HABITAT USE BY BATS IN TWO INDIANA FORESTS PRIOR TO SILVICULTURAL TREATMENTS FOR OAK REGENERATION

Jeremy J. Sheets, Joseph E. Duchamp, Megan K. Caylor, Laura D'Acunto, John O. Whitaker, Jr., Virgil Brack, Jr., and Dale W. Sparks[1]

Abstract.—As part of a study examining the effects of silvicultural treatments for oak regeneration on habitat use by bats, we surveyed forest stands prior to the implementation of treatments in two state forests in Indiana. Interior forest sites corresponding to areas designated for silvicultural treatments were surveyed for 2 nights each during the summers of 2007 and 2008. Additionally, three types of existing forest openings (pre-existing harvest openings, forest edges, and open corridors) were surveyed during 2007 in the same area. We assessed bat habitat use by recording echolocation calls using ANABAT II bat detectors. We characterized a location as experiencing high levels of activity, experiencing low levels of activity, or being unused by a species of bat based on recorded call minutes. We used occupancy models to account for differences in detection probability.

Stands designated for uneven-aged harvest had a greater probability of experiencing high activity by a species of bat when compared to areas designated for other silvicultural treatments. Existing forest openings had probabilities of high activity levels that were similar to each other, but high activity levels in these habitats were less likely for Indiana myotis (*Myotis sodalis*) and northern myotis (*M. septentrionalis*) when compared to forest interior locations. At interior forest sites, northern myotis were more likely than other species to have high activity levels. These results provide some insight into the potential responses of bats to forest management practices and serve as a baseline for future experimental treatments.

INTRODUCTION

Bats are one of the most diverse mammals in both feeding habits and numbers of species, making up 20 percent of extant mammalian species (Nowak 1994, Altringham 1996). Being the only volant mammals, they provide important ecosystem services, such as regulating insect populations and distributing forest nutrients (Duchamp et al. 2010, Kunz and Fenton 2005). Because bats are widespread and can consume >50 percent of their body weight in insects during a night, they play an important role in reducing insect populations (Cleveland et al. 2006). Several studies have confirmed that bats can reduce the amount of insects in a landscape (Kalka et al. 2008, Williams-Guillén et al. 2008). The estimated annual value of bats to North American agriculture is $3.7 billion (Boyles et al. 2011).

Bats can also be important biological indicators. Studies have shown that bats respond rapidly to

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[1] Biologist (JJS), JF New & Associates, 708 Roosevelt Rd., Walkerton, IN 46574; Assistant Professor (JED) and Graduate Student (LD), Indiana University of Pennsylvania, Department of Biology, 975 Oakland Ave., Indiana, PA 15705; Professor (JOW) and Graduate Student (MKC), Indiana State University, Department of Biology, Terre Haute, IN 47809; Principal Scientist (VB) and Scientist (DWS), Environmental Solutions and Innovations, Inc., 4526 Este Ave., Cincinnati, OH 45232. JED is corresponding author: to contact, call 724-357-1299 or email at jduchamp@iup.edu.

changes in the environment (Jones et al. 2009, Kunz et al. 2007, Lacki et al. 2007). Their ability to fly lets them move from less desirable habitats to more suitable ones. Thus, a presence, absence, or change in bat diversity and activity can help determine the environmental effects of human activities on ecological communities in a landscape. For example, one study showed that bat activity was reduced in areas of poor water quality as a result of sewage outfalls (Vaughan et al. 1996).

Bats also can accumulate heavy metals, pesticides, and other pollutants found in the environment. Researchers in Britain have found that bat activity and diversity increased on organic farms versus traditional farms that used pesticides (Wickramasinghe et al. 2003). Additionally, heavy metals such as mercury and lead have been found in high concentrations in bats, probably due to bioaccumulation from feeding on insects in polluted areas (O'Shea et al. 2001). Bats' ability to respond to landscape changes and pollution makes them valuable indicators of ecosystem health.

The suitability of forests for bats can be described by four factors: the density of forest structure or "clutter" and the availability of roosts, prey, and water (Hayes and Loeb 2007). All of these characteristics can be drastically affected by timber harvests, and previous studies have shown a strong relationship between timber harvests and forest use by resident bat species (Hayes and Loeb 2007, Patriquin and Barclay 2003). Bats' ability to maneuver through dense forest environments, and the efficiency with which they can use large forest openings, can be predicted to some extent by their wing morphology and body size. Larger-bodied bats with long, narrow wings tend to fly faster and more efficiently and make use of forest openings (Norberg and Rayner 1987). In contrast, smaller bats with a wing-tip shape that aids in their maneuverability can carefully pick their way through a cluttered forest environment (Norberg and Rayner 1987).

Bats' response to timber harvest is typically measured by use, either flight activity represented by recorded echolocation calls or selection of roosting habitat (Hayes and Loeb 2007). Although characteristics of a forest can affect the ability to record echolocation calls, with some exceptions (Duchamp et al. 2006, Yates and Muzika 2006) previous studies of bat activity have not typically estimated detection probability when measuring use. Additionally, to our knowledge, response to timber harvest has been measured only after a timber harvest. A true experimental manipulation involving the measurement of pre-harvest activity levels followed by long-term post-harvest monitoring of activity has not occurred.

The present study measures bats' pre-harvest use of intact forest stands based on echolocation calls and analyses that incorporate detection probability. Additionally, we monitored activity levels in a variety of existing openings for comparison with future activity levels in openings created by silvicultural treatments. Our study had two objectives: 1) compare habitat use by bats among existing forest openings prior to silvicultural treatment, and 2) compare habitat use by bats among our proposed treatment areas.

