

The effects of prescribed fire on bat communities in the longleaf pine sandhills ecosystem

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The historical exclusion of fire from the longleaf pine–wiregrass (sandhills) ecosystem has resulted in a tremendous net loss of this important habitat. Prescribed fire is recognized as an essential tool for the maintenance of natural successional dynamics in this system, and its positive effects on native tree, shrub, and ground-layer plant communities are well documented. However, little is known about the influence of fire periodicity on many of the wildlife species occupying these forests. Our goal was to determine the relative degree to which a forest's structural characteristics and insect abundance and biomass influence the activity of different ecomorphological guilds of insectivorous bats and whether either of these factors was influenced by the periodicity of prescribed fire. We conducted a 2-year echolocation-monitoring study of bats in sandhills forests experiencing 3 categories of fire periodicity: 1–2 years, 3–5 years, and >8 years. We found significant differences in tree, shrub, and ground-layer characteristics among these burn-frequency categories, but few differences in abundance or biomass of most orders of nocturnal insects. However, the biomass of Lepidoptera was greatest at sites with the longest time between burns and was positively associated with fire-dependent deciduous tree and shrub densities. Bat activity below the canopy was significantly lower in the sites with >8-year burn frequencies than in either of the other treatments and was positively associated with height of canopy closure (a fire-dependent variable). Species-specific activity patterns confirmed ecomorphological predictions. Small-bodied species with low wing loadings and aspect ratios replaced larger, less-maneuverable species below the canopy at sites with >8-year burn frequencies. We provide support for the hypothesis that the structural characteristics of a habitat have primacy over prey availability in habitat choice by large and fast-flying species of bats. We suggest that frequency of fire is an important indirect determinant in structuring the communities of bats that forage in forests.

Key words: Chiroptera, foraging, habitat selection, indirect effects, insects, longleaf pine, management, prescribed fire, sandhills

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The integrity of many ecosystems relies on periodic disturbances to disrupt the trajectory of the system's shift between successional states (Beisner et al. 2003; Scheffer et al. 2001; Sousa 1984). In natural forests and grasslands, fire, drought, and grazing are 3 principal disturbances shaping species assemblages (Belsky 1992; Collins et al. 1998; Hobbs and Huenneke 1992; Roques et al. 2001). It is widely recognized that suppression of natural fire periodicity in a wide variety of forest ecosystems significantly influences the structure and dynamics of the local community (e.g., Glitzenstein et al. 1995; Hutchinson et al. 2005; Peterson and Reich 2001; Waldrop et al. 1992).

The longleaf pine (*Pinus palustris*) forests of the southeastern United States are composed of a longleaf pine–dominated canopy, with a ground layer primarily composed of wiregrass (*Aristida stricta*) and a diversity of herbaceous taxa (Ricketts et al. 1999). Longleaf pines and many ground-layer plants have unique pyrogenic adaptations that function to more quickly spread fire while allowing the burned plant to survive (McCune 1988; Mutch 1970). Thus, periodic fires



clear the shrub layer of juvenile hardwoods, and positively reinforce the high levels of ground-layer species richness and endemism (Brockway and Lewis 1997; Gilliam and Platt 1999; Outcalt 2006). During the interval between fires, oak species (primarily turkey oak [*Quercus laevis*]) become established in the shrub layer and develop into a thick midstory within a decade's time (Glitzenstein et al. 1995; Varner et al. 2005; Waldrop et al. 1992). Therefore, sustainment of this community is entirely dependent on periodic fire, which has prompted landowners and managers to use prescribed burning as an alternative to natural fire (e.g., Glitzenstein et al. 1995; Varner et al. 2005).

Because sandhills plant communities respond strongly to fire, it is probable that higher trophic levels, such as herbivores and their predators, respond to bottom-up pressures caused by postburn succession (Wootton 1998). Insects perform a myriad of ecological roles in temperate forests as herbivores, decomposers, pollinators, parasites, predators, and prey (Miller 1993). Therefore, decisions of habitat management should explicitly investigate the role of insects within the community, and in fire-climax ecosystems one must consider the influence of prescribed burning on insect abundance and diversity.

The dynamics of insect communities vary in response to prescribed fire, exhibiting positive, negative, or neutral effects depending on the species studied, location of the study, burn season, burn frequency, and type of habitat burned (McCullough et al. 1998; Panzer and Schwartz 2000; Swengel 2001). One pathway through which prescribed fire may influence insect communities is by altering the overall abundance of plant resources. Plants provide the majority of insects with food resources, either directly (herbivory or detritivory) or indirectly (predation on herbivores and detritivores). Insects also use plant structures for shelter and oviposition (Strauss and Zangerl 2001). Therefore, the gradual increase in plant biomass in areas that do not experience fire should increase the carrying capacity of insects that use fire-intolerant plants. Conversely, because high levels of herbaceous endemism are maintained by frequent fires, and because phytophagous insects are often highly specialized on certain host plants, a shift to a hardwood-dominated forest with the cessation of burning also may manifest a decrease in overall insect abundance, due to local extirpation of specialist species.

Empirical studies suggest that the quality of forage for insects is a determinant of their overall abundance (Perez-Harguindeguy et al. 2003) and that plant quality is often partially a product of fire history (DeLuca et al. 2006; Erwin et al. 2001). Although fire may reduce the abundance of herbivorous insect species by reducing the abundance of food supply, the food that remains may be of higher quality. Thus, predictions with regard to the effect of fire on insect abundance are confounded by the fact that although the quantity of a food resource may decrease following fire, its quality may respond in a variety of ways (Kay et al. 2007).

Forests provide roosting habitat for greater than one-half of all North American bat species (Barclay and Kurta 2007) as

well as foraging habitat for bats that utilize all roost types. However, information on the use of forests by commuting and foraging bats is limited, relative to information on roost use (Lacki et al. 2007). The question of how to best manage forests to promote bat diversity and abundance has only recently been addressed in response to heavy losses of populations of listed species. Most of the applied research that has investigated effects of forest management activities on bats has examined the response of bats to timber harvests (Lacki et al. 2007). Few studies have addressed the influence of fire on the forest bat community, and most of this research has focused on roost site selection rather than foraging habitat selection (Boyles and Aubrey 2006; Carter et al. 2002; Fisher and Wilkinson 2005; Hayes and Loeb 2007; Johnson et al. 2009; Rodrigue et al. 2001; Schwab 2006).

