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Bat response to prescribed fire and overstory thinning in hardwood forest on the Cumberland Plateau, Tennessee

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A B S T R A C T

Across the Southeastern U.S., including the Cumberland Plateau of Tennessee, prescribed fire and overstory thinning are being used to restore areas of closed-canopy hardwood forest to open woodland and savanna. We used acoustic recording of bat echolocation call sequences to examine bat activity (relative use of an area for foraging) in hardwood forest stands subject to 4 prescribed fire and residual basal area treatments (spring prescribed fire with woodland [SpW] and savanna [SpS] residual basal areas, and fall prescribed fire with woodland [FaW] and savanna [FaS]) basal areas, as well as untreated controls, during summer of 2013 and 2014. When possible, we classified recorded echolocation call sequences to species using automated identification software (Sonobat™ 3.1.4, SonoBat™ Inc., Arcata, California). To minimize errors in species classification of recorded bat passes, we combined similar species in groups based on call characteristics prior to conducting analyses. Total bat activity ($P \leqslant 0.001$), as well as LABO/NYHU (eastern red bat [*Lasiurus borealis*] and evening bat [*Nycticeius humeralis*]; $P = 0.001$), EPFU/LANO (big brown bat [*Eptesicus fuscus*] and silver-haired bat [*Lasionycteris noctivagans*]; $P \leqslant 0.001$), PESU (tricolored bat [*Perimyotis subflavus*]; $P = 0.001$), and LACI (hoary bat [*Lasiurus cinereus*]; $P = 0.005$) activity was generally higher in SpS and FaS stands, where overstory basal area was lower, than in control, SpW, and FaW stands, where overstory basal area was higher ($P \leqslant 0.001$). Our results suggest these treatments reduce clutter (physical obstructions to flight and foraging including foliage, branches, and stems), leading to improved foraging conditions for bats, particularly larger bodied species with lower call frequencies that are adapted to fly and forage in open conditions. We found no evidence nocturnal flying insect prey abundance or biomass influenced activity of bats in treatment stands, indicating clutter is more important than prey availability in determining habitat use by bats in this system. Our study provides support for continued use of prescribed fire and overstory thinning to restore hardwood forest to woodland and savanna and as a strategy to maintain and enhance habitat for forest bats in the Southeastern U.S.

1. Introduction

In recent years, land managers have begun to increase their use of prescribed fire and overstory thinning in upland hardwood forests across the Southeastern U.S. in an attempt to restore and maintain the open woodland and savanna conditions that existed before the era of fire suppression (Delcourt and Delcourt, 1998; Brose et al., 2001, 2012). This includes upland hardwood forests of the Cumberland Plateau, where a number of oak woodland and savanna restoration projects are ongoing. The use of prescribed fire and overstory thinning in the region can modify habitat conditions for numerous bat species (Boyles and Aubrey, 2006). Understanding bat responses to such habitat modifications is critical given the unprecedented conservation crisis and population declines many species are facing as a result of multiple threats. Over the past decade, a rise in the number of wind energy installations (i.e., wind turbines) in the U.S. has caused increased mortality of numerous migratory tree-roosting bats (e.g., eastern red bat [*Lasiurus borealis*], hoary bat [*Lasiurus cinereus*], and silver-haired bat [*Lasionycteris noctivagans*]), all of which roost and forage in hardwood forest systems and can be influenced by management and restoration activities (Cryan and Veilleux, 2007; Lacki et al., 2007; Cryan and Barclay, 2009). More recently, White-nose Syndrome (WNS), a disease caused by the fungus *Pseudogymnoascus destructans*, has caused catastrophic population declines in numerous cave-hibernating bat species across the Eastern U.S., threatening once abundant populations with regional extirpation (Frick et al., 2010; Turner et al., 2011; Langwig et al., 2012). The disease currently infects 7 bat species, 5 of which are federally listed or being considered for listing (gray bat [*Myotis grisescens*], Indiana

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bat [*M. sodalis*], northern long-eared bat [*M. septentrionalis*], little brown bat [*M. lucifugus*], and tricolored bat (*Perimyotis subflavus*); United States Fish and Wildlife Service, 2015). All of these species use Southeastern hardwood forest systems for roosting and foraging, particularly during the pre- and post-hibernation and maternity periods (i.e., spring, summer, and early fall; Barclay and Kurta, 2007; Lacki et al., 2007). This is an important time in the life-history of cave-hibernating bats because of the energetics associated with reproduction and entering and recovering from hibernation, especially if affected by WNS. Therefore, managing hardwood forests in proximity to hibernacula to provide high quality habitat during this period may be critical for population persistence and species recovery (Johnson et al., 2010).