STUDY AREA

This study was conducted on Morgan-Monroe State Forest and Yellowwood State Forest in Morgan, Monroe, and Brown Counties in south-central Indiana (Fig. 1). Both forests (19,000 ha combined) were established in the 1920s after the high ridges, steep slopes, and narrow streams proved unsuitable for agriculture (Carman, this publication; Sheldon 2007). Today, these sites are covered in upland forests dominated by oaks (*Quercus* spp.) and hickories (*Carya* spp.), broken by occasional corridors (mostly logging roads) and previously harvested areas. Previous timber management consisted of single-tree and group selection in both forests (Sheldon 2007).

During the next 100 years, nine management units totaling 3,603 ha within these forests will be subjected to a variety of silvicultural treatments: even-aged (clearcuts and shelterwood cuts) and uneven-aged (single-tree selection and patch cuts) harvest, and control areas of no harvest (Kalb and Mycroft, this publication).

MATERIALS AND METHODS

Sampling

During 2007 and 2008, bats were acoustically sampled at locations relative to planned timber harvests within the nine experimental management units (Kalb and Mycroft, this publication). Within even-aged and control management units, the four areas designated

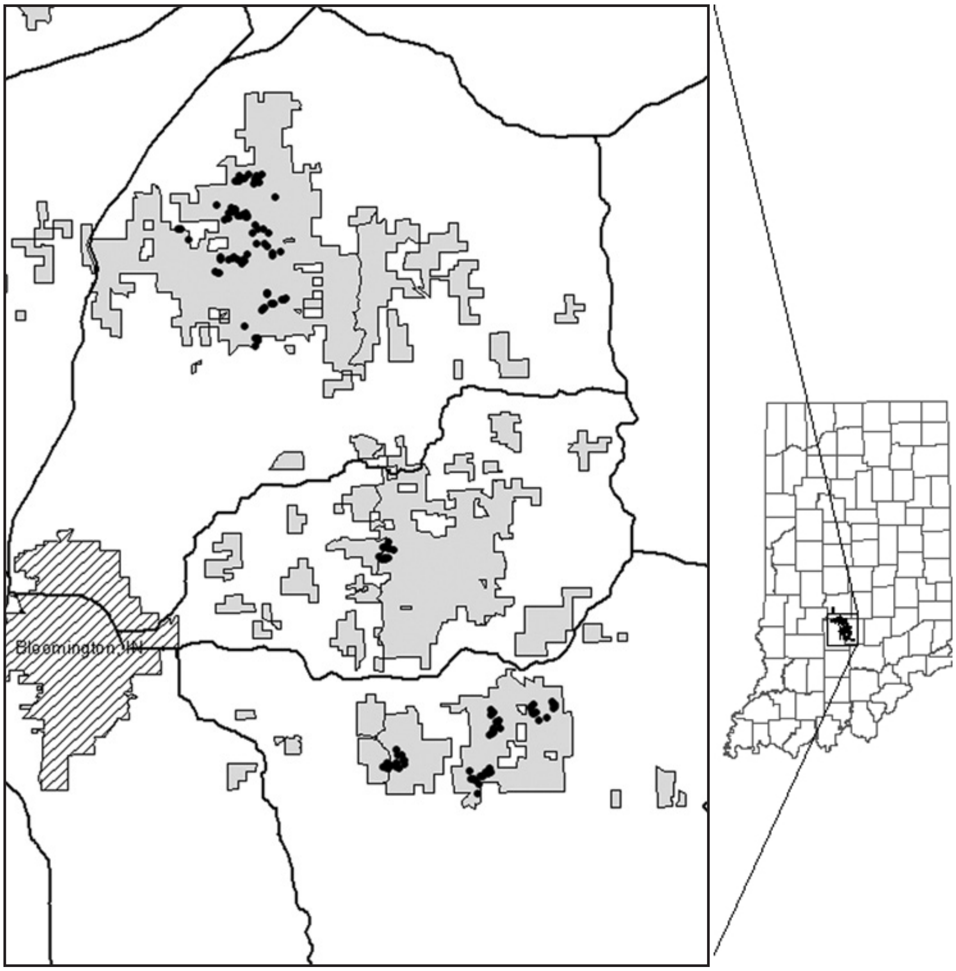

Figure 1.—Location of Morgan-Monroe (MM) and Yellowwood (YW) State Forests (gray areas) in relation to Bloomington, IN (hash mark). Solid circles denote sample sites.

for silvicultural treatments were sampled. Within the uneven-aged management units, four areas were randomly selected from the eight total areas designated for silvicultural treatments. For each sampled treatment area, detectors were placed at least 40 m apart at three locations relative to expected harvest area: inside, adjacent to, or outside the timber harvest. For control sites where no harvest was to occur, locations were still based on the area that potentially could have been harvested. Each detector location was considered to be an independent sample.

During 2007, in addition to the forest interior sites described above, we sampled three forest habitats that represented existing structural heterogeneity prior to timber harvests: forest edge, pre-existing harvest openings, and open corridors. Forest edge habitat was the interface of the forest with open lands, largely agricultural fields. Pre-existing harvest openings were non-linear openings (<2 ha) in the forest canopy. Corridors were linear openings within the forest such as fire and hiking trails, logging and access roads, and utility corridors. Locations for forest edge, pre-existing harvest openings, and open corridor samples were selected by identifying multiple, suitable sites for each habitat throughout the study area and then randomly selecting among these using a random numbers table. Additional corridor sites were chosen at established sites where bats were captured with mist nets along existing logging trails. Sampling occurred at 108 forest interior locations, 13 forest edges, 12 pre-existing harvest openings, and 24 corridors.

At each sample location, echolocation calls were digitally recorded to a CF card during 2 entire nights per year using an ANABAT II detector with a CF ZCAIM (Titley Electronics, Ballina, New South Wales, Australia). One sample occasion occurred during the early summer (15 May-8 July) and the other later in the summer (9 July-15 August). These time periods correspond to typical formation and then dispersion of maternity colonies in the area. Each ANABAT detector was set about 1 m from the ground on a polyvinyl chloride (PVC) pipe and housed within a plastic storage container with a 45° PVC elbow at one end (Duchamp et al. 2006). Microphones were placed 1 cm from the PVC elbow. Detectors were aligned on a random azimuth selected from a random numbers table, and areas of dense vegetation were avoided.