Forests contain high insect biomass and diversity, making them attractive habitats for foraging insectivorous bats. However, forests are structurally complex habitats, in which some bats have difficulties capturing insects. Factors such as the aspect ratio (AR), wing loading (WL), and echolocation capabilities influence the maneuverability and insect-detection capabilities of each species, which in turn dictate the ability of each species to utilize cluttered habitat. Less-maneuverable species are those with high WLS or ARs, and that are adapted to rapid flight in open habitats (Findley and Black 1983; Kingston et al. 2000; Lee and McCracken 2004; Norberg and Rayner 1987).

Bat species that are physically constrained to flying in open habitat have several foraging options. In some cases, these less-maneuverable species forage above the canopy (Hayes and Gruber 2000; Kalcounis et al. 1999; Menzel et al. 2005). Under other circumstances they select more open forested habitats, such as recent clear-cuts (Patriquin and Barclay 2003), thinned stands (Humes et al. 1999; Loeb and Waldrop 2008), or forest edges (Hein et al. 2009; Morris et al. 2010). Because periodic fires temporarily suppress the midstory layer of forests and cause a turnover in plant and insect communities, less-maneuverable species should increase their foraging within recently burned stands. This was the case in Kentucky, where overall insect abundance increased as a result of prescribed burning and corresponded to a shift in the foraging ranges of large-bodied bats toward burned areas (Lacki et al. 2009). In South Carolina, however, the activity of a number of bat species was greater in mechanically thinned stands than intact stands, and intermediate in stands receiving prescribed burns (Loeb and Waldrop 2008).

Although bats may choose habitats based on whether or not they are physically capable of hunting in an area, prey availability also is an important factor in their selection of foraging grounds (Brigham et al. 1997; Clark et al. 1993; Erickson and West 2003; Fenton 1990; Grindal and Brigham 1998; Jacobs 1999; Lacki et al. 2007; Saunders and Barclay 1992). Experimental evidence supports both claims, but the structural habitat characteristics appear to have primacy over prey abundance in the limited number of studies to compare these factors (Adams et al. 2009; Entwistle et al. 1996;

Kalcounis and Brigham 1995; Schnitzler and Kalko 2001). The objectives of this study are to determine which stand, shrub, and ground-level vegetation characteristics are sensitive to the periodicity of prescribed fire; how the abundance and biomass of nocturnal insects differ in response to varying prescribed fire periodicities; and the relative contributions of insect prey availability and structural habitat complexity in explaining vertical and horizontal activity patterns of ecomorphological guilds of bats.

MATERIALS AND METHODS

Study forests.—Our study took place within 2 of the largest remaining extents of fire-managed sandhills in the United States: the Citrus Tract of the Withlacoochee State Forest (28°45'N, 82°25'W, Citrus County, Florida), and the Ordway-Swisher Biological Station (29°42'7.47"N, 82°1'8.39"W, Putnam County, Florida). We obtained prescribed fire histories dating at least 15 years for each forest and categorized portions of land as belonging to 1 of 3 fire frequencies: burned within the previous 1 year and having a burn frequency of at least once every 1–2 years; last burned 3–5 years prior and with a burn frequency of 3–5 years; and >8 years since last burn and with burn frequency >8 years. Using a custom routine in ArcGIS (ESRI, Inc., Redlands, California), we randomly generated 24 square, 40-ha sites within each study forest, evenly distributed across burn categories in area classified as sandhills habitat. These sites were selected to be as far away as possible from one another to reduce autocorrelative effects.

Vegetation measurements.—During September and October of 2008 and 2009, we assessed the stand, canopy, shrub, and ground cover characteristics at four 15-m-radius circular plots at each of the 24 sites in the 2 study areas. The 1st plot at each site was centered on the random Universal Transverse Mercator location. We then established three 15-m transects directed outward at 0°, 120°, and 240° from the center of each plot. At the distal end of each of these transects we continued in a 30-m straight line to establish the centers of the 2nd, 3rd, and 4th plots. Three transects also were measured in each additional survey plot. We used the means of measurements taken in all 4 plots at each site for the various metrics to characterize the vegetative structure and composition at each site.

We estimated canopy cover using a concave spherical densiometer held at breast height at the center of each plot. The height of crown closure (the average height of the base of the crowns of trees in the canopy layer) and the average heights of coniferous and deciduous trees were measured in the same fashion, using a tall staff incrementally marked every 50 cm. We estimated snag density by counting the total number of snags (diameter at breast height > 7.5 cm) occupying the entire area visible from the center of each plot.

To calculate coniferous, deciduous, and total basal areas, we counted and measured the diameter at breast height of all trees >3 m tall in each of the 4 circular plots at each site. Along the

three 15-m transects in each circular plot we measured the percent ground cover of bare ground, leaf litter, and grass.

We calculated an index of the concentration of deciduous trees, using the formula: concentration = $10.5 - BA_{\text{decid}}/BA_{\text{total}}$, where BA_{decid} is the basal area (m^2/ha) of deciduous trees at the site and BA_{total} is the overall basal area of the site. Values closer to 0.5 indicate a greater homogeneity in tree type (coniferous or deciduous) in each stand.

Insect sampling.—During May–August 2008 and 2009, we sampled insects at 2 or 3 sites per week. We used the total number of captures per night at each trap as an index of insect abundance. Each night, we sampled from at least 2 different burn treatment sites at which bats were not simultaneously being monitored. At the center of each site we suspended 3 m off the ground a Universal Black Light Trap on a dusk–dawn timer (Bioquip Inc., Rancho Dominguez, California). This trap setup provides a good index of phototropic nocturnal insect activity among sites and its relatively small effective radius does not lure insects from outside the sampling unit (Ober and Hayes 2008; Ricketts et al. 2002; Spalding and Parsons 2004).