Few studies have examined the effect of prescribed fire or silvicultural practices on bats in hardwood forest systems of the Southeastern U.S. Those studies that have been conducted generally focus on response of a single bat species to treatments with relatively few examining the bat community as a whole (Menzel et al., 2002; Owen et al., 2004; Lacki et al., 2009). No studies have been conducted examining the combined effect of prescribed fire and overstory thinning. Studies that have been conducted examining bat response to prescribed fire and silvicultural practices in other North American forest systems, have found prescribed fire and overstory thinning affect bat activity (relative use of an area for foraging) through changes in forest structure and availability of nocturnal flying insect prey (Grindal and Brigham, 1998; 1999; Loeb and Waldrop, 2008; Titchenell et al., 2011; Armitage and Ober, 2012). Changes in forest structure alter the degree of clutter (physical obstructions including foliage, branches, and stems, that impede flight and limit prey detection by reflecting echolocation calls) with which bats must contend (Lacki et al., 2007). Morphological variations in body size and wing shape, particularly wing loading (mass of the bat divided by its total wing area; WL) and aspect ratio (length of the wing squared divided by its surface area; AR), along with differences in echolocation call frequency and structure determine whether bats can fly and capture prey in clutter and, in turn, their habitat use and activity in a forest stand (Aldrich and Rautenbach, 1987; Norberg and Rayner, 1987). However, while bats may use a forest stand for foraging based on their adaptations to that environment, the availability of nocturnal insect prey may also play an important role in determining use, and in turn, activity in an area (Erickson and West, 2003; Fenton, 1990; Brigham et al., 1997; Jacobs, 1999; Lacki et al., 2007).

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

2. Methods

2.1. Study area

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

2.2. Experimental design

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

2.3. Bat activity

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

We repeated this process for an additional 2 monitoring periods each summer.

We stored digitally recorded bat call sequences on compact flash cards inside detectors, downloading them to a computer once per week. Bat call sequences from a given 7-day sampling period were uploaded to SonoBat™ D500x file attributer 2.3 (SonoBat™ Inc., Arcata, California) and batch-processed through scrubbing, using default settings, to remove noise and poor quality files. We analyzed bat passes that remained post-scrubbing using SonoBat™ 3.1.4 Kentucky-Tennessee (SonoBat™ Inc., Arcata, California) default settings, with a bat pass defined as a search-phase echolocation call sequence of $\geqslant 2$ echolocation call pulses (Gannon et al., 2003; Armitage and Ober, 2010; Weller and Baldwin, 2011). SonoBat 3.1.4 uses a decision engine, based on the quantitative analysis of know echolocation call recordings from species across Tennessee and Kentucky to try and classify each unknown bat pass to species. This decision engine uses a spectrogram of the calls comprising each pass and measurements of 76 call parameters to characterize call structure. We used the default discriminant probability threshold for classification of 0.90 and acceptable call quality of 0.80. When using automated identification software the accuracy of species identification can vary from 60% to 95% (Parsons and Jones, 2000; Redgwell et al., 2009; Armitage and Ober, 2010; Britzke et al., 2011). Therefore, to reduce classification errors, we only included in our analysis bat passes that had a discriminant probability threshold $\geqslant 0.90$ and consistency among all identification categories ("by vote", "by consensus," and "mean classification").

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

Table 1
Bat groupings, based on call frequency and wing morphology, used in a study examining bat response to prescribed fire and overstory thinning in hardwood forest stands conducted at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013–2014.

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

[a] Species with similar call frequencies grouped together.
[b] Wing loading and aspect ratio values.

2.4. Forest clutter

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

2.4.1. Live overstory basal area

To determine live overstory basal area (m^2/ha), we measured dbh (diameter at breast height) of all live overstory trees with a dbh $\geqslant$ 12.7 cm within an 11.3 m radius subplot centered on each sampling point (Fig. 1).

2.4.2. Midstory stem density

To assess midstory stem density (stems/m^2), we counted all tree saplings, shrubs, woody vines, and semi-woody plants >1.4 m tall and with a diameter at breast height (dbh) < 12.7 cm within 7 3-m radius subplots around each sampling point. The first of these subplots was centered on the sampling point. Two subplots were located on either side of the sampling point at 12.5 m intervals and parallel to the slope. Two additional subplots were located perpendicular to the slope, 12.5 m from the sampling point (one upslope and one down slope; Fig. 1).

2.5. Insect sampling

We sampled nocturnal flying insects in all study stands 3 times each summer (May–July) for 2 years (2013–2014) using Universal Black Light Traps (Bioquip Products Inc., Rancho Dominquez, California; Spalding 2004) powered by rechargeable 12 volt batteries. We deployed light traps at the center of each study stand, suspended 3 m above the ground (Armitage and Ober, 2012). We deployed light traps every other night from sunset to sunrise over a 7 day period in 5 study stands (1 detector in each treatment type

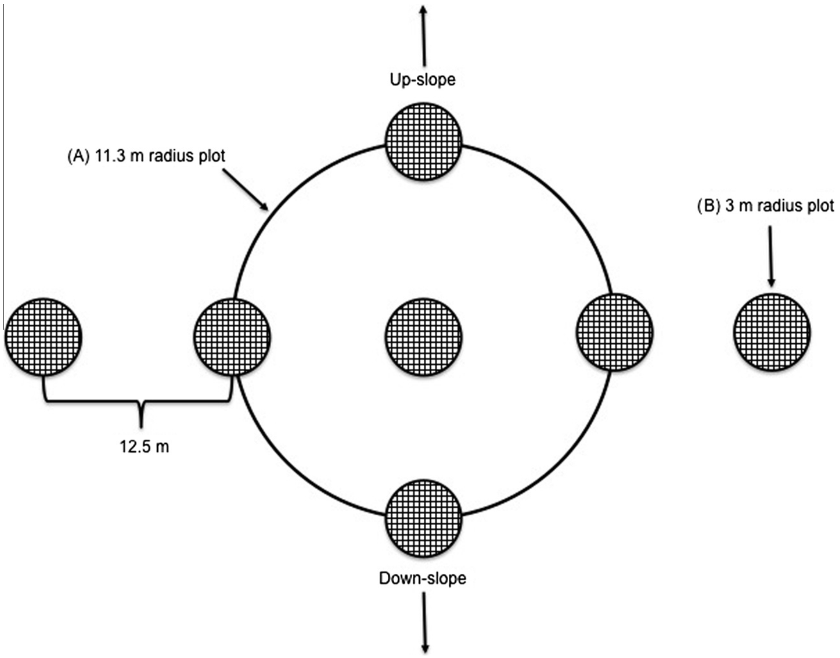

Fig. 1. Sampling layout for assessing forest clutter in hardwood forest stands used to examine bat response to prescribed fire and overstory thinning at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013–2014. (A) 11.3 m radius plot used to measure live overstory tree basal area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