Bat Echolocation Call Identification

To identify recorded bat call sequences, we cleaned digital recordings with a filter in program ANALOOK (v. 4.8; Corben 2001) according to settings proposed by Britzke and Murray (2000). Call sequences were screened visually for irregular calls, and only regular search-phase calls were retained and measured in ANALOOK. We identified species by comparing measured parameters of a recorded call to the same parameters of calls in a reference library of echolocation calls collected from bat communities across the eastern United States (Britzke et al. 2011). We reduced the species included in the reference library to summer residents regularly captured during extensive mist-net surveys occurring within the study area: big brown bat (*Eptesicus fuscus*), eastern red bat (*Lasiurus borealis*), hoary bat (*L. cinereus*), little brown myotis (*Myotis lucifugus*), northern myotis (*M. septentrionalis*), Indiana myotis (*M. sodalis*), and tri-colored bat (*Perimyotis subflavus*)[2].

We then used the remaining call reference library to train 20 feed-forward, back-propagation neural networks, each with a single hidden layer of 24 nodes and skip layer connections (R v. 2.1; package ‘‘nnet’’) (Britzke et al. 2011, R Development Core Team 2011, Venables and Ripley 2002). Each network assigned a species identity to each call. We then assigned a final identity to each call by taking the mode of species assignments from the 20 neural networks. Similarly, we determined the identification of a call sequence by taking the mode of the species assignments for

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[2] Formerly eastern pipistrelle (*Pipistrellus subflavus*)

calls within that sequence. Sequences were deemed unidentified if the mode of identified calls either was less than four calls or less than 60 percent of all calls in the sequence.

To quantify bat activity levels for each species, we counted the number of minutes within which a species of bat was recorded and identified during a night of sampling. We categorized the amount of activity during a night into three categories: no activity, low-level activity, and high-level activity. Failure to detect a call during a night resulted in categorization as no activity for that location x species combination. If the number of minutes was in the upper quartile of all levels of activity for a species, then that location was considered to have a high level of activity during a night. If the number of minutes was in the lower three quartiles for a species, the location was considered to have a low level of activity during the night in question. The level of activity at a site was summarized into a detection history for each location across all sample nights. The activity level for each species of bat was considered independent.

Statistical Models

Due to differences in the years sampled, we analyzed bat activity data collected during 2007 at existing forest openings separately from data collected during both 2007 and 2008 at interior forest locations prior to silviculture treatments. Diversity and activity levels recorded during 2007 for the three types of existing forest openings and interior forest locations were compared using an analysis of variance (ANOVA) and Tukey's method of post-hoc comparisons (R Development Core Team 2011, Yandell 1997). The sample unit was considered to be the sample site with activity pooled across both sample nights. Minutes of activity were log transformed to improve assumptions of normality. Diversity was calculated using the exponential of the Shannon-Wiener index (Jost 2006) and was considered only for sample locations with >10 minutes of recorded activity. We also used these methods to compare overall bat activity and diversity between areas designated for silvicultural treatments. For these data the forest stand was considered the sample unit and minutes of activity were pooled across the three sample sites within each stand, and across all sample nights for both years of the study (2007 and 2008).

We relied on occupancy models to make species-specific comparisons of bat activity that would account for potential differences in the probability of detection among species and between habitats. Because bats can easily travel among our sampling locations, our occupancy models provide a relative probability of use rather than "occupancy" for our sample locations (MacKenzie 2006). We use the term "activity" to describe this use to remain consistent with existing bat literature. For data collected at existing forest openings during 2007, we used a single-state occupancy model (MacKenzie et al. 2006) to estimate two parameters: the probability of detecting high activity levels (p) and the probability of high activity levels occurring at a site for a species of bat (Ψ). The models resulting from this process were based on two detection nights at each sample site during a single year.

For data collected during 2007 and 2008 at interior forest sites, we used a multi-state occupancy model to estimate the probability of either low activity levels or high activity levels for a species of bat at a sample site (Nichols et al. 2007). The models resulting from this process were based on 4 detection nights at each sample site: 2 nights of sampling each year. The multistate occupancy models estimated five types of parameters. Two probabilities of detection were estimated: the probability of detecting low activity levels (p_1) and the probability of detecting high activity levels (p_2). Additionally, two probabilities of occurrence were estimated: the probability of low activity for a species occurring at a site (ψ_1) and the probability of high activity for a species occurring at a site (ψ_2). The fifth estimated parameter was for the probability that a site with high activity levels would appear to have low activity levels for a species during a sample night (δ).

The highest level of activity detected for a species at a site was considered to characterize activity at that site. Inconsistencies in the detections of the highest level activity were attributed to imperfect detection of activity levels at a site. Statistical models were run in program MARK (White 2011) using an extension package RMark (Laake and Rexstad 2011) within program R (R Development Core Team 2011).

With both types of models, we used a similar approach to building models. When modeling the parameters detection probability (*p*) and probability of activity levels occurring at a site (ψ), we tested a null model estimating a single value for each parameter against models where the values of parameters would be estimated separately for particular factors. The types of factors fell into two general categories: location differences and species differences. For the models examining forest openings, location factors were based on the type of forest opening sampled: forest edge, pre-existing harvest openings, and open corridors. For the models examining interior forest plots over 2 years, the location factors were based on the planned experimental silvicultural treatments: even-aged, uneven-aged, and non-harvest treatments. Species factors were the individual species included in the models. Models allowing for factor effects were built in a forward step-wise fashion, beginning with single factor effects and then testing additional additive effects. We first built models describing detection probability (*p*), followed by models describing probability of activity level occurring at a site (ψ). Model comparisons were based on AICc values (Burnham and Anderson 2002).