All insects were collected the morning after sampling and sorted to order in the laboratory. We measured the body length of each insect and estimated order-specific biomass using allometric equations from the literature. These equations relate body size to mass and were derived from insect measurements taken in the United States (Benke et al. 1999; Ober and Hayes 2008; Sabo et al. 2002; Sample et al. 1993). We included both total and order-specific biomass estimates with insect abundance in our analyses because they are probably relevant factors in the optimal foraging decisions made by bats and should generally be considered alongside abundance in studies of trophic interactions (Saint-Germain et al. 2007).

Echolocation monitoring.—We deployed Anabat II (Titley Electronics Inc., Ballina, Australia) detectors to remotely monitor bat echolocation calls. Echolocation monitoring provides an index of bat activity at a site, useful for comparing relative use among sites; it does not provide a measure of abundance (Hayes 2000). Each detector was programmed to begin recording 30 min prior to sunset and shut off 30 min after sunrise. Microphones were housed in weatherproof containers. The sensitivities of all bat detectors were calibrated to 30 m once per month (Larson and Hayes 2000).

We set up detectors 1 m off the ground to assess bat activity below the canopy at all burn categories. We also conducted acoustic monitoring above the canopy layer at the 2 extreme burn categories (1–2 years and >8 years between burns). To monitor above the canopy, we 1st used a pneumatic launcher (AK Biocca Engineering, Berkeley, California) to propel a weighted tennis ball attached to a nylon rope between the crowns of 2 tall trees as near as possible to the global positioning system position of each site. We then set up permanent pulley systems at each of these sites, allowing us to hoist an Anabat transducer on a 30-m cable to the height of the 2 trees (approximately 20–25 m).

Four evenings per week, we deployed bat detectors at 6 randomly chosen sites (2 sites per night for each burn

category). Ground detectors were placed directly underneath the canopy detectors at the high and low burn-frequency sites, and at the centers of the medium frequency sites. The following day we relocated the detectors to new sites, which allowed us to sample all 24 of a study area's sites every other week, switching between forests each week. Weather patterns (temperature, wind, and precipitation) were very consistent throughout the study period and did not correlate with insect and bat activity. All surveys were completed in accordance with guidelines approved by the American Society of Mammalogists (Sikes et al. 2011).

Bat activity at a site was quantified as the mean number of passes recorded by each detector per night. We defined a pass as a sequence of ≥ 2 identifiable search-phase echolocation calls. Bat calls were classified to species using 1 high-quality search-phase echolocation call per pass (for specific selection criteria, see Armitage and Ober [2010]). We classified these calls using the random forest machine learning algorithm trained on a library of North Florida bat species (Breiman 2001). The call library was composed of 7 species groups we expected to find in the region (Marks and Marks 2006). The calls of 2 species, *Lasiurus borealis* (red bat) and *L. seminolus* (Seminole bat), are too similar to reliably classify to species and were combined into a single group. The random forest technique uses a randomized ensemble of decision trees and has proved successful in classifying local bats to species with $>85\%$ accuracy and carries fewer assumptions than the commonly used discriminant functions in call classification (Armitage and Ober 2010). We qualitatively verified the classification results by visually comparing unknown calls with voucher calls, and attempted to categorize fragmentary calls that were missed by the quantitative analysis. Calls classified differently by the quantitative and qualitative techniques were labeled as "unknown" and only included in analyses of total bat activity.

We grouped bat species into ecomorphological guilds based on their average WLs and ARs (Menzel et al. 2003). Bats categorized as having high WL/AR values were defined as those having a relative AR and WL $\geq 1 SE$ above the mean for bats in the region, whereas low WL/AR bats had values $\geq 1 SE$ below the mean (AR $\bar{X} = 2.56 \pm 0.120 SE$; WL $\bar{X} = 1.59 \pm 0.086 SE$). *L. borealis* and *L. seminolus* both fell within 1 SE of the mean, and were included in a 3rd group.

Data analysis.—We used the R statistical computing language (R Development Core Team 2011) for all analyses. Nonnormal data were transformed by taking the square-root, natural logarithm, or natural logarithm + 1. Heteroscedasticity was evaluated using the Breusch–Pagan test.

An analysis of variance (ANOVA) was used to test for fire-treatment effects on vegetation characteristics and insect biomass. We found evidence of overdispersion in the insect abundance count data ($\phi = 3$) and used a negative binomial model parameterized with dummy variables for the fire-treatment categories. To investigate whether differences existed in biomass or the abundance of insect orders among burn treatments, we used Wald's F -test and the likelihood-

ratio test, respectively. If the test statistics for the parameterized model were significantly different from the null model ($\alpha = 0.05$), we took this as evidence for the effect of fire treatment on the response variable.

To determine which vegetation characteristics best explained variation in insect abundance and biomass among sites, we fit the data to a series of generalized linear models made up of stand, canopy, shrub, and ground-layer predictors. A negative binomial link function was chosen to model the overdispersed abundance data, and biomass was modeled as a normal distribution. We used an information-theoretic approach to select models based on Akaike's information criterion (AIC—Burnham and Anderson 2002). For models predicting biomass, we used AIC_c , a small sample size-corrected version of AIC. Because abundance data were overdispersed, we used $QAIC_c$, a small sample size- and overdispersion-corrected information criterion. We calculated Δ_i by subtracting from each model the lowest AIC value corresponding to the model with the most support, given the evidence. This value corresponds to the expected information loss between the best and i th models (Burnham and Anderson 2002). Models with $\Delta_i \leq 2$ were considered equally plausible and were all considered as the best approximations of reality given the data (Burnham and Anderson 2002). We also used Akaike weights (w_i s), to estimate the probability that model i is the best model of those considered. If any of the top-ranked models ($\Delta_i \leq 2$) contained variables representing vegetation characteristics previously shown to have fire-treatment effects, and if the null model was not a running candidate model, we viewed this as evidence for the indirect effect of fire on that insect parameter (Burnham and Anderson 2002).

We used ANOVA to test for differences in bat activity among burn frequencies. We also compared the differences in activity above and below the canopy between low and high burn-frequency sites. All comparisons were carried out for total bat activity and for activity of each ecomorphological guild.

