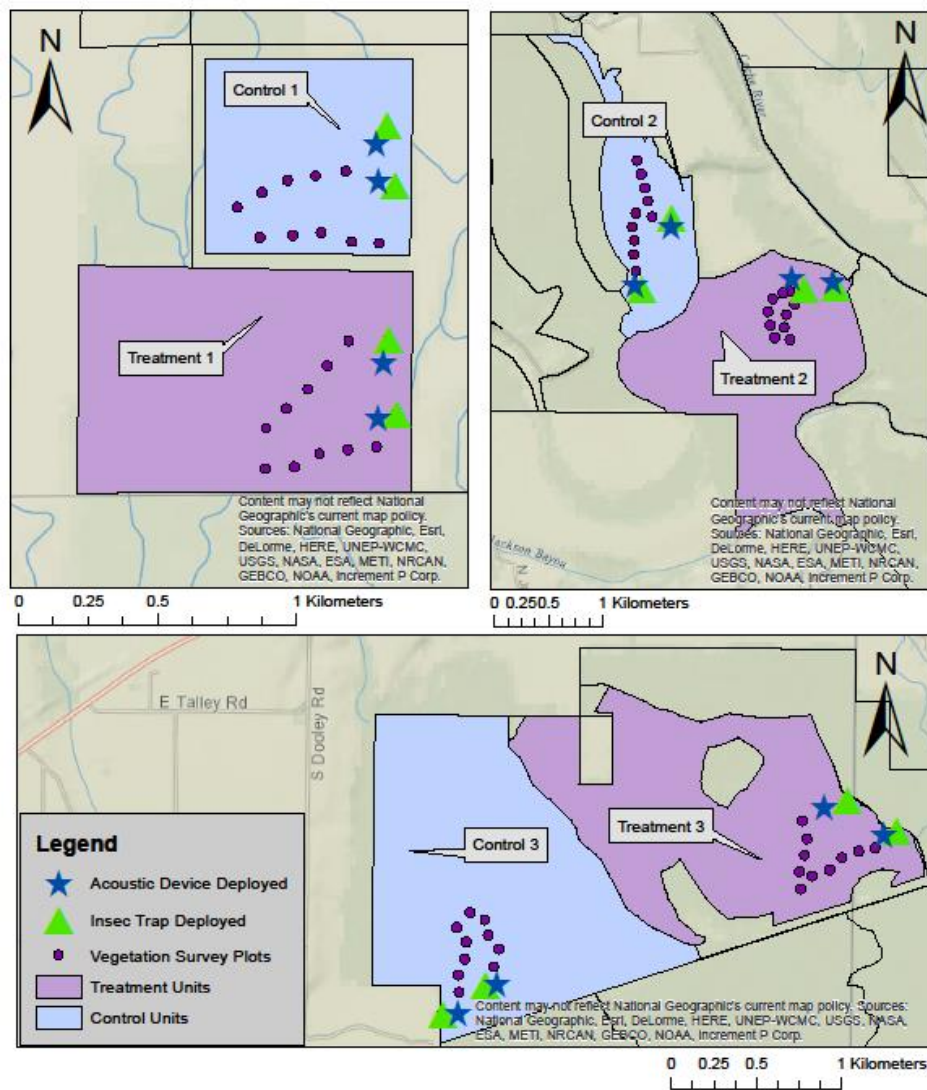


Fig. 3.2. Acoustic survey locations, insect abundance survey locations, and vegetation survey plots are depicted within the 2014 field season's treatment and reference stands at Cache River National Wildlife Refuge, Arkansas.