collecting 4 insect sub-samples/7 night sample period). These study stands were different than those being monitored for bat echolocation calls (a study stand was not simultaneously sampled for insects and monitored for echolocation calls). At the end of the 7 nights, we relocated light traps to the remaining 5 study stands and collected insects every other night for a further 7 nights. We repeated this process for an additional 2 sampling periods each summer.

We used Nuvan Prostrip© (Amvac Chemical Corp., Los Angeles, California) kill strips to euthanize all insects captured in light traps and collected insect samples after each trap night. After collection, we placed insects in a container of 70% isopropyl alcohol until they could be sorted to order, counted, and body length of each measured (mm) from the anterior of the head to the posterior of the last abdominal segment using a dissecting microscope. We used insect counts as a measure of relative abundance (no. of individuals). From body length measurements, we estimated total biomass of insects (g) and biomass of individual insect orders (g) collected using order specific length-mass equations derived from other studies conducted in the United States (Sample et al., 1993; Benke et al., 1999; Sabo et al., 2002 and Ober and Hayes, 2008). We used abundance and biomass estimates as indices of nocturnal flying insect prey availability.

2.6. Data analysis

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

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

3. Results

3.1. Bat activity

We monitored bat activity within our 10 study stands for 210 nights (21 nights/stand) from May–July 2013 and 2014 for a total of approximately 4920 monitoring hours (12 h/night). Over two summers, we recorded 17,460 bat passes, of which we classified 62.74% ($n = 10{,}955$) as belonging to one of our 6 species groups (MYOT, LABO/NYHU, EPFU/LANO, PESU, CORA, and LACI; Table 1). EPFU/LANO constituted 62.48% ($n = 6845$) of classified passes, LABO/NYHU 15.82% ($n = 1733$), PESU 11.76% ($n = 1288$), MYOT 4.74% ($n = 519$), LACI 4.78% ($n = 524$), and CORA 0.42% ($n = 46$).

Total bat activity (classified and unclassified bat passes) and activity of LABO/NYHU, EPFU/LANO, PESU, and LACI were affected by treatment alone (Fig. 2). There was no difference in total bat activity between control and SpW stands. However, total bat activity was higher in SpS, FaW, and FaS compared to control stands. The highest total activity occurred in SpS stands and differed from that seen in FaW and FaS stands. Similarly, there was no difference in EPFU/LANO activity between control and SpW stands. However, activity of this species group was higher in SpS, FaW, and FaS than control stands. Again, the highest EPFU/LANO activity occurred in SpS stands and differed from that seen in FaW and FaS stands. For LABO/NYHU and PESU, activity in control, SpW, and FaW stands was similar. LABO/NYHU activity was higher in SpS and FaS stands compared to control stands. The highest LABO/NYHU activity occurred in SpS stands and differed from that seen in FaS stands. PESU activity was also higher in SpS and FaS compared to control stands, but did not differ between these two treatments. LACI activity was similar in control, SpW, FaW, and FaS stands but higher in SpS compared to control stands. MYOT and CORA activity were unaffected by prescribed fire and overstory thinning and did not differ among treatment and control stands ($P \geqslant 0.067$).

3.2. Forest clutter

Live overstory basal area was affected by treatment alone (Fig. 3). There was no difference in live overstory basal area among control, SpW and FaW stands. Overstory basal area was lower in SpS and FaS stands compared to control stands, but did not differ between these two treatments. Midstory density was affected by a treatment $*$ year interaction (Fig. 4), in addition to treatment alone. In 2013, there was no difference in midstory density between control and FaW stands. However, midstory density was lower in SpW and SpS compared to control stands and greater in FaS compared to control stands. In 2014, midstory density was higher in SpW, SpS, FaW and FaS compared to control stands, but did not differ between these four treatments.

3.3. Nocturnal flying insect availability

We collected nocturnal flying insects within our 10 study stands for 120 nights from May–July 2013 and 2014 (12 nights/stand/year), for a total of 2880 collection hours (i.e., 12 h/night) over 2 years. A total of 40,220 individuals were captured (18,309 [45.52%] in 2013 and 21,911 [54.48%] in 2014), with a combined biomass of 242.95 g (105.61 g [43.47%] in 2013 and 137.34 g [56.53%] in 2014). Captured individuals were identified as belonging to 1 of twelve orders. We grouped any order that had $\leqslant 250$ total captures across both study years for analysis purposes due to low sample size. This left us with 4 insect orders and 1 insect group: (1) Coleoptera, (2) Diptera, (3) Hemiptera, (4) Lepidoptera, or (5) Other (Blattodea, Ephemeroptera, Hymenoptera, Neuroptera, Odonata, Orthoptera, Plecoptera, and Trichoptera). Coleoptera constituted 53% ($n = 21{,}316$) of total insects collected followed by Lepidoptera 34.74% ($n = 13{,}972$), Diptera 9.15% ($n = 3680$), Hemiptera 1.77% ($n = 710$), and Other 1.35% ($n = 546$). In terms of biomass, Lepidoptera constituted 135.86 g (55.92%), Coleoptera 94.43 g, (38.87%), Other 3.15% (7.64 g), Diptera 1.07% (2.61 g), and Hemiptera 0.99% (2.40 g) of insects collected.