RESULTS

Summary of Recorded Echolocation Calls

All seven species known to be summer residents in the area were detected via echolocation call recordings (Table 1). We recorded bat echolocation calls during

Table 1.—Summary of (a) number of minutes with a call recorded from each bat species for each treatment plot during 2007-08 and (b) additional sampled habitats in 2007.

(a)	2007			2008			
	Uneven	Even	Control	Uneven	Even	Control	Total
Big brown bat	11	6	2	2	3	5	29
Eastern red bat	8	5	1	11	7	6	38
Hoary bat	0	0	0	0	0	0	0
Little brown myotis	0	7	1	21	7	6	42
Northern myotis	89	35	31	136	89	58	438
Indiana myotis	62	24	7	122	34	47	296
Tri-colored bat	32	25	28	69	35	72	261
Total	202	102	70	361	175	194	1,104

(b)	Corridors	Edges	Gaps	Total
Big brown bat	106	268	203	577
Eastern red bat	158	176	451	785
Hoary bat	6	8	0	14
Little brown myotis	19	66	17	102
Northern myotis	181	22	23	226
Indiana myotis	144	34	20	198
Tri-colored bat	239	113	401	753
Total	853	687	1,115	2,655

3,759 minutes on 516 nights across 157 locations. During 2007, detected activity levels differed among habitat types ($F_{3,153}$ = 48.8 and P < 0.001). Detected activity was lowest at interior forest locations (mean = 2.38±5.01 SD) compared to pre-existing harvest openings (mean = 45.71±30.56 SD; P < 0.001), forest edge (mean = 31.88±42.37SD; P < 0.001), and corridors (mean = 19.13±24.96 SD; P < 0.001). Pre-existing harvest openings also had greater activity than corridors (P < 0.001), but were not statistically different from edge locations (P = 0.127; Table 1). The species diversity of bat activity at locations with more than 10 minutes of activity was similar across all four forest habitats ($F_{3,43}$ = 0.609; P = 0.613): forest edges (mean = 3.4±0.9 SD), forest corridors (mean = 3.1±0.9 SD), interior (mean = 3.1±1.2 SD), and pre-existing harvest openings (mean = 2.8±1.0 SD).

Among interior forest locations in both 2007 and 2008, minutes of bat activity among stands designated for the three silvicultural treatment types were similar ($F_{2,33}$ = 1.629 and P = 0.211): stands designated for uneven-aged harvest (mean = 46.9±61.19 SD), stands designated for no harvest (mean = 22.0±30.1 SD), and stands designated for even-aged harvest (mean = 23.1±27.8 SD) (Table 1). Diversity at treatment areas with greater than 10 minutes of activity appeared to be higher in stands designated for even-aged management (mean = 3.8±0.9 SD) relative to stands designated for no harvest (mean = 2.7±0.2 SD) ($F_{2,33}$ = 3.357; P = 0.058). Diversity of bats in stands designated for uneven-aged harvest (mean = 3.1±1.0 SD) was similar to the other two treatments.

Bat Activity Levels in Treatment Plots

We used a multi-state occupancy model to describe the low and high activity levels of bats at the interior forest plots prior to silvicultural treatments. Only species with activity recorded on more than 20 nights were included in statistical models: eastern red bats (22 nights), northern myotis (95 nights), Indiana myotis (56 nights), and tri-colored bats (127 nights). The best of 73 models considered for describing detection probabilities for both low activity (p_1) and high activity (p_2) included terms for a lower probability of detecting activity for eastern red bats for both measures, a higher probability of detecting low activity levels (p_1) of tri-colored bats, and higher probability of detecting bat activity during the second year of sampling (2008) for both measures (Tables 2, 3, and 4).

Table 2.—Rankings for occupancy models describing high activity levels by bats at interior forest locations of treatment stands before implementation of silvicultural treatments. All models estimated detection probabilities as described in Table 3. Twenty-one models were tested, and those within 2 AICc of the highest ranking model were considered competing models. All models within 5 AICc of the highest ranking model along with those that were nested within competing models are shown.

Models for high activity levels ψ_2	Parameters	AICc	Δ AICc	Weight
Northern myotis + uneven treatment stands	12	1679.993	0.000	0.735
Northern myotis + harvest treatment stands	12	1682.897	2.904	0.172
Northern myotis	11	1684.632	4.639	0.072
Uneven treatment stands	11	1687.549	7.556	0.017
Constant	10	1690.823	10.830	0.003

Table 3.—Regression coefficients and uncertainty estimates for highest ranking occupancy model describing high activity levels by bats at interior forest locations of treatment stands before implementation of silvicultural treatments.

Model parameters	Regression model coefficients	Standard error	Lower 95% CI	Upper 95% CI
ψ_1 = *Pr* (low activity)				
Intercept	2.801	1.536	-0.209	5.813
ψ_2 = *Pr* (high activity)				
Intercept	-1.660	0.460	-2.563	-0.758
Northern myotis	1.143	0.386	0.387	1.900
Uneven treatment stands	0.934	0.375	0.198	1.671
δ = *Pr* (detecting low activity at high-activity site)				
Intercept	-0.967	0.239	-1.436	-0.498
p_1 = *Pr* (detection of low activity)				
Intercept	-1.979	0.280	-2.527	-1.430
Tri-colored bat	1.627	0.321	0.998	2.255
Eastern red bat	-1.368	0.659	-2.661	-0.076
Year 2008	-1.401	0.405	-2.195	-0.608
p_2 = *Pr* (detection of high activity)				
Intercept	-0.800	0.216	-1.225	-0.376
Eastern red bat	-1.273	0.425	-2.106	-0.440
Year 2008	0.814	0.269	0.286	1.342

Table 4.—Occupancy model parameter and uncertainty estimates based on highest-ranking model describing high-level use by bats at interior forest locations of treatment stands before implementation of silvicultural treatments.