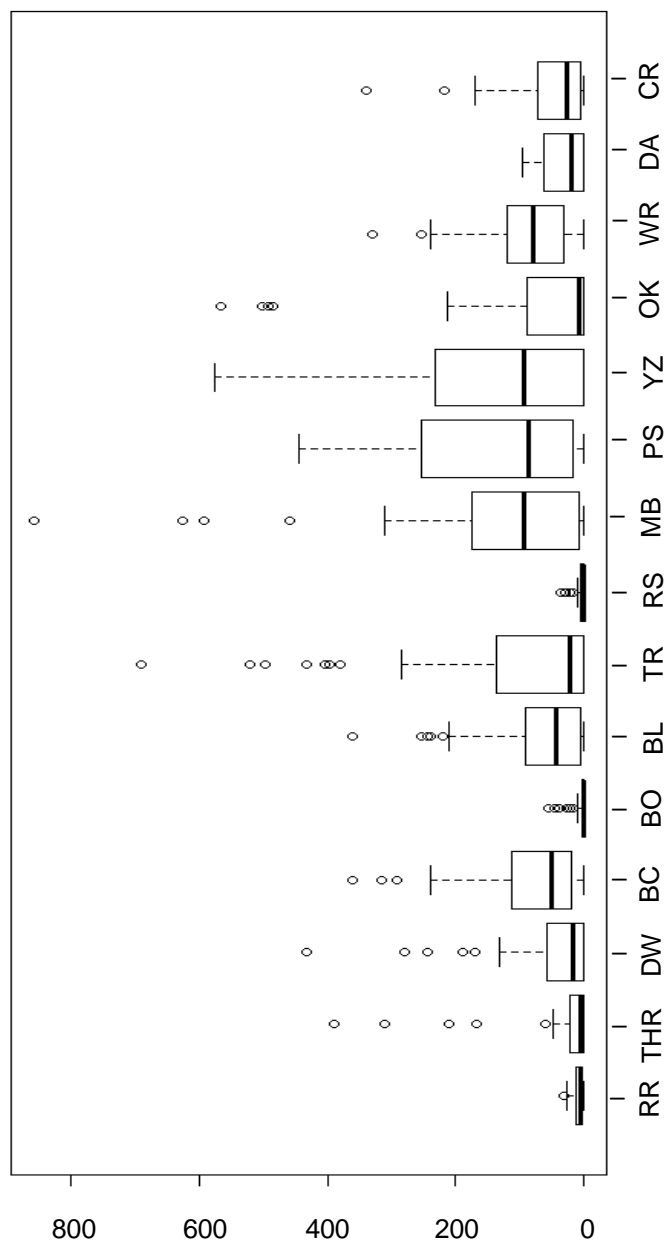


Fig 3.3. Mean bat call recordings across locations surveyed in chronological order in the Mississippi Alluvial Valley 2013-2014. Locations coded as: RR = Red River WMA, THR = Three Rivers WMA, DW = Dewey Wills WMA, BC = Bayou Cocodrie NWR, BO = Boeuf WMA, BL = Big Lake WMA, TR = Tensas River NWR, RS = Russell Sage WMA, MB = Morgan Brake NWR, PS = Panther Swamp NWR, YZ = Yazoo NWR, OK = O'Keefe WMA, WR = White River NWR, CR = Cache River NWR.