We fit a series of linear mixed-effects models to data on bat activity above and below the canopy, and the relative differences in activity between the vertical strata. This modeling framework accounts for variation in response variables between forests and years (random effects). Fixed effects included structural (stand) and prey base (insect) variables. Parameters were estimated using maximum likelihoods to facilitate model comparisons (Bolker et al. 2009; Pinheiro and Bates 2000). Because bat activity also can be explained by landscape features, we compared models including the site's distance to the nearest open body of water and distance to the nearest urban land. We used a hierarchical approach to compare the relative importances of these 3 categories by 1st determining the best explanatory models for each class of models independently (i.e., structure, landscape, and prey-only comparisons) and then directly comparing the best explanatory structure, landscape, and prey models. Models were ranked using AIC_c . We considered all models with $\Delta_i \leq 2$, and $\Delta_{\text{null}} > 2$ as competitive hypotheses for variance in bat activity. We only considered bat activity to be indirectly

TABLE 1.—Mean (\pm SE) for vegetation characteristics under different prescribed fire frequencies, and results of ANOVAs for differences.

Vegetation characteristics	Fire frequency			$F_{2,93}$	P
	1–2 years	3–5 years	>8 years		
Total basal area (m ² /ha)	10.41 \pm 0.47	10.84 \pm 0.63	13.46 \pm 0.86	4.12	0.0193
Deciduous basal area (m ² /ha)	2.08 \pm 0.31	1.50 \pm 0.23	4.56 \pm 0.68	14.68	\leq 0.0001
Coniferous basal area (m ² /ha)	8.32 \pm 0.57	9.34 \pm 0.65	8.90 \pm 0.66	0.67	0.5148
Concentration of trees (index)	0.29 \pm 0.03	0.36 \pm 0.02	0.24 \pm 0.02	6.47	0.0023
Canopy closure height (m)	15.97 \pm 0.42	14.92 \pm 0.52	13.84 \pm 0.41	6.47	0.0055
Canopy density (%)	17.45 \pm 2.05	22.31 \pm 1.79	38.67 \pm 3.31	16.65	\leq 0.0001
Density of tall deciduous woody shrubs (transect ⁻¹)	0.48 \pm 0.07	0.87 \pm 0.13	3.77 \pm 0.46	49.23	\leq 0.0001
Density of short deciduous woody shrubs (transect ⁻¹)	11.69 \pm 1.80	11.82 \pm 1.4	11.10 \pm 1.18	0.06	0.9397
Sand–ash ground cover (%)	0.16 \pm 0.03	0.02 \pm 0.01	0.03 \pm 0.01	23.76	\leq 0.0001
Grass ground cover (%)	0.50 \pm 0.03	0.60 \pm 0.04	0.30 \pm 0.04	17.55	\leq 0.0001
Leaf litter ground cover (%)	0.17 \pm 0.02	0.22 \pm 0.03	0.55 \pm 0.04	32.13	\leq 0.0001
Snag density (ha ⁻¹)	0.84 \pm 0.23	2.97 \pm 0.44	2.13 \pm 0.42	3.45	0.0357

affected by prescribed fire periodicity if activity differed significantly among burn treatments; and if activity was best explained by vegetation or insect characteristics shown to be fire-dependent. If bat activity for any guild or stratum showed fire-treatment effects that could not be explained by any fire-dependent vegetation or insect variables, we considered the hypothesis plausible, but unexplained by our data set.

RESULTS

Fire-treatment effects.—We found significant differences between categories of prescribed fire frequencies for 10 of the 12 vegetation characteristics investigated (Table 1): overall basal area; deciduous basal area; canopy closure; density of tall, woody deciduous shrubs; grass ground cover; leaf litter ground cover; sand–ash ground cover; average crown heights; snag density; and tree concentration. We found no evidence of fire-treatment effects on the basal area of coniferous trees or the density of short (<0.5 m) broadleaf shrubs.

We captured approximately 34,000 insects representing 10 orders over 40 nights of sampling. The most common orders of insects captured were Coleoptera (56.5% of all individuals), Hymenoptera (22.2%), Lepidoptera (13.5%), Hemiptera (3.3%), Homoptera (2.2%), and Diptera (1.5%). Other orders represented 0.7% of the total captures and were not used for analyses. The overall biomass of the captures was 215,934 mg. Coleopterans accounted for the majority of insect biomass (84.2%) followed by lepidopterans (17%), hymenopterans (2.7%), and all other groups (<1%). We found significant differences among the 3 categories of fire frequency for abundance of all insects ($\chi^2_{2,36} = 6.89$, $P < 0.05$) and abundance of Hemiptera ($\chi^2_{2,36} = 8.75$, $P < 0.05$), which both increased with burn frequency; and for biomass of Lepidoptera ($F_{2,37} = 7.07$, $P < 0.005$), which decreased with burn frequency. No other insect groups showed fire-treatment effects.

Prey availability.—When attempting to determine which vegetation characteristics best explained variation in insect

abundance and biomass, we found that the variables we investigated did not adequately predict most a priori hypotheses (Appendix I). However, we did find a few biologically meaningful associations, all with relatively low model probabilities. Coleopteran abundance was best explained by total basal area and tall shrub densities ($w_i = 0.42$), and hemipteran abundance by total basal area and percent cover of sand–ash and leaf litter ($w_i = 0.37$). Abundances of Hemiptera and Diptera also were explained by distances to water ($w_i = 0.12$ and 0.59 , respectively). Variation in total insect biomass was best explained by deciduous basal area and tree concentration ($w_i = 0.65$), and lepidopteran biomass by deciduous foliage and tall shrub density ($w_i = 0.79$). Thus, models explaining abundance of Coleoptera and models explaining biomass of all insects and Lepidoptera included fire-dependent vegetation characteristics.