Model parameters	Parameter estimates	Standard error	Lower 95% CI	Upper 95% CI
ψ_1 = *Pr* (low activity)				
Constant	0.943	0.083	0.802	1.000
ψ_2 = *Pr* (high activity)				
Even and control experimental plots	0.400	0.047	0.313	0.494
Uneven experimental plots	0.870	0.077	0.639	0.962
Even and control experimental plots by northern myotis	0.761	0.104	0.509	0.907
Uneven experimental plots by northern myotis	0.774	0.120	0.472	0.929
δ = *Pr* (detecting low activity at high-activity site)				
Constant	0.362	0.064	0.248	0.494
p_1 = *Pr* (detection of low activity)				
Tri-colored bat in 2007	0.413	0.070	0.306	0.567
Eastern red bats in 2007	0.034	0.021	0.115	0.178
Other bats in 2007	0.121	0.030	0.069	0.189
Tri-colored bats in 2008	0.148	0.039	0.075	0.229
Eastern red bats in 2008	0.009	0.007	0.003	0.032
Other bats in 2008	0.033	0.015	0.011	0.070
p_2 = *Pr* (detection of high activity)				
Eastern red bats in 2007	0.111	0.042	0.040	0.224
Other bats in 2007	0.311	0.046	0.229	0.411
Eastern red bats in 2008	0.221	0.074	0.085	0.400
Other bats in 2008	0.503	0.063	0.386	0.628

The probability that low activity levels would be detected at a location with high activity levels (δ) was left constant. We then tested a series of 21 models that estimated the probability of high and low bat activity levels at sample locations. The best model estimated a single probability of low-level activity (ψ_1) across our sites, and the probability of high activity levels (ψ_2) occurring at a sample location was greater for northern myotis and for all bats in areas designated for uneven-aged silvicultural treatments (Tables 2, 3, and 4).

Bat Use of Existing Forest Openings

We used a simpler single-state occupancy model to describe the probability of high bat activity levels within existing forest openings during the first year of sampling (2007). We included only species with at least 10 nights of high activity: big brown bats (24 nights), eastern red bats (34 nights), northern myotis (12 nights), Indiana myotis (10 nights), and tri-colored bats (25 nights). The best of 15 models considered for describing probability of detecting high activity levels included terms for a greater probability of detection (p) for eastern red bats (Tables 5, 6, and 7). We then tested a series of 34 models that estimated the probability of high activity levels (ψ) occurring in open habitats. Our model comparisons resulted in two competing models that described a lower probability of high activity levels within existing forest openings by Indiana myotis and northern myotis relative to other species (Tables 5, 6, and 7). One of the competing models also described an even lower probability of high activity levels for northern myotis along forest edges (Tables 5, 6, and 7).

Table 5.—Rankings for models describing high activity levels by bats within existing forest openings. All models estimated detection probabilities as described in Table 6. Fifteen models were tested and those within 2 AICc of the highest ranking model were considered competing models. All models within 5 AICc of the highest ranking model along with those that were nested within competing models are shown.

Models for high activity levels ψ	Parameters	AICc	Δ AICc	Weight
Indiana myotis + northern myotis along forest edges	5	450.568	0.000	0.494
Indiana myotis + northern myotis	5	452.263	1.695	0.212
Indiana myotis + big brown bats in forest corridors	5	454.538	3.970	0.068
Indiana myotis + big brown bats along forest edges	5	454.584	4.015	0.070
Indiana myotis + Eastern red bats in forest corridors	5	455.027	4.458	0.053
Indiana myotis + tri-colored bats	5	455.047	4.479	0.053
Indiana myotis	4	455.950	5.381	0.034
Northern myotis along forest edges	4	457.881	7.312	0.013
Northern myotis	4	461.048	10.479	0.003
Constant	3	461.451	10.883	0.002

Table 6.—Model-averaged regression coefficients and uncertainty estimates for competing models describing high activity levels by bats within existing forest openings.

Model parameters	Regression model coefficients	Standard error	Lower 95% CI	Upper 95% CI
$\psi = Pr$ (high activity)				
Intercept	1.447	0.796	-0.113	3.007
Indiana myotis	-2.141	0.817	-3.742	-0.540
Northern myotis along forest edges	-2.216	1.076	-4.325	-0.107
Northern myotis	-0.537	0.479	-1.476	0.402
$p = Pr$ (detection of high activity)				
Intercept	-0.690	0.257	-1.194	-0.186
Eastern red bats	0.696	0.339	0.032	1.360

Table 7.—Model-averaged parameter and uncertainty estimates based on competing models describing high activity levels by bats within existing forest openings in stands before implementation of silvicultural treatments.

Model parameters	Parameter estimates	Standard error	Lower 95% CI	Upper 95% CI
$\psi = Pr$ (high activity)				
Indiana myotis	0.333	0.117	0.151	0.585
Northern myotis along forest edges	0.236	0.197	0.035	0.725
Northern myotis in other habitats	0.695	0.202	0.260	0.937
Other bat species	0.809	0.122	0.475	0.952
$p = Pr$ (detection of high activity)				
Eastern red bats	0.501	0.096	0.321	0.682
Other bat species	0.334	0.057	0.233	0.453

DISCUSSION

After accounting for the probability of detection, we found that forest stands proposed for uneven-aged silvicultural treatments had a greater probability of high bat activity when compared to forest stands designated for other treatments. When examining the existing data for these stands, we could find no obvious reason to account for this difference. Also, interior forest locations prior to silvicultural treatment were more likely to experience high activity levels by northern myotis relative to other species. In contrast, the probability of high activity levels within existing forest openings was lower for both northern myotis and Indiana myotis relative to other species. Among pre-existing forest openings, northern myotis activity appeared to be especially low along forest edges.