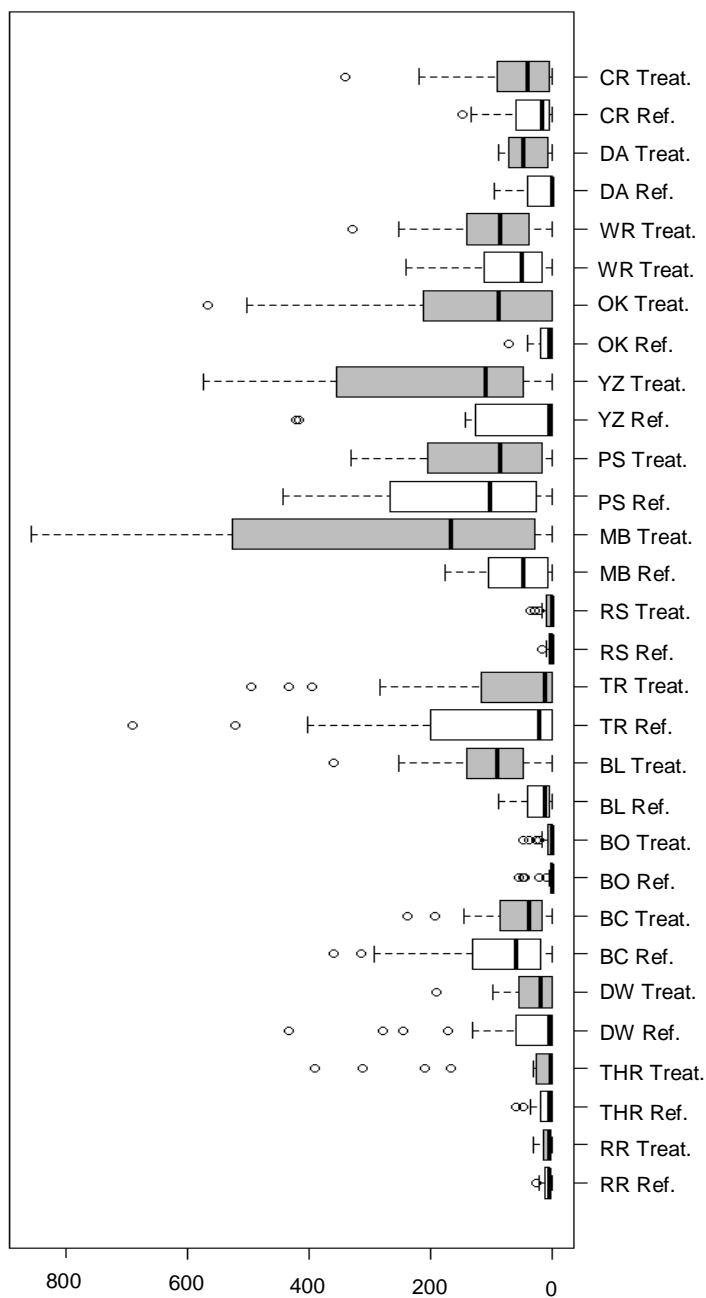


Fig. 3.4. Mean bat call recordings from reference (Ref., white) and treatment (Treat., gray) stands for locations surveyed in chronological order in the Mississippi Alluvial Valley 2013-2014. Locations coded as: RR = Red River WMA, THR = Three Rivers WMA, DW = Dewey Wills WMA, BC = Bayou Cocodrie NWR, BO = Boeuf WMA, BL = Big Lake WMA, TR = Tensas River NWR, RS = Russell Sage WMA, MB = Morgan Brake NWR, PS = Panther Swamp NWR, YZ = Yazoo NWR, OK = O'Keefe WMA, WR = White River NWR, CR = Cache River NWR.

Table 3.1. Comparison of mean ( $\bar{x}$ ), minimum, and maximum values for bat species recordings summed per stand of bottomland hardwood forests in the Mississippi Alluvial Valley 2013-2014.

Species	Treatment			Reference			ANOVA Statistics	
	$\bar{x}$	Min	Max	$\bar{x}$	Min	Max	F*	P-value**
Total Bats	439	0	2597	300	0	2178	3.53	0.063
Evening bat	245	0	1406	166	0	1677	2.63	0.105
Eastern red bat/Seminole bat	93	0	1190	51	0	793	2.99	0.087
Tri-colored bat	65	0	840	39	0	427	3.2	0.077
Silver-haired bat	0.3	0	5	0.3	0	10	0.02	0.877
Hoary bat	0.3	0	4	0.5	0	13	0.61	0.435
Rafinesque's big-eared bat	6	0	217	1	0	25	2.20	0.141
Big brown bat	9	0	163	6.7	0	180	0.29	0.589
Mexican free-tailed bat	1	0	10	0.8	0	21	0.27	0.607
Myotis bats	21	0	54	34	0	368	2.22	0.139

\* F-statistics calculated with numerator degrees of freedom = 1, denominator degrees of freedom = 111.

\*\* P-value presents the difference between treatment and reference stand means performed using a randomized block analysis of variance.

Table 3.2. Comparison of mean ( $\bar{x}$ ), minimum, and maximum values for insect biomass (non-transformed) in the Mississippi Alluvial Valley, 2013-2014. Number of traps = 128. Biomass weighed to the nearest 0.01g, biomass <0.01g not considered. Other orders = Total Biomass – Lepidoptera, Coleoptera, Diptera.