Bat activity.—We recorded 9,854 sequences of bat calls over 825 detector-nights during May–August 2008 and 2009. Of these sequences, we categorized 8,380 (85%) as high-quality search-phase sequences. The remaining 15% of sequences generally was composed of fragmentary or approach-phase calls and were not used. The most commonly recorded group was *L. borealis–seminolus* (41%), followed by *Myotis austroriparius* (southeastern bat; 25%), *Perimyotis subflavus* (tricolored bat; 9%), *Nycticeius humeralis* (evening bat; 8%), *Eptesicus fuscus* (big brown bat; 2%), *Lasiurus intermedius* (northern yellow bat; 1.5%), and *Tadarida brasiliensis* (Brazilian free-tailed bat; 1%). The remainder (12%) of the search-phase calls was classified differently by the quantitative and qualitative techniques and was categorized as “unknown.” We categorized *M. austroriparius*, *P. subflavus*, and *N. humeralis* as low WL/AR species and *T. brasiliensis*, *E. fuscus*, and *L. intermedius* as high WL/AR species.

In the understory (Fig. 1A), total bat activity was lowest in burn sites >8 years in age and showed fire-treatment effects ($F_{2,93} = 7.27$, $P < 0.005$). Low WL/AR species were equally active among the 3 burn treatments, but the activities of high

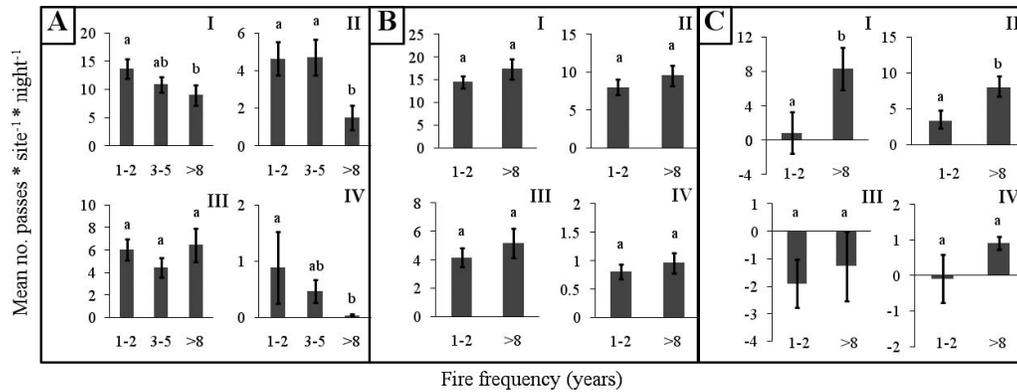


FIG. 1.—Average bat activity (\pm SE) A) below the canopy, B) above the canopy, and C) between vertical strata for I) all bats, II) *Lasiurus borealis–seminolus*, III) low wing loadings/aspect ratios, and IV) high wing loadings/aspect ratios guilds in stands with different prescribed fire frequencies. Different letters above bars indicate significant pairwise differences ($\alpha = 0.05$).

WL/AR species, and *L. borealis–seminolus* were significantly different among fire treatments ($F_{2,93} = 3.56$, $P < 0.05$; $F_{2,93} = 16.00$, $P < 0.001$). Variation in activity below the canopy of all bats combined, of *L. borealis–seminolus*, and of the high WL/AR guild was best explained by the height of crown closure at each site, with bat activity increasing as height of crown closure increased. Activity of low WL/AR bats below the canopy was best explained by the site's distance to urban land (Table 2A).

Above the canopy (Fig. 1B), activity patterns of all bats and of each ecomorphological guild did not significantly differ among fire treatments (i.e., no difference between 1–2 years and >8 years). Variation in overall bat activity and activity of high WL/AR bats above the canopy was not explained by any stand, insect, or landscape variable. Variation in low WL/AR bat activity above the canopy was explained by the biomass of Lepidoptera. Variation in the activity of the *L. borealis–seminolus* species group above the canopy was best explained by abundance of Diptera (Table 2B).

The difference between above-canopy and below-canopy activity (Fig. 1C) for all bats and *L. borealis–seminolus* was significantly greater at fire-infrequent sites than at sites with 1- to 2-year fire periodicities ($F_{1,62} = 4.69$, $P < 0.05$; $F_{1,62} = 5.09$, $P < 0.05$; respectively). Stratification of bat activity at a site was generally related to both forest structure and prey availability. Mean height of crown closure best explained stratification of overall activity and high WL/AR species activity. Additionally, abundances of all insects, Hymenoptera, and Homoptera also explained stratification of activity for all bats, low WL/AR species, and *L. borealis–seminolus*, respectively. In all cases, the relative differences in bat activity below versus above the canopy were negatively associated with prey availability and tree crown height, suggesting a preference for foraging below the canopy under low-clutter conditions (Table 2C).

DISCUSSION

Our study reveals strong effects of fire periodicity on vegetative characteristics of the sandhills ecosystem. Specifically,

fire periodicity affected deciduous basal area, tall deciduous shrub density, canopy cover, average height of crown closure, tree concentration, and ground cover composition. As expected, the basal area of deciduous trees was greatest at sites with the longest histories of fire exclusion. This result confirms the general observation that periodic fire suppresses the development of a hardwood midstory (Glitzenstein et al. 1995; Provencher et al. 2001). Likewise, the densities of tall deciduous shrubs also were greatest at most infrequently burned sites, but short deciduous shrubs were equally abundant across all burn categories. Deciduous saplings (generally *Quercus*) are quick to resprout after burning, but experience heavy mortality at sites with quick fire-return intervals (Glitzenstein et al. 1995; Plocher 1999). The accumulation of deciduous biomass with increased time between burns also results in increased canopy cover and decreased average height of crown closure. Tree concentration was greatest at 1- to 2-year and >8 -year sites, suggesting that intermediate periods of burning (every 3–5 years) might maintain a more heterogeneous mixture of tree types. Dominant ground cover also differed among burn categories. Leaf litter, which was greatest at the >8 -year burn sites, is an important fuel, and its absence from sites with short burn intervals may cause those fires to burn more patchily, creating a heterogeneous habitat for plant and insect recolonization, which may promote species richness (Slocum et al. 2003; Thaxton and Platt 2006).