Total insect abundance and abundance of Coleoptera, Diptera, and Lepidoptera were not affected by prescribed fire and overstory thinning and did not differ among treatment and control stands ($P \geqslant 0.220$). Abundance of Other was affected by treatment alone (Fig. 5). There was no difference in Other abundance between control, SpW, FaW, and FaS stands. However, Other abundance was lower in SpS compared to control, FaW, and FaS stands.

Hemiptera abundance was affected by a treatment $*$ year and treatment $*$ sample period interaction (Fig. 6). In 2013, Hemiptera abundance was similar among control, SpW, SpS, and FaW stands. However, Hemiptera abundance was greater in FaS compared to all other treatment and control stands. In 2014 there was no difference in Hemiptera abundance between control and all treatment stands. During the May sampling period there was no difference in Hemiptera abundance among control and all treatment stands. Hemiptera abundance was similar in control, SpW, SpS, and FaW stands, but greater in FaS compared to control and SpW stands during the June sampling period. During the July sampling period Hemiptera abundance was similar in control, SpS, FaW, and FaS stands but greater in SpW than control stands. Total insect biomass and biomass of Coleoptera, Diptera, Hemiptera, Lepidoptera, and Other were not affected by prescribed fire and overstory thinning and did not differ between treatment stands ($P \geqslant 0.290$).

3.4. Effects of clutter and nocturnal flying insect availability on bat activity

Three models were the best predictors of total bat activity. These models contained the variables live overstory basal area, insect abundance, and insect biomass (Table 2). Total bat activity was inversely related to live overstory basal area. Insect abundance and insect biomass had a weak effect on total bat activity (Table 3). Four models, containing the variables live overstory basal area, insect abundance, insect biomass, and distance to water were the best predictors of LABO/NYHU activity (Table 2). LABO/NYHU activity was also inversely related to live overstory basal area. Insect abundance, insect biomass, and distance to water had a weak effect on activity of this group (Table 3). Two models were the best predictors of EPFU/LANO activity. These models contained the variables basal area and insect biomass (Table 2). LABO/NYHU activity was again inversely related to basal area but insect biomass had a weak effect on activity. Three models were the best predictors of PESU activity and contained the variables live overstory basal area, midstory density, insect abundance, and insect biomass (Table 2). PESU activity was inversely related to both live overstory basal area and midstory density. Insect abundance and insect biomass had a weak effect on PESU activity. Ten models, including the null, were the best predictors of LACI activity. These models contained the variables live overstory basal area, midstory density, insect biomass and insect abundance (Table 2). All of these variables had a weak effect on activity of this species (Table 3).

4. Discussion

Our results indicate that, in upland hardwood forests on Tennessee's Cumberland Plateau, prescribed fire and overstory thinning treatments increase activity in and use of previously closed-canopy hardwood forest stands by foraging bats. We found