Insect Taxa	Treatment			Reference			ANOVA Statistics	
	$\bar{x}$	Min	Max	$\bar{x}$	Min	Max	F*	P-value**
Total Biomass	41.14	0	346.13	35.51	0	160.35	0.4	0.6
Macro-Lepidoptera	0.59	0	5.53	0.82	0	6.5	1.3	0.27
Micro-Lepidoptera	0.24	0	1.64	0.43	0	2.58	4.6	0.04
Macro-Coleoptera	30.58	0	209.67	28.72	0	135.65	0.1	0.77
Micro-Coleoptera	8.91	0	239.5	4.72	0	54.5	1.2	0.29
Diptera	0.05	0	1.22	0.38	0	0.44	0.5	0.50
Other	0.8	0.02	3.85	1.1	0.23	20.01	0.9	0.34

\* F-statistics calculated with numerator degrees of freedom = 1, denominator degrees of freedom = 111.

\*\* P-value presents the difference between treatment and reference stand means performed using a randomized block analysis of variance.

Table 3.3. Comparison of mean ( $\bar{x}$ ), minimum, and maximum values for forest structural characteristics measured in silviculturally treated and reference stands at 15 study areas in the Mississippi Alluvial Valley 2013-2014.

Parameter	Treatment			Reference			ANOVA Statistics	
	$\bar{x}$	Min	Max	$\bar{x}$	Min	Max	F*	P-value**
Canopy Closure (%)	79	76	89	79	76	86	2.9	0.09
Basal Area (m <sup>2</sup> /ha)	27.22	5	71	33.85	14	81	12.5	0.0006
Stem Density (#/ha)	3746	200	14100	3803	133	11483	0.05	0.8
Snag Density (#/ha)	13	2	60	10	0	45	4.4	0.04
Dead Downed Wood Density (#/ha)	9	0	37	10	0	33	0.7	0.40
Tree Species Richness	10	3	18	10	5	18	3.5	0.07

\* F-statistics calculated with numerator degrees of freedom = 1, denominator degrees of freedom = 111.

\*\* P-value presents the difference between treatment and reference stand means performed using a randomized block analysis of variance.

Table 3.4. Factor loadings rotated using the varimax score to identify relationships between original characteristics measured and principal components in silviculturally treated and reference stands at 15 study areas in the Mississippi Alluvial Valley 2014-2015. Eigenvalues and cumulative variance included.

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Date	0.13	0.00	0.07	0.80	-0.23
Basal Area	-0.20	0.20	0.72	0.20	-0.06
Canopy Closure	-0.12	-0.34	-0.51	0.11	-0.57
Stem Density	-0.04	-0.09	-0.13	-0.14	0.86
Snag Density	0.04	0.83	-0.08	0.26	0.03
Down Wood Density	0.02	0.84	0.17	-0.18	-0.01
Tree Species Richness	-0.05	-0.15	0.86	-0.03	-0.03
Macro-Lepidoptera	0.72	0.08	-0.10	0.28	0.05
Micro-Lepidoptera	0.85	0.12	0.01	0.14	-0.04
Macro-Coleoptera	0.68	-0.24	-0.13	-0.46	-0.06
Micro-Coleoptera	0.72	0.04	0.02	-0.37	-0.39
Diptera	0.37	0.39	-0.12	-0.35	-0.26
Other Orders	0.71	0.03	-0.10	-0.03	0.10
Eigenvalue	3.17	2.02	1.46	1.32	1.11
Cumulative Variance	0.24	0.40	0.51	0.61	0.70

Table 3.5. Best approximating generalized linear mixed models ( $\Delta AIC_c \leq 2.00$ ) used to evaluate responses of bat call frequencies to silvicultural treatments to promote desired forest conditions for wildlife in bottomland hardwood forests of the Mississippi Alluvial Valley, 2013-2014. Degrees of freedom (K), -2 log-likelihood (-2LL),  $AIC_c$  and  $\Delta AIC_c$  values presented.  $AIC_c$  weights ( $w_i$ ) represent the relative likelihood of each model and were calculated after model averaging for species with multiple top models, otherwise weights were calculated across all possible models.