We found no clear associations between fire frequency and insect biomass and abundance for most orders. Time and resources did not allow us to identify plants and insects at a high taxonomic resolution, but we recommend that future studies do so. The responses of insect groups to prescribed burning likely depend on the spatial arrangement, timing, and intensity of the fire, and thus differ according to species-specific life-history traits that facilitate or prohibit postfire recolonization (Hanula and Wade 2003; Knight and Holt 2005; Provencher et al. 2003).

We predicted that bat activity below the canopy would diminish with increasing time between burns because morphological constraints prevent many species from foraging

TABLE 2.—Rankings and comparisons of the 3 best explanatory models for each predictive category (stand, prey, and landscape) for all groups of bats (excluding the groups with only null models) below and above the canopy, and for the relative difference in vertical stratification at a site. Direction column indicates the association of each model’s variables. w_i = Akaike weight; WL = wing loading; AR = aspect ratio. Δ_i is defined in the “Materials and Methods.”

Response variable	Model type	Best explanatory model	Δ_i	w_i	Direction
A) Below the canopy					
Total calls	1) Stand	Average height of crown closure	0.00	0.78	+
	2) Landscape	Distance to urban land	2.91	0.18	+
	3) Prey	Homoptera + Diptera + Coleoptera + Hymenoptera (abundance)	6.83	0.04	- - ++
High WL/AR	1) Stand	Average height of crown closure	0.00	0.96	+
	2) Prey	Homoptera (abundance)	7.49	0.02	-
	3) Landscape	Null (intercept-only)	8.37	0.02	0
Low WL/AR	1) Landscape	Distance to urban land	0.00	0.73	+
	2) Prey	Hymenoptera + Diptera (abundance)	2.14	0.26	+ -
	3) Stand	Average height of crown closure + total basal area	9.50	0.01	++
<i>Lasiurus borealis</i> – <i>seminolus</i>	1) Stand	Average height of crown closure	0.00	0.99	+
	2) Prey	Coleoptera (abundance)	9.29	0.01	+
	3) Landscape	Distance to water	17.80	0.00	+
B) Above the canopy					
Low WL/AR	1) Prey	Lepidoptera (biomass)	0.00	0.80	+
	2) Stand	Null (intercept-only)	4.24	0.10	0
	2) Landscape	Null (intercept-only)	4.24	0.10	0
<i>L. borealis</i> – <i>seminolus</i>	1) Prey	Diptera (abundance)	0.00	0.72	-
	2) Stand	Null (intercept-only)	3.34	0.14	0
	2) Landscape	Null (intercept-only)	3.34	0.14	0
C) Difference (above – below)					
Total calls	1) Prey	Total insects (abundance)	0.00	0.57	-
	1) Stand	Average height of crown closure	0.63	0.41	-
	2) Landscape	Null (intercept-only)	6.74	0.02	0
High WL/AR	1) Stand	Average height of crown closure	0.00	0.74	-
	2) Prey	Total insects (abundance)	2.54	0.21	-
	3) Landscape	Null (intercept-only)	5.22	0.05	0
Low WL/AR	1) Prey	Hymenoptera (abundance)	0.00	0.97	-
	2) Landscape	Null (intercept-only)	8.30	0.02	0
	3) Stand	Average height of crown closure	8.65	0.01	-
<i>L. borealis</i> – <i>seminolus</i>	1) Prey	Homoptera (abundance)	0.00	0.74	-
	2) Stand	Average height of crown closure	2.81	0.18	-
	3) Landscape	Null (intercept-only)	4.39	0.08	0

in heavily cluttered habitats. We did indeed find strong indirect effects of fire on bat activity below the canopy. In our study, basal area, canopy cover, and average height of crown closure increased with increasing time between fires, creating greater structural clutter. Areas with higher densities of mature hardwoods were characterized by a lower height of crown closure, which is directly related to the volume of space underneath the canopy in which a bat may forage. This finding highlights the importance of fire’s effects on structural clutter in driving bat activity beneath the canopy.

Dividing bats into guilds based on ecomorphological predictions of clutter tolerance sheds light on the relative contributions of prey availability and structural clutter in determining vertical habitat use. Because lower WLs and ARs allow bats to forage in more complex habitat, we predicted the activity of low WL/AR bats in this system (*M. austroriparius*, *P. subflavus*, and *N. humeralis*) would not be strongly affected

by habitat structure. Our findings supported this hypothesis; these maneuverable bats showed equal activity across burn categories in both vertical strata. Furthermore, the activity of these species below the canopy was better explained by a site’s distance to urban land (including roads and buildings) than by any fire-dependent stand or insect variable. Above the canopy, variation in activity of these agile species was explained by Lepidoptera biomass. All 3 species are known to roost in man-made structures and prey on Lepidoptera (Lacki et al. 2007).

Activity of poorly maneuverable, high WL/AR bats (*E. fuscus*, *L. intermedius*, and *T. brasiliensis*) was expected to sharply decline below the canopy with increasing time between burning due to the development of a hardwood midstory. As expected, although the activity levels of these species were equal among sites above the canopy, they sharply dropped below the canopy at fire-infrequent (>8-years) sites,

and especially at those with the lowest heights of tree crowns. These results suggest that the volume of open space beneath the crowns of trees is an important driver of foraging for these less-agile species. We arrived at very similar conclusions regarding the activity patterns of *L. borealis-seminolus*, suggesting that this group also is intolerant of the structural clutter characteristic of the fire-infrequent sites. This is somewhat surprising, given that activity of *L. borealis-seminolus* did not differ between cluttered and open habitats in other longleaf pine forests (Menzel et al. 2005).