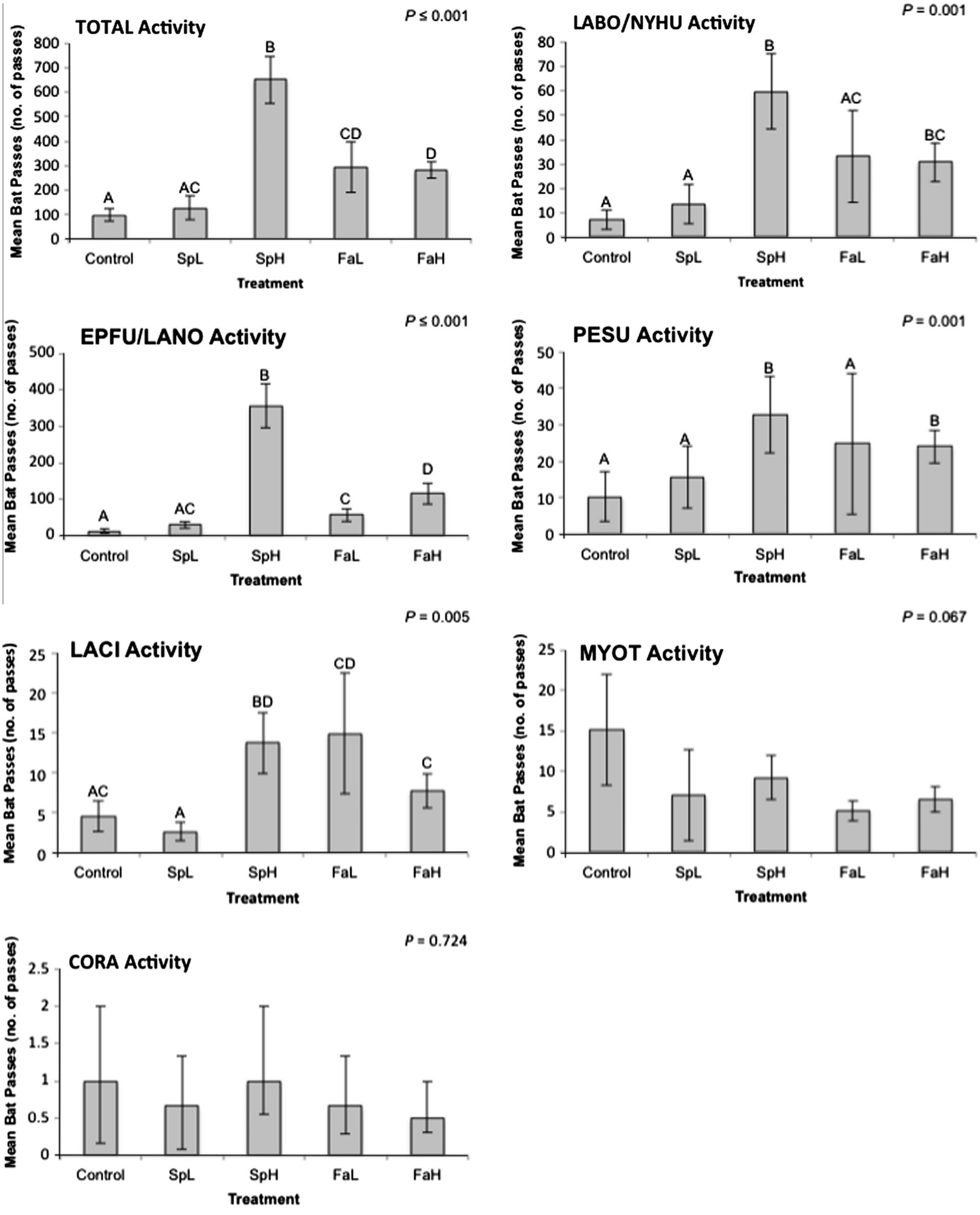

Fig. 2. Effect of treatment on bat activity in hardwood forest stands subject to prescribed fire and overstory thinning treatments at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013–2014. Total = all bats (identified and unidentified); LABO/NYHU = eastern red bat (*Lasiurus borealis*) and evening bat (*Nycticeius humeralis*); EPFU/LANO = big brown bat (*Eptesicus fuscus*) and silver-haired bat (*Lasionycteris noctivagans*); PESU = tricolored bat (*Perimyotis subflavus*), LACI = hoary bat (*Lasiurus cinereus*). Treatments: SpW = Spring prescribed fire with woodland residual basal area (low overstory thinning with target residual basal area of 14 m^2/ha), SpS = Spring prescribed fire with savanna residual basal area (high overstory thinning with target residual basal area of 7 m^2/ha), FaW = Fall prescribed fire with woodland residual basal area, FaS = Fall prescribed fire with savanna residual basal area. Bars with same uppercase letter not different ($P > 0.05$).

total bat activity within control stands to be relatively low; comprising only 6.8% of the activity recorded across all study stands. This is comparable to other studies that have found low levels of bat activity in closed canopy pine (Grindal and Brigham, 1998; Humes et al., 1999; Erickson and West, 2003; Menzel et al., 2005; Loeb and Waldrop, 2008) and hardwood (Titchenell et al., 2011) forest. Total bat activity was highest in SpS stands, where 64% of bat passes were recorded. LABO/NYHU, EPFU/LANO and

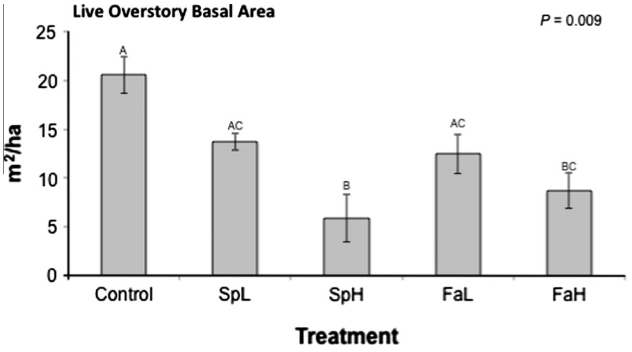

Fig. 3. Effect of treatment on live overstory basal area in hardwood forest stands subject to prescribed fire and overstory thinning treatments at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013–2014. Treatments: SpW = Spring prescribed fire with woodland residual basal area (low overstory thinning with target residual basal area of 14 m^2/ha), SpS = Spring prescribed fire with savanna residual basal area (high overstory thinning with target residual basal area of 7 m^2/ha), FaW = Fall prescribed fire with woodland residual basal area, FaS = Fall prescribed fire with savanna residual basal area. Bars with same uppercase letter not different ($P > 0.05$).

LACI activity were also highest in SpS stands. Higher total bat activity and LABO/NYHU and EPFU/LANO activity were also observed in FaS compared to control, SpW, and SpS stands. However, activity levels were lower in FaS than SpS stands. PESU was the only species with activity highest in SpS and FaS stands, with no difference observed between these two treatments. It is likely the higher activity observed in certain treatment stands compared to others was a result of these stands being selected by bats as foraging areas (Titchenell et al., 2011).