Bat Species Models	K	-2LL	$AIC_c$	$\Delta AIC_c$	$w_i$
Evening bat					
PC1 <sup>a</sup> +PC3 <sup>c</sup> +PC4 <sup>d</sup>	10	-2768.91	5558.1	0	0.31
PC1+PC2 <sup>b</sup> +PC3+PC4+PC5 <sup>e</sup>	12	-2767.68	5559.8	1.66	1.13
PC1+PC2+PC3+PC4	11	-2768.86	5560.1	1.96	0.12
Eastern red bat/Seminole bat					
PC1+PC2+PC5	10	-1996.22	4012.7	0	1
Tri-colored bat					
PC3+PC4+treatment/age <sup>f</sup>	9	-1668.55	3355.3	0	0.30
PC3+PC4+PC5+treatment/age	10	-1668.18	3356.7	1.31	0.16
PC1+PC3+PC4+treatment/age	10	-1668.4	3357.1	1.75	0.13
PC2+PC3+PC4	10	-1668.52	3357.3	1.99	0.11
Silver-haired bat					
PC2+PC3	9	-114.25	246.7	0	0.39
PC1+PC2+PC3	10	-114.17	248.6	1.89	0.15
Hoary bat					
PC2+PC3+PC5	10	-138.79	297.9	0	0.73
PC1+PC2+PC3+PC5	11	-138.74	299.8	1.95	0.27
Rafinesque's big-eared bat					
PC2+PC3	9	-369.42	757.1	0	1
Big brown bat					
PC1+PC2+PC3+PC4	11	-731.67	1485.7	0	0.61
PC1+PC2+PC3+PC4+PC5	12	-731.59	1487.6	1.9	0.24
Mexican free-tailed bat					
NULL	7	-255.98	526.1	0	0.15
PC5	8	-255.37	526.9	0.84	0.10
PC2	8	-255.53	527.3	1.16	0.09
PC1	8	-255.81	527.8	1.72	0.06
PC3	8	-255.85	527.9	1.79	0.06
Myotine bats					
PC3+PC5	9	-1479.95	2978.1	0	0.24
PC1+PC3+PC5	10	-1479.64	2979.6	1.43	0.12
PC3	8	-1481.76	2979.7	1.57	0.11
PC3+PC4+PC5	10	-1479.81	2979.9	1.77	0.10
PC2+PC3+PC5	10	-1479.93	2980.2	2.01	0.09

<sup>a</sup> PC1 (principal component 1) is interpreted as the positive association of the biomasses of moths, beetles, and other orders.

<sup>b</sup> PC 2 (principal component 2) is interpreted as the positive association of snags and dead downed wood.

<sup>c</sup> PC 3 (principal component 3) is interpreted as the positive association of large tree basal area and tree species richness.

<sup>d</sup> PC 4 (principal component 4) is interpreted as survey date.

<sup>e</sup> PC 5 (principal component 5) is interpreted as the positive association of stem density and decreasing canopy closure.

<sup>f</sup> Treatment/age is a random factor incorporating age of treatment within treatment.



Species	Intercept	PC1	PC2	PC3	PC4	PC5
Evening bat	3.06(0.23)	0.22(0.10)	0.03(0.10)	0.29(0.10)	-0.23(0.10)	-0.16(0.11)
Eastern red bat/Seminole bat	1.20(0.55)	0.18(0.18)	0.03(0.19)	0.50(0.19)	0.04(0.18)	-0.25(0.16)
Tri-colored bat	0.80(0.37)	-0.09(0.16)	0.04(0.17)	1.15(0.18)	0.39(0.16)	-0.14(0.17)
Silver-haired bat	-1.24(0.72)	-0.12(0.30)	-0.48(0.30)	-0.96(0.33)	-	-
Hoary bat	-7.88(0.80)	-0.14(0.42)	-0.09(0.38)	-0.12(0.40)	-	-0.19(0.41)
Rafinesque's big-eared bat	-6.42(0.56)	-0.31(0.29)	-0.21(0.27)	0.27(0.27)	-	0.15(0.23)
Big brown bat	-1.43(0.36)	0.23(0.20)	-0.35(0.20)	0.67(0.19)	-0.42(0.19)	0.08(0.19)
Mexican free-tailed bat	-6.22(0.74)	-0.16(0.29)	-0.25(0.29)	0.14(0.28)	-	-0.30(0.27)
Myotis bats	0.63(0.16)	-0.10(0.13)	-0.02(0.13)	0.74(0.14)	-0.07(0.13)	-0.24(0.13)