The actual estimates of probability of use in general had wide confidence intervals. This variation likely reflects the minimal sampling of two occasions when estimating detection probability during a year. Given this caveat, the trends in our current modeling effort can help develop expectations of the effect of planned silvicultural treatments on the activity of foraging bats (Yates and Muzika 2006). Although use by Indiana myotis and northern myotis appeared to differ relative to other species, the actual estimates for the probability of high activity levels were similar at both forest interior locations and within existing forest openings. Other bat species had higher activity levels in existing forest openings when compared to interior forest locations. Based on these results, we expect that creating forest openings via silvicultural treatments in our experimental stands will increase the frequency of high activity levels by other species of bats, and maintain a similar level of activity by both Indiana myotis and northern myotis.

The probability of an interior forest location's experiencing low activity levels was estimated to be high with upper confidence intervals nearing 1. High activity levels were described as greater than 4 minutes of recorded activity during a night, which was the upper quartile of all recorded activity across all species. Low activity levels in interior forest sites were common, but inconsistent on a nightly basis. These low activity levels could reflect the lower probability of detecting bat activity at interior forest sites relative to existing forest openings. It also could be representative of the behavioral pattern of bats foraging in a cluttered environment.

The greater activity by bats in existing forest openings is likely due to a reduction in structural density, or "clutter." Our results were consistent with previous studies of bats using forested habitats in the eastern United States (Menzel et al. 2002, Owen et al. 2004, Titchenell et al. 2011). The greatest amount of nightly activity was recorded in pre-existing harvest openings and along the forest edge. Bats that cannot tolerate clutter spend much of their time foraging in these types of openings within forest stands (Hogburg et al. 2002, Owen et al. 2004, Patriquin and Barclay 2003, Titchenell et al. 2011). Additionally previous studies have found that forest edges may experience lower levels of activity by some species in the genus *Myotis*, such as the northern myotis, that roost and forage in the forest (Menzel et al. 2001, 2005a; Patriquin and Barclay 2003). Forest interior sites, which are characterized by greater clutter, appeared to be avoided by most bat species (Loeb and O’Keefe 2006) and thus were occupied least.

Activity by Bat Species

As expected, higher levels of activity by big brown and eastern red bats were recorded in pre-existing harvest openings and edges compared to other habitats. This difference is consistent with wing morphology that is specialized for habitats with minimal clutter (Elmore et al. 2004, Norberg and Rayner 1987). Big brown bats forage in open uncluttered environments (Duchamp et al. 2004, Loeb and O’Keefe 2006). Although this species typically exploits human structures for roosts, it is known to commute several kilometers between roosting and foraging locations (Duchamp et al. 2004). This species may commute into and out of Morgan-Monroe and Yellowwood State Forests from human structures outside of the study area. In contrast, eastern red bats roost in foliage (Mager and Nelson 2001, O’Keefe et al. 2009) within the forest and characteristically exploit gaps within the forest. Yates and Muzika (2006) found that eastern red bat habitat use was more likely in stands with more open understory.

The northern myotis, Indiana myotis, and the tri-colored bat used forest interior habitat at relatively high levels. However, the northern myotis and the Indiana myotis used forest openings less relative to other species. The northern myotis, a clutter-adapted species, is considered to prefer continuous forests and older forest stands (Loeb and O’Keefe 2006, Owen et al. 2003), and could be negatively affected by openings created during silvicultural treatments. However, Yates and Muzika (2006) found no evidence that northern myotis were negatively affected by fragmentation. With silvicultural treatments that create larger openings that are less cluttered, northern myotis may prefer forest structured like Morgan-Monroe and Yellowwood State Forests as of 2007: 30-80 years in age and a timber harvest regime based primarily on single-tree and small-group selection cuts. Indiana myotis can tolerate some clutter, but are more often detected along forest edges, forest openings, and corridors (Sparks et al. 2005). The tri-colored bat is considered a clutter-adapted species (Menzel et al. 2005b). In our study, however, it appeared to exploit both forest interior and forest openings on a regular basis and should perhaps be considered a habitat generalist (Loeb and O’Keefe 2006).

High activity levels were rarely recorded for little brown myotis and hoary bats during our study, and neither was included in our occupancy models. The echolocation call (Arita and Fenton 1997) and medium wing loading (Broders et al. 2004) of little brown myotis suggest this species uses a moderately cluttered habitat. They are known to forage along edges (Hogburg et al. 2002) and over still water (Barclay and Brigham 1991), which was rare in the upland study area. A lack of still water for foraging and few anthropogenic structures for day-roosts may explain the relative rarity of this species in Morgan-Monroe and Yellowwood State Forests. Little brown myotis, like big brown bats, may use corridors to commute from roosts outside the forest. The echolocation calls and high wing loading of hoary bats suggest the use of a clutter-free environment (Barclay et al. 1999, Norberg and Rayner 1987).

Although all seven species of bats captured during concurrent mist-net surveys (Sheets, Whitaker, et al., this publication) also were detected acoustically, two additional species, silver-haired bat (*Lasionycteris noctivagans*) and evening bat (*Nycticeius humeralis*), occur in this region of Indiana (Whitaker et al. 2007). Evening bats were not captured during 3 years of mist-net surveys (Sheets, Whitaker, et al. this publication) and were not included as potential species to be identified during acoustic surveys. Silver-haired bats are not thought to be summer residents in the area (Whitaker et al. 2007). The evening bat does occur in the region during the summer months, but the distribution is spotty and it is most often found in lowland areas rather than upland forests such as those sampled for this study (Whitaker et al. 2007).