Our results are comparable to those of other studies examining bat response to prescribed fire and overstory thinning or similar silvicultural treatments. Little brown bats have been found to forage more in burned stands than unburned stands of mixed hardwood forest, with differences attributed to the less cluttered canopies occurring in burned areas (Lacki et al., 2009). Other studies examining the effects of fire on bats have mostly been conducted in pine forests. Bat activity was higher in recently burned Florida longleaf pine-wiregrass stands and was positively associated with height of canopy closure, suggesting benefits to certain species of reduced clutter (Armitage and Ober, 2012). Humes et al. (1999) found bat activity was higher in thinned Douglas fir (*Pseudotsuga menziesii*) stands than un-thinned stands of the same age. They concluded that the structural changes resulting from thinning may benefit bats by creating a habitat structure they are able to use more effectively. Loeb and Waldrop (2008) also found that total bat activity was higher in thinned southern pine stands than in control stands, but stands that were burned and thinned didn't vary from that of controls. However, thinning of red pine (*Pinus resinosa*) stands in Michigan did not lead to an increase in their use by bats, despite significant changes in their structural complexity. Even after thinning, red pine plantations may be too structurally complex for use by foraging bats (Tibbels and Kurta, 2003). Another study, conducted in boreal forest, also found thinning had minimal effect on habitat use by bats. However, this study emphasized the practice may have different effects on different species that may be obscured if the community is studied as a single entity (Patriquin and Barclay, 2003), an issue we avoided by studying individual species or groups of species with similar call characteristics and wing morphology.

Our results imply forest clutter is the primary driver in determining bat activity in treatment stands, with availability of nocturnal insect prey having little influence over whether bats will use a stand. In our study, live overstory basal area, a variable that has been shown to provide an effective quantitative measure of clutter (O'Keefe et al., 2014), was lower in SpS and FaS stands than control and SpW and FaW stands. These same stands had higher activity of LABO/NYHU, EPFU/LANO, LACI and PESU than did control, SpW and FaW stands. This suggests overstory basal area may play a role in determining activity of these species in a stand The role of basal area in determining bat activity was supported by our multiple regression models, which found total bat activity and activity of LABO/NYHU, EPFU/LANO, PESU and LACI was inversely related to live overstory basal area. PESU activity was the only species whose activity was also inversely related to midstory density, another frequently used quantitative measure of clutter.

A bat's ability to maneuver in clutter and capture insect prey depends on a number of factors including body size and wing morphology, particularly wing aspect ratio and wing loading. Larger-bodied bat species with high WLs or ARs tend to be less maneuverable and more adapted to flight in more open, less cluttered areas (Findley and Black, 1983; Aldrich and Rautenbach, 1987; Crome and Richards, 1988; Kalcounis et al., 1999; Kingston et al., 2000; Lee and McCracken, 2004). A bat's capacity to maneuver in and capture insect prey in clutter also depends on its echolocation call capabilities. The structure of search-phase

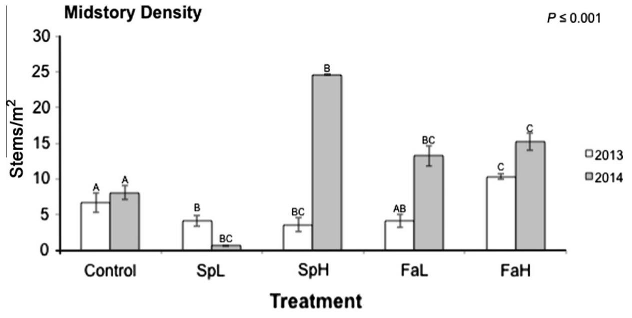

Fig. 4. Effect of a treatment ∗ year interaction on midstory density in hardwood forest stands subject to prescribed fire and overstory thinning treatments at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013–2014. Treatments: SpW = Spring prescribed fire with woodland residual basal area (low overstory thinning with target residual basal area of 14 m^2/ha), SpS = Spring prescribed fire with savanna residual basal area (high overstory thinning with target residual basal area of 7 m^2/ha), FaW = Fall prescribed fire with woodland residual basal area, FaS = Fall prescribed fire with savanna residual basal area. Bars with same uppercase letter not different ($P > 0.05$).

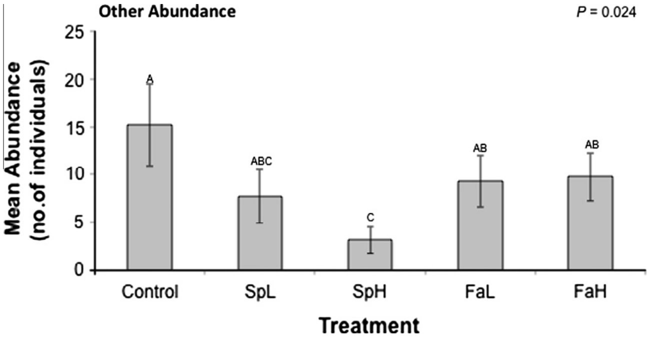

Fig. 5. Effect of treatment on Other (Blattodea, Ephemeroptera, Hymenoptera, Neuropetera, Odonta, Orthoptera, Plecoptera, and Trichoptera) nocturnal flying insect abundance in hardwood forest stands subject to prescribed fire and overstory thinning at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013–2014)· Treatments: SpW = Spring prescribed fire with woodland residual basal area (low overstory thinning with target residual basal area of 14 m^2/ha), SpS = Spring prescribed fire with savanna residual basal area (high overstory thinning with target residual basal area of 7 m^2/ha), FaW = Fall prescribed fire with woodland residual basal area, FaS = Fall prescribed fire with savanna residual basal area. Bars with same uppercase letter not different ($P > 0.05$).