Table 3.7. Parameter weights ( $w_i$ ) summed for bat species' call frequencies in the Mississippi Alluvial Valley 2013-2014. Species with multiple selected top models with  $\Delta AIC_c \leq 2$  have weights recalculated after model averaging, otherwise weights are calculated for all possible subsets. Evidence ratios ( $w_1/w_2$ ) presented as the relative evidence to favor one parameter over another. Bat species are named by conventional code.

Taxon Parameters	$\Sigma w_i$	$\Sigma w_1/\Sigma w_2$
Evening bat		
pc1 <sup>a</sup>	1.00	100
pc2 <sup>a</sup>	1.00	100
pc5 <sup>a</sup>	1.00	100
pc3 <sup>b</sup>	<0.01	
pc4 <sup>b</sup>	<0.01	
Eastern red bat/Seminole bat		
pc1 <sup>a</sup>	1	100
pc2 <sup>a</sup>	1	100
pc5 <sup>a</sup>	1	100
pc3 <sup>b</sup>	<0.1	
pc4 <sup>b</sup>	<0.1	
Tri-colored bat		
pc3 <sup>a</sup>	1.00	1.30
pc4+treatment/age <sup>b</sup>	0.77	
pc4	0.23	
pc5	0.23	
pc1	0.18	
pc2	0.16	
Silver-haired bat		
pc2 <sup>a</sup>	1.00	3.57
pc3 <sup>a</sup>	1.00	3.57
pc1 <sup>b</sup>	0.28	
Hoary bat		
pc2 <sup>a</sup>	1.00	3.70
pc3 <sup>a</sup>	1.00	3.70
pc5 <sup>a</sup>	1.00	3.70
pc1 <sup>b</sup>	0.27	
Rafinesque's big-eared bat		
pc2 <sup>a</sup>	1.00	100
pc3 <sup>a</sup>	1.00	100
pc1 <sup>b</sup>	<0.1	
pc5 <sup>b</sup>	<0.1	
Big brown bat		
pc1 <sup>a</sup>	1.00	3.45
pc2 <sup>a</sup>	1.00	3.45
pc3 <sup>a</sup>	1.00	3.45
pc4 <sup>a</sup>	1.00	3.45

pc5 <sup>b</sup>	0.29	
Mexican free-tailed bat		
pc5 <sup>a</sup>	0.30	1.11
pc2 <sup>b</sup>	0.27	
pc1	0.12	
pc3	0.12	
Myotine bats		
pc3 <sup>a</sup>	1.00	1.21
pc5 <sup>b</sup>	0.83	
pc1	0.18	
pc4	0.15	
pc2	0.13	

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<sup>a</sup> Highest parameter  $w_i = w_1$

<sup>b</sup> Second-highest parameter  $w_i = w_2$

## VITA

After completing her work at Booker T. Washington High School in Pensacola, Florida, in 2002, Lorraine Ketzler entered the University of Florida at Gainesville, Florida. She studied Wildlife Ecology and Conservation and received the degree of Bachelor of Science from the University of Florida in May 2006. She joined the Peace Corps in June 2006 and served as a Protected Areas Management Volunteer in Honduras, Central America, until October 2008. Upon return to the United States, she worked as a field technician for Texas A&M, the Missouri Department of Conservation/University of Missouri, and the U.S. Fish and Wildlife Service until February 2013. In February 2013, she entered the Graduate School of Stephen F. Austin State University, and received the degree of Master of Science in Forestry in December 2015. She now works for the US Fish and Wildlife Service in Florida.

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