Fire is a temporary disturbance that promotes habitat heterogeneity at the landscape scale. By limiting the development of a hardwood midstory, fire may temporarily improve the ability of clutter-intolerant bats to forage beneath the canopy. This stratum of the forest may provide the best foraging opportunities for bats because insect abundance tends to be greater closer to ground level than near the canopy (Adams et al. 2009). Although the degree to which interspecific competition structures bat assemblages is still unclear (Patterson et al. 2003), it is likely that clutter tolerances of bat species are dependent on traits such as body size, call structure, and morphology, which confer a selective advantage (via foraging success) to individual bats (Swartz et al. 2003). This theory is well supported by distinct vertical and horizontal segregation of bat species in highly diverse tropical assemblages (Altringham 1996). If interspecific interactions are important in structuring bat assemblages, then clutter-tolerant species may fare best in unburned patches, where they could avoid competitive interactions with clutter-intolerant species. Because different species of bats respond differently to the exclusion of fire, a mosaic of frequently and infrequently burned patches sites may be optimal for promoting effective foraging of both clutter-adapted and clutter-intolerant bats across a landscape scale.

We determined that the structural characteristics of a forest have primacy over prey availability in dictating foraging activity for poorly maneuverable species (those with moderate to high WL/AR). Highly maneuverable, low WL/AR bats, which are capable of foraging under most local clutter conditions, are primarily associated with other characteristics, such as distance to urban land, and Lepidoptera biomass. Habitat management using prescribed fire should take account of the potential differences in habitat use among bat species. Overall, it appears that management with frequent prescribed burns would allow more bat species to forage below the canopy and increase overall bat activity. However, clutter-adapted species may benefit when some hardwood-dominated stands are left unburned for long periods of time, because these areas may provide decreased competition among foraging bats. Fire also provides increased roosting opportunities for many bat species (Boyles and Aubrey 2006; Johnson et al. 2009; Schwab 2006). Therefore, prescribed fire should be used judiciously to promote landscape heterogeneity and connectivity in order to best accommodate the specific prey, flight, and roosting requirements of all species in the local bat community.

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APPENDIX I

Information theoretic comparison of models' evidence ratios (Akaike weights [w_i]) using vegetation and stand characteristics to predict insect abundance and biomass. $QAIC_c$ = small sample size- and overdispersion-corrected Akaike information criterion; AIC_c = small sample size-corrected version of Akaike's information criterion.

Explanatory variable	$\Delta QAIC_c$	w_i	Direction
Overall abundance			
Volume of foliage			
Basal area	0.00	0.11	
Deciduous basal area	1.75	0.05	
Coniferous basal area	1.27	0.06	
Short shrub density	1.35	0.06	
Tall shrub density	0.06	0.11	
Total shrub density	0.74	0.07	
Total deciduous foliage	0.74	0.07	
Average height of crown closure	2.54	0.03	
Homogeneity of vegetation			
Tree concentration	2.53	0.03	
Ground cover composition			
Sand-ash	0.00	0.11	
Grass	2.13	0.04	
Leaf litter	0.75	0.07	
Dead tree abundance			
Snag density	2.26	0.04	
Landscape feature			
Distance to water	1.58	0.04	
Null (intercept-only)	0.07	0.10	
Lepidopteran abundance			
Volume of foliage			
Basal area	0.00	0.17	
Deciduous basal area	1.47	0.08	
Coniferous basal area	0.55	0.13	
Short shrub density	0.34	0.15	
Tall shrub density	1.66	0.08	
Total shrub density	0.44	0.14	
Total deciduous foliage	1.33	0.07	
Average height of crown closure	1.65	0.06	
Homogeneity of vegetation			
Tree concentration	1.65	0.06	
Null (intercept-only)	1.68	0.06	
Coleopteran abundance			
Volume of foliage			
Basal area	1.35	0.14	+
Deciduous basal area	2.53	0.08	
Coniferous basal area	3.54	0.05	
Short shrub density	3.87	0.04	
Tall shrub density	0.00	0.28	+
Total shrub density	3.15	0.06	
Average height of crown closure	4.54	0.03	
Homogeneity of vegetation			
Tree concentration	4.18	0.03	
Ground cover composition			
Sand-ash	3.54	0.05	
Grass	4.54	0.03	
Leaf litter	3.87	0.04	
Dead tree abundance			
Snag density	4.64	0.03	
Landscape feature			
Distance to water	3.34	0.05	
Null (intercept-only)	2.23	0.09	

APPENDIX.—Continued.

Explanatory variable	$\Delta QAIC_c$	w_i	Direction
Hymenopteran abundance			
Volume of foliage			
Basal area	2.24	0.06	
Deciduous basal area	2.15	0.06	
Coniferous basal area	2.49	0.05	
Short shrub density	2.42	0.05	
Tall shrub density	2.46	0.05	
Total shrub density	2.45	0.05	
Average height of crown closure	2.49	0.05	
Homogeneity of vegetation			
Tree concentration	2.08	0.06	
Ground cover composition			
Sand-ash	1.43	0.09	
Grass	2.05	0.06	
Leaf litter	0.81	0.12	
Dead tree abundance			
Snag density	2.30	0.06	
Landscape feature			
Distance to water	1.76	0.07	
Null (intercept-only)	0.00	0.17	
Hemipteran abundance			
Volume of foliage			
Basal area	0.70	0.15	-
Deciduous basal area	4.91	0.02	
Coniferous basal area	2.00	0.08	
Short shrub density	5.11	0.02	
Tall shrub density	3.18	0.04	
Total shrub density	4.67	0.02	
Average height of crown closure	5.15	0.02	
Homogeneity of vegetation			
Tree concentration	4.74	0.02	
Ground cover composition			
Sand-ash	0.00	0.22	+
Grass	4.76	0.02	
Leaf litter	0.31	0.19	-
Dead tree abundance			
Snag density	5.08	0.02	
Landscape feature			
Distance to water	1.13	0.12	-
Null (intercept-only)	2.77	0.06	
Homopteran abundance			
Volume of foliage			
Basal area	3.60	0.04	
Deciduous basal area	3.94	0.04	
Coniferous basal area	3.48	0.05	
Short shrub density	3.48	0.05	
Tall shrub density	3.75	0.04	
Total shrub density	3.79	0.04	
Total deciduous foliage	3.95	0.04	
Average height of crown closure	2.76	0.06	
Homogeneity of vegetation			
Tree concentration	3.74	0.04	
Ground cover composition			
Sand-ash	3.36	0.05	
Grass	3.75	0.04	
Leaf litter	3.68	0.04	
Dead tree abundance			
Snag density	3.92	0.04	
Landscape feature			

APPENDIX.—Continued.