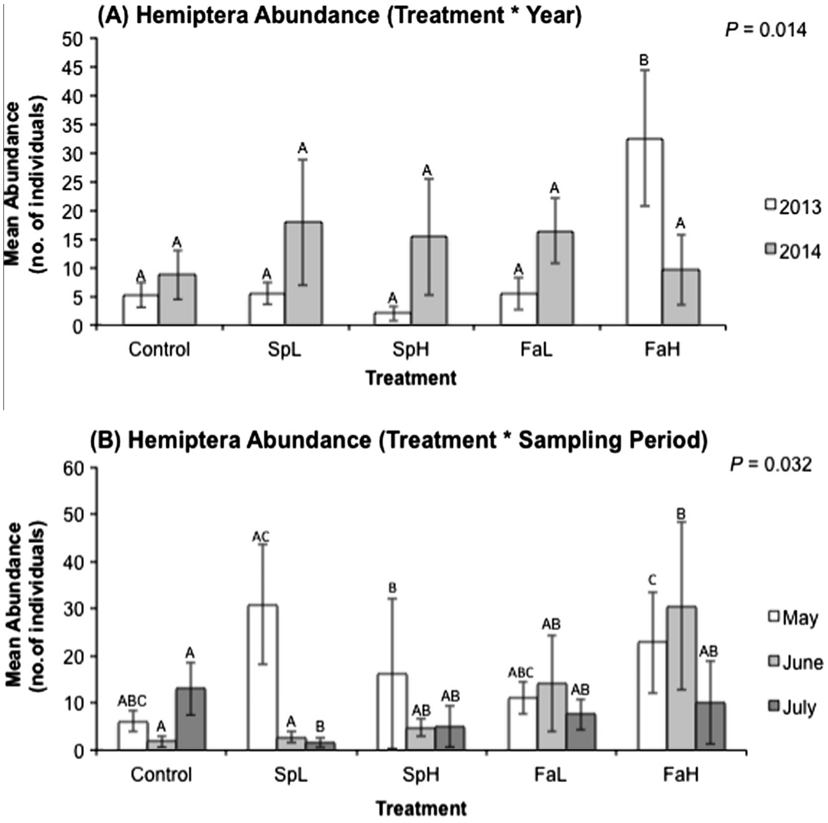

Fig. 6. Effect of a (A) treatment ∗ year interaction and (B) treatment ∗ sampling period interaction on nocturnal flying Hemiptera abundance in hardwood forest stands subject to prescribed fire and overstory thinning at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013–2014. Treatments: SpW = Spring prescribed fire with woodland residual basal area (low overstory thinning with target residual basal area of 14 m^2/ha), SpS = Spring prescribed fire with savanna residual basal area (high overstory thinning with target residual basal area of 7 m^2/ha), FaW = Fall prescribed fire with woodland residual basal area, FaS = Fall prescribed fire with savanna residual basal area. Bars with of same color with same uppercase letter not different ($P > 0.05$).

calls emitted by bats when looking for prey, are related to habitat and foraging strategy (Schnitzler and Kalko, 1998). Species with broadband calls of high frequency are better suited to foraging in more cluttered forest locations (Simmons and Stein, 1980). In contrast, species with narrowband calls of low frequency are more suited to open locations (Neuweiler, 1983). This is largely consistent with our observations. LABO/NYHU, EPFU/LANO, and LACI, which all have relatively low frequency calls and/or moderate to high WL/AR values exhibited greater activity in stands with less clutter than in more cluttered control stands, likely due to the increased efficiency of flight during foraging and easier prey capture. A study in Kentucky hardwood forest found a shift in the foraging ranges of larger-bodied bats with high ARs and WLs toward burned areas with less clutter (Lacki et al., 2009b). These species also had low frequency calls. In Florida longleaf pine stands, small-bodied bat species with low ARs and WLs replaced large-bodied, less maneuverable species below the canopy at sites with >8-year burn frequencies due to increased mid-story growth and clutter (Armitage and Ober, 2012). In areas with high overstory density, canopy cover, and midstory/understory clutter, EPFU, and other species with high ARs and WLs, will often fly and forage above the canopy (Armitage and Ober, 2012). This would explain why, in our control, SpW, and FaW stands where overstory basal area and, therefore clutter, were high, we recorded EPFU, and similar sized species, less frequently on our ground based ultrasonic detectors. Once overstory canopy cover and, in turn clutter were reduced, these species likely moved closer to the ground to forage, where our ultrasonic detectors recorded them. Certainly, in the southern U.S., EPFU are often found in early successional habitats, indicating they prefer areas with low clutter (Ellis et al., 2002; Menzel et al., 2005; Loeb and O'Keefe, 2006). Loeb and Waldrop (2008) found thinning and clutter reduction benefitted both EPFU and LABO in Southern pine stands. Because of their smaller size and low WLs and ARs, we expected PESU to be more clutter adapted than some of the other species examined, such as EPFU and LABO. As a result, we did not expect prescribed fire and overstory thinning to have much of an effect on their activity and anticipated recording them as frequently in controls as treatment stands. However, like the larger bodied species, their activity was higher in SpS and FaS stands than control, SpW, and SpS stands. Several other studies have found PESU use low clutter habitats such as early successional areas more than mid- and late-successional stands (Ellis et al., 2002; Menzel et al., 2005; Loeb and O'Keefe, 2006) and Loeb and Waldrop (2008) found their activity was five times higher in thinned than control or burned stands. As proposed for myotine species (Titchenell et al., 2011), PESU may be better able to exploit forest habitat regardless of clutter and therefore forage in areas that are most profitable.