Like every sampling method, bat detectors have biases. In forests, clutter from vegetation, vertical vegetation layering, call intensity, weather conditions, theft, and vandalism, among others, may affect the accuracy, quantity, and quality of calls detected (Duchamp et al. 2006, Hayes 2000, Weller and Zabel 2002). We estimated variation in detection probability between species and habitat types so that it did not bias our comparisons of activity levels. We also maintained a uniform sampling space directly in front of our microphones by directing bat detectors away from roads and heavily cluttered stands of vegetation. Neither vandalism nor theft occurred. We avoided sampling on nights with prolonged periods of adverse weather conditions. On occasion, temporary adverse weather conditions may have occurred, but they should not have affected overall activity levels during an entire night.

CONCLUSIONS

When testing for differences in the use of forest stands selected for silvicultural treatments, we found that stands selected for uneven-aged management had higher levels of bat activity than our other stands. Although we are not sure of the reasons, we will need to be aware of this pre-disposition as we monitor the response to silvicultural treatments as part of the Hardwood Ecosystem Experiment. We also found differences in our ability to detect bats acoustically among bat species and between forest habitats. These differences emphasize the importance of continuing to estimate detection probability as the Hardwood Ecosystem Experiment proceeds.

Finally, our results also provide some insight into the potential responses of bats to silvicultural treatments. When interior forest locations were compared to a variety of forest openings, there was a consistent response of increased use of openings by bat species that are adapted to foraging in open spaces. Bats adapted to foraging in an environment with higher densities of vegetation used these forest openings along with the interior forest locations during foraging flights.

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LITERATURE CITED

Altringham, J.D. 1996. **Bats: biology and behavior.** London, UK: Oxford University Press. 262 p.

Arita, H.T.; Fenton, M.B. 1997. **Flight and echolocation in the ecology and evolution of bats.** Trends in Ecology and Evolution. 12(2): 53-58.

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

Barclay, R.M.R.; Fullard, J.H.; Jacobs, D.S. 1999. **Variation in the echolocation calls of the hoary bat (*Lasiurus cinereus*): influence of body size, habitat structure, and geographic location.** Canadian Journal of Zoology. 77(4): 530-534.

Boyles, J.G.; Cryan, P.M.; McCracken; G.F.; Kunz T.H. 2011. **Economic importance of bats in agriculture.** Science. 332(6025): 41-42.

Britzke, E.R.; Duchamp, J.E.; Murray, K.L.; Swihart, R.K.; Robbins, L.W. 2011. **Acoustic identification of bats in the eastern United States: a comparison of parametric and nonparametric methods.** Journal of Wildlife Management. 75(3): 660–667.

Britzke, E.R.; Murray, K.L. 2000. **A quantitative method for selection of identifiable search-phase calls using the Anabat system.** Bat Research News. 41: 33-36.

Broders, H.G.; Findlay, C.S.; Zheng, L. 2004. **Effects of clutter on echolocation call structure of *Myotis septentrionalis* and *M. lucifugus*.** Journal of Mammalogy. 85(2): 273-281.

Burnham, K.P.; Anderson, D.R. 2002. **Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed.** New York: Springer-Verlag. 488 p.

Cleveland, C.J.; Betke, M.; Federico, P.; Frank, J.D.; Hallam, T.G.; Horn, J.; López, J.D., Jr.; McCracken, G.F.; Medellín, R.A.; Moreno-Valdez, A.; Sansone, C.G.; Westbrook, J.K.; Kunz, T.H. 2006. **Economic value of the pest control service provided by Brazilian free-tailed bats in south-central Texas.** Frontiers in Ecology and the Environment. 4(5): 238-243.

Duchamp, J.E.; Sparks, D.W.; Swihart, R.K. 2010. **Exploring the “nutrient hot spot” hypothesis at trees used by bats.** Journal of Mammalogy. 91(1): 48-53.

Duchamp, J.E.; Sparks, D.W.; Whitaker, J.O., Jr. 2004. **Foraging-habitat selection by bats at an urban-rural interface: comparison between a successful and a less successful species.** Canadian Journal of Zoology. 82(7): 1157-1164.

Duchamp, J.E.; Yates, M.; Muzika, R.M.; Swihart, R.K. 2006. **Estimating probabilities of detection for bat echolocation calls: an application of the double-observer method.** Wildlife Society Bulletin. 34(2): 408-412.

Elmore, L.W.; Miller, D.A.; Vilella, F.J. 2004. **Selection of diurnal roosts by red bats (*Lasiurus borealis*) in an intensively managed pine forest in Mississippi.** Forest Ecology and Management. 199(1): 11-20.

Hayes, J.P. 2000. **Assumptions and practical considerations in the design and interpretation of echolocation-monitoring studies.** Acta Chiropterlogica. 2(2): 225-236.

Hayes, J.P.; Loeb, S.C. 2007. **The influences of forest management on bats in North America.** In: Lacki, M.J.; Hayes, J.P.; Kurta, A., eds. Bats in forests: conservation and management. Baltimore, MD: Johns Hopkins University Press: 207-234.

Hogburg, L.K.; Patriquin, K.J.; Barclay, R.M.R. 2002. **Use by bats of patches of residual trees in logged areas of the boreal forest.** The American Midland Naturalist. 148(2): 282-288.

Jones, G.; Jacobs, D.S.; Kunz, T.H.; Willig, M.R.; Racey, P.A. 2009. **Carpe noctem: the importance of bats as bioindicators.** Endangered Species Research. 8(1-2): 93-115.

Jost, L. 2006. **Entropy and diversity.** Oikos. 113(2): 363-375.

Kalka, M.B.; Smith, A.R.; Kalko, E.K.V. 2008. **Bats limit arthropods and herbivory in a tropical forest.** Science. 320(5872): 71.

Kunz, T.H.; Arnett, E.B.; Erickson, W.P.; Hoar, A.R.; Johnson, G.D.; Larkin, R.P.; Strickland, M.D.; Thresher, R.W.; Tuttle, M.D. 2007. **Ecological impacts of wind energy development on bats: questions, research needs, and hypotheses.** Frontiers in Ecology and the Environment. 5(6): 315-324.