Explanatory variable	ΔQAIC_c	w_i	Direction
Distance to water	0.00	0.28	
Null (intercept-only)	1.49	0.13	
Dipteran abundance			
Volume of foliage			
Basal area	5.36	0.04	
Deciduous basal area	6.83	0.02	
Coniferous basal area	5.91	0.03	
Short shrub density	5.69	0.03	
Tall shrub density	7.02	0.02	
Total shrub density	5.79	0.03	
Average height of crown closure	7.01	0.02	
Homogeneity of vegetation			
Tree concentration	7.01	0.02	
Ground cover composition			
Sand-ash	7.00	0.02	
Grass	4.98	0.05	
Leaf litter	6.19	0.03	
Dead tree abundance			
Snag density	5.14	0.05	
Landscape feature			
Distance to water	0.00	0.59	—
Null (intercept-only)	4.54	0.06	
Explanatory variable	ΔAIC_c	w_i	Direction
Overall biomass			
Volume of foliage			
Basal area	3.73	0.05	
Deciduous basal area	0.29	0.30	—
Coniferous basal area	6.93	0.01	
Short shrub density	4.63	0.03	
Tall shrub density	4.79	0.03	
Total shrub density	3.97	0.05	
Total deciduous foliage	3.97	0.05	
Average height of crown closure	6.68	0.01	
Homogeneity of vegetation			
Tree concentration	0.00	0.35	+
Ground cover composition			
Sand-ash	6.82	0.01	
Grass	5.86	0.02	
Leaf litter	6.71	0.01	
Dead tree abundance			
Snag density	6.51	0.01	
Landscape feature			
Distance to water	5.92	0.02	
Null (intercept-only)	4.64	0.03	
Lepidopteran biomass			
Volume of foliage			
Basal area	6.36	0.02	
Deciduous basal area	6.13	0.02	
Coniferous basal area	6.00	0.02	
Short shrub density	5.84	0.02	
Tall shrub density	0.05	0.39	+
Total shrub density	6.36	0.02	
Total deciduous foliage	0.00	0.40	+
Average height of crown closure	4.29	0.05	
Homogeneity of vegetation			
Tree concentration	6.35	0.02	
Null (intercept-only)	4.02	0.05	
Coleopteran biomass			

APPENDIX.—Continued.

Explanatory variable	ΔAIC_c	w_i	Direction
Volume of foliage			
Basal area	1.68	0.08	
Deciduous basal area	0.70	0.14	
Coniferous basal area	3.15	0.04	
Short shrub density	2.79	0.05	
Tall shrub density	2.23	0.06	
Total shrub density	2.50	0.06	
Average height of crown closure	3.03	0.04	
Homogeneity of vegetation			
Tree concentration	0.00	0.19	
Ground cover composition			
Sand-ash	3.26	0.04	
Grass	2.50	0.06	
Leaf litter	3.19	0.04	
Dead tree abundance			
Snag density	2.74	0.05	
Landscape feature			
Distance to water	3.26	0.04	
Null (intercept-only)	0.93	0.12	
Hymenopteran biomass			
Volume of foliage			
Basal area	3.10	0.05	
Deciduous basal area	2.73	0.06	
Coniferous basal area	3.41	0.04	
Short shrub density	3.33	0.04	
Tall shrub density	3.38	0.04	
Total shrub density	3.32	0.04	
Average height of crown closure	3.22	0.04	
Homogeneity of vegetation			
Tree concentration	2.39	0.07	
Ground cover composition			
Sand-ash	2.33	0.07	
Grass	2.56	0.06	
Leaf litter	0.00	0.22	
Dead tree abundance			
Snag density	3.40	0.04	
Landscape feature			
Distance to water	1.85	0.09	
Null (intercept-only)	1.06	0.13	
Hemipteran biomass			
Volume of foliage			
Basal area	3.59	0.10	
Deciduous basal area	4.64	0.06	
Coniferous basal area	8.21	0.01	
Short shrub density	9.49	0.00	
Tall shrub density	8.74	0.01	
Total shrub density	9.20	0.01	
Average height of crown closure	9.36	0.01	
Homogeneity of vegetation			
Tree concentration	8.50	0.01	
Ground cover composition			
Sand-ash	0.00	0.57	+
Grass	9.27	0.01	
Leaf litter	6.57	0.02	
Dead tree abundance			
Snag density	9.97	0.00	
Landscape feature			
Distance to water	2.23	0.19	
Null (intercept-only)	7.63	0.01	

APPENDIX.—Continued.

Explanatory variable	ΔAIC_c	w_i	Direction
Homopteran biomass			
Volume of foliage			
Basal area	3.78	0.11	
Deciduous basal area	8.31	0.01	
Coniferous basal area	6.29	0.03	
Short shrub density	7.26	0.02	
Tall shrub density	9.13	0.01	
Total shrub density	7.45	0.02	
Total deciduous foliage	9.20	0.01	
Average height of crown closure	8.20	0.01	
Homogeneity of vegetation			
Tree concentration	9.00	0.01	
Ground cover composition			
Sand-ash	7.87	0.01	
Grass	9.13	0.01	
Leaf litter	9.13	0.01	
Dead tree abundance			
Snag density	8.88	0.01	
Landscape feature			
Distance to water	0.00	0.72	—
Null (intercept-only)	6.80	0.02	
Dipteran biomass			
Volume of foliage			
Basal area	3.87	0.04	
Deciduous basal area	4.03	0.03	
Coniferous basal area	4.18	0.03	
Short shrub density	3.92	0.04	
Tall shrub density	4.06	0.03	
Total shrub density	4.02	0.03	
Average height of crown closure	4.21	0.03	
Homogeneity of vegetation			
Tree concentration	3.51	0.05	
Ground cover composition			
Sand-ash	3.79	0.04	
Grass	0.00	0.26	
Leaf litter	2.15	0.09	
Dead tree abundance			
Snag density	1.99	0.10	
Landscape feature			
Distance to water	1.42	0.13	
Null (intercept-only)	1.89	0.10	