All bats inhabiting North American forests are insectivorous and rely on insects as a prey base (Lacki et al., 2007). Although specializations have been reported, most species consume insects from multiple orders, their diet varying by geographic location, time of night, season, and year, presumably as a result of shifts in the availability of insects of different types (Whitaker, 1972; Whitaker and Clem, 1992; Kurta and Whitaker, 1998; Murray and Kurta, 2002; Lee and McCracken, 2001; Lacki et al., 2007). However, we found no difference in nocturnal flying insect abundance or biomass among treatment and control stands, suggesting insect availability was not influencing bat activity. Although insect abundance or biomass frequently appeared in supported AIC models, model averaging resulted in 95% confidence intervals for these variables crossing 0, indicating they had a weak effect on bat activity and were not informative in explaining differences in activity among stands.

Table 2
Supported models of variables affecting bat activity in hardwood forest stands subject to prescribed fire and overstory thinning treatments at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013–2014.

Species group[a]	Model[b]	k	AICc	ΔAICc	w_i
Total	BA	2	851.20	0.00	0.22
	BA + IB	3	851.35	0.15	0.21
	BA + IC	3	852.62	1.12	0.11
LABO/NYHU	BA	2	625.78	0.00	0.18
	BA + IB	3	626.15	0.38	0.15
	BA + DW	3	627.47	1.69	0.08
	BA + IC	3	627.67	1.89	0.07
EPFU/LANO	BA	2	764.95	0.00	0.28
	BA + IB	3	765.61	0.66	0.20
PESU	BA + MD	3	608.15	0.00	0.19
	BA + MD + IC	4	608.74	0.58	0.14
	BA + MD + IB	4	610.15	1.99	0.06
LACI	MD + IB	3	491.11	0.00	0.11
	MD + IB + IC	4	491.60	0.49	0.09
	MD	2	491.73	0.62	0.08
	BA + IB	3	492.36	1.25	0.06
	BA	2	492.42	1.31	0.06
	IB	2	492.58	1.47	0.05
	IB + IC	3	492.77	1.66	0.04
	BA + IB + IC	4	492.83	1.72	0.05
	MD + IC	3	492.99	1.88	0.04
	Null	1	493.01	1.90	0.04

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

[b] Variables: BA = live overstory basal area (m^2/ha); MD = midstory density (stems/m^2), IB = insect biomass (g); IC = insect abundance (no. of individuals); DW = distance to water (m).

Table 3
Coefficients from supported models of variables affecting bat activity in hardwood forest stands subject to prescribed fire and overstory thinning at Catoosa Wildlife Management Area, Cumberland County, Tennessee, USA, 2013–2014.

Species group[a]	Variable[b]	β	SE	95% CI	
				Lower	Upper
Total	BA	−20.77	6.10	−32.73	−8.81
	IB	−13.20	9.17	−31.17	4.76
	IC	−0.05	0.06	−0.17	0.06
LABO/NYHU	BA	−2.28	0.99	−4.22	−0.35
	IB	−1.91	1.40	−4.66	0.84
	DW	−0.04	0.05	−0.15	0.06
	IC	−0.01	−0.01	−0.02	0.01
EPFU/LANO	BA	−15.32	2.97	−21.15	−9.49
	IB	−5.64	4.49	−14.44	3.15
PESU	BA	−2.41	1.08	−4.53	−0.29
	MD	−2.61	1.00	−4.56	−0.66
	IB	0.74	1.22	−1.65	3.13
	IC	−0.01	0.01	−0.02	0.00
LACI	BA	−0.48	0.31	−1.08	0.12
	MD	0.52	0.28	−0.03	1.06
	IB	−0.79	0.46	−1.70	0.11
	IC	0.00	0.00	0.00	0.01

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

[b] Variables: BA = live overstory basal area (m^2/ha), MD = midstory density (stems/m^2), IB = insect biomass (g), IC = insect abundance (no. of individuals), DW = distance to water (m).

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

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

5. Conclusions

Our study indicates SpS or FaS treatments used to restore hardwood savanna provide improved foraging conditions for and are beneficial to numerous larger bodied bat species with high WLs and ARs (EPFU, LABO, LANO, NYHU, and LACI), as well as smaller bodied bats with lower WLs and ARs (PESU). The most beneficial treatment appears to be SpS, which generally results in the highest activity of these species. Bat activity, particularly of PESU, is also high following FaS treatments and this treatment provides managers with an alternative season for fire application, while still benefiting bats. Bat activity is generally not affected by SpW and FaW treatments used for woodland restoration. Although these treatments do not benefit bats through improvements in foraging conditions, they also do not seem to negatively affect the species we examined. Our study provides support for continued use of prescribed fire and overstory thinning to restore hardwood forest to woodland and savanna and as a strategy to maintain or enhance foraging conditions for forest bats in the Southeastern U.S.

We do recognize our study was only conducted for two years and that foraging conditions are likely to change over time depending on frequency of prescribed fire application. Therefore, long-term research that focuses on forest structure and clutter must be implemented in stands that have been subject to overstory thinning and are being burned under varying fire frequencies to aid forest managers in making sound management decisions. In addition, the effects of prescribed fire and thinning treatments on roost trees, another critical component of bat habitat, needs to be investigated before the role of these treatments in bat management and conservation can be fully understood.

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