Kunz, T.H.; Fenton, M.B., eds. 2005. **Bat ecology.** Chicago, IL: University of Chicago Press. 798 p.

Laake, J.; Rexstad, E. 2011. **RMark: an alternative approach to building linear models.** In: Cooch, E.; White, G., eds. Program MARK: a gentle introduction. 10th ed.: 6.15(88). Available: http://www.phidot.org/software/mark/docs/book/. (Accessed 4 October 2012).

Lacki, M.J.; Amelon, S.K.; Baker, M.D. 2007. **Foraging ecology of bats in forests.** In: Lacki, M.J.; Hayes, J.P.; Kurta, A., eds. Bats in forests: conservation and management. Baltimore, MD: Johns Hopkins University Press: 83-127.

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

MacKenzie, D.I. 2006. **Modeling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly.** Journal of Wildlife Management. 70(2): 367-374.

MacKenzie, D.I.; Nichols, J.D.; Royle, J.A.; Pollock, K.H.; Bailey, L.L.; Hines, J.E. 2006. **Occupancy modeling and estimation: inferring patterns and dynamics of species occurrence.** San Diego, CA: Elsevier Academic Press. 324 p.

Mager, K.J.; Nelson, T.A. 2001. **Roost-site selection by eastern red bats (*Lasiurus borealis*).** The American Midland Naturalist. 145(1): 120-126.

Menzel, J.M.; Ford, W.M.; Menzel, M.A.; Carter, T.C.; Gardner, J.E.; Garner, J.D.; Hofmann, J.E. 2005a. **Summer habitat use and home-range analysis of the endangered Indiana bat.** Journal of Wildlife Management. 69(1): 430-436.

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

Menzel, M.A.; Carter, T.C.; Menzel, J.M.; Ford, W.M.; Chapman, B.R. 2002. **Effects of group selection silviculture in bottomland hardwoods on the spatial activity patterns of bats.** Forest Ecology and Management. 162(2-3): 209-218.

Menzel, M.A.; Menzel, J.M.; Carter, T.C.; Ford, W.M.; Edwards, J.W. 2001. **Review of the forest habitat relationships of the Indiana bat (*Myotis sodalis*).** Gen. Tech. Rep. NE-284. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 21 p.

Nichols, J.D.; Hines, J.E.; MacKenzie, D.I.; Seamans, M.E.; Gutiérrez, R.J. 2007. **Occupancy estimation and modeling with multiple states and state uncertainty.** Ecology. 88(6): 1395-1400.

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

Nowak, R. 1994. **Walker's bats of the world.** Baltimore, MD: Johns Hopkins University Press. 287 p.

O'Keefe, J.M.; Loeb, S.C.; Lanham, J.D.; Hill, H.S., Jr. 2009. **Macrohabitat factors affect day roost selection by eastern red bats and eastern pipistrelles in the southern Appalachian Mountains, USA.** Forest Ecology and Management. 257(8): 1757-1763.

O'Shea, T.J.; Everette, A.L.; Ellison, L.E. 2001. **Cyclodiene insecticide, DDE, DDT, arsenic, and mercury contamination of big brown bats (*Eptesicus fuscus*) foraging at a Colorado Superfund site.** Archives of Environmental Contamination and Toxicology. 40(1): 112-120.

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

Owen, S.F.; Menzel, M.A.; Ford, W.M.; Chapman, B.R.; Miller, K.V.; Edwards, J.W.; Wood, P.B. 2003. **Home-range size and habitat used by the northern myotis (*Myotis septentrionalis*).** The American Midland Naturalist. 150(2): 352-359.

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

R Development Core Team. 2011. **R: a language and environment for statistical computing.** Vienna, Austria: R Foundation for Statistical Computing. Available at www.R-project.org. [Date accessed unknown].

Sparks, D.W.; Ritzi, C.M.; Duchamp, J.E.; Whitaker, J.O., Jr. 2005. **Foraging habitat of the Indiana bat (*Myotis sodalis*) at an urban-rural interface.** Journal of Mammalogy. 86(4): 713-718.

Titchenell, M.A.; Williams, R.A.; Gehrt, S.D. 2011. **Bat response to shelterwood harvests and forest structure in oak-hickory forests.** Forest Ecology and Management. 262(6): 980-988.

Vaughan, N.; Jones, G.; Harris, S. 1996. **Effects of sewage effluent on the activity of bats (Chiroptera: Vespertilionidae) foraging along rivers.** Biological Conservation. 78(3): 337-343.

Venables, W.N.; Ripley, B.D. 2002. **Modern applied statistics with S.** New York: Springer. 512 p.

Weller, T.J.; Zabel, C.J. 2002. **Variation in bat detections due to detector orientation in a forest.** Wildlife Society Bulletin. 30(3): 922-930.

Whitaker, J.O., Jr.; Brack, V., Jr.; Sparks, D.W.; Cope, J.B.; Johnson, S. 2007. **Bats of Indiana.** Terre Haute, IN: Indiana State University Center for North American Bat Research and Conservation. 59 p.

White, G.C. 2011. **Program MARK: mark and recapture survival rate estimation software, v. 6.1.** Fort Collins, CO: Colorado State University.

Wickramasinghe, L.P.; Harris, S.; Jones, G.; Vaughan, N. 2003. **Bat activity and species richness on organic and conventional farms: impact of agricultural intensification.** Journal of Applied Ecology. 40(6): 984-993.

Williams-Guillén, K.; Perfecto, I.; Vandermeer, J. 2008. **Bats limit insects in a neotropical agroforestry system.** Science. 320(5872): 70.

Yandell, B.S. 1997. **Practical data analysis for designed experiments.** London, UK: Chapman and Hall. 437 p.

Yates, M.D.; Muzika, R.M. 2006. **Effect of forest structure and fragmentation on site occupancy of bat species in Missouri Ozark forests.** Journal of Wildlife Management. 70(5): 1238-1248.