

# Hardwood Forest

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# A Comparison of Bat Activity in a Managed Central Hardwood Forest

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**ABSTRACT.**—Bats exploit forest resources based on species-specific adaptations, resulting in differences in activity across forested landscapes. Forest management practices alter forests, impacting species differently and presumably affecting bat activity. Application of forest management that promotes species-specific bat conservation requires further understanding of bat response to silvicultural practices. We surveyed timber harvest treatments on two Indiana State Forests to compare bat activity across forest management treatments, in forests adjacent to harvests, and at locations across the harvest-forest gradient from May to July in 2013 and 2014. We used Wildlife Acoustics Song Meter SM2BAT+ detectors and Kaleidoscope Pro analysis software to survey bats in relation to four treatment types: clear cut, patch cut, shelterwood preparatory cut, and intact forest. Detectors were deployed at two points within each treatment and three points on the forested periphery of treatments and recorded for three consecutive nights. We examined bat activity using  $N$ -mixture models that estimate abundance and probability of detection for an open population and used Akaike's Information Criterion to select the best models. Based on identification of acoustic calls, eastern red bats and hoary bats were more active in harvest treatments than control treatments. Big brown, eastern red, and tri-colored bats were most active at harvest edges. Northern long-eared and Indiana/little brown bats were most active at harvest edges and in adjacent forest and hoary bats were most active at harvest centers. Differences in bat activity across these managed forests suggest bat assemblages benefit from management that employs an array of silvicultural methods, provides edge habitat, and maintains adjacent forest stands. Our results can be used to predict effects of forest management practices on species-specific bat activity to maximize bat usage of forests.

## INTRODUCTION

Approximately 75% of forest cover has been lost in the state of Indiana over the last two centuries due to agricultural expansion, logging practices, urban development, and human population growth (Carman, 2013). Indiana's forests are recovering as better management practices are implemented and farmland reverts to forest, yet forests are scarce and fragmented on much of the landscape. Additionally, increased land development and slowing in farmland reversion suggests Indiana's forested land may be nearing a peak (Gormanson *et al.*, 2016). Silvicultural practices that alter remaining forests must be well understood in regard to their ecosystem impacts to ensure the continual conservation of forest-dependent bats (Grindal, 1996; Hayes and Adam, 1996; Menzel *et al.*, 2002). This is especially true in light of the recent drastic population declines associated with White-nose Syndrome (Blehert *et al.*, 2009; and *see* USFWS, 2018).

Forest ecosystems serve as the primary habitat for many temperate bat species by providing essential foraging and roosting habitat (Barclay and Brigham, 1991; Barclay and Kurta, 2007). Bats are thought to select forested habitats based on four key characteristics: density of forest structure, roost availability, prey abundance, and water availability (Hayes and Loeb, 2007). All of these characteristics can be affected by forest management practices (Krusic *et al.*, 1996; Fenton, 2001; Menzel *et al.*, 2005). In particular timber harvests can directly alter forest structure and number of available roosts (Jones *et al.*, 2000; Loeb and Waldrop, 2008; Adams *et al.*, 2009).

Bats vary in terms of morphology and echolocation call characteristics and these traits affect how bats forage in different habitats (Aldridge and Rautenbach, 1987; Norberg and Rayner, 1987; Humes *et al.*, 1999; Menzel *et al.*, 2002; Patriquin and Barclay, 2003). Larger-bodied bats have high wing loadings and high aspect ratios resulting in faster flight with less maneuverability. These bats use lower frequency calls than smaller-bodied bats and calls of large bats attenuate at slower rates (Aldridge and Rautenbach, 1987). These morphological and echolocation characteristics promote in-flight prey capture and allow larger-bodied bats to forage efficiently in open areas (Aldridge and Rautenbach, 1987; Jones *et al.*, 2000; Menzel *et al.*, 2005). In contrast, smaller-bodied bats have lower wing loadings, wing aspect ratios, and higher frequency echolocation calls; therefore, these bats are slower and more maneuverable in flight but also have a shorter call range when compared to larger bats (Aldridge and Rautenbach, 1987; Norberg and Rayner, 1987). Smaller-bodied bats typically are categorized as clutter-adapted due to their ability to forage within forest clutter where they may glean prey from vegetation surfaces in addition to capturing prey in flight (Norberg and Rayner, 1987).

Previous work has shown that bats are generally more active in timber harvest areas than in unharvested forests (Grindal and Brigham, 1998; Humes *et al.*, 1999; Menzel *et al.*, 2005; Titchenell *et al.*, 2011); however, effects vary by species due to differences in morphology and echolocation call structure. In particular, big brown bats (*Eptesicus fuscus*), eastern red bats (*Lasiurus borealis*), hoary bats (*Lasiurus cinereus*), and tri-colored bats (*Perimyotis subflavus*) show higher activity in cut areas in the coastal plain of the Carolinas (Menzel *et al.*, 2002; Morris *et al.*, 2010). Titchenell *et al.* (2011) found higher overall bat activity in shelterwood harvests, and Menzel *et al.* (2002) found more bat activity in group selection harvests compared to unharvested forest. Additionally, Patriquin and Barclay (2003) found an increase in total bat activity in clear cuts compared to unharvested forest in Alberta, Canada, but northern long-eared bats (*Myotis septentrionalis*), a clutter-adapted species, were less active in clear cuts. Clearly a more detailed understanding of timber harvest influence on bat species is needed to apply forest management strategies that promote bat conservation.

Forest management practices such as timber harvests can create hard edges at the harvest-forest interface. Bats use these edges for navigation, commuting, and foraging (Clark *et al.*, 1993; Walsh and Harris, 1996; Grindal and Brigham, 1999; Hogberg *et al.*, 2002). Forest edges may also offer greater insect availability (Grindal and Brigham, 1999; Morris *et al.*, 2010), because these boundaries potentially act as windbreaks that concentrate large amounts of insects (Pasek, 1988; Swystun *et al.*, 2001). Higher bat activity along harvest edges, rather than in harvest centers or forest interiors, has been widely documented (Menzel *et al.*, 2002; Patriquin and Barclay, 2003). Krusic *et al.* (1996) found overall higher concentrations of bat activity at forest edges than at locations within forest interiors in a study in New Hampshire and Maine, but calls were not classified to species. A study in Alberta, Canada showed greater activity of northern long-eared and little brown bats (*Myotis lucifugus*) at harvest edges over harvest center (Hogberg *et al.*, 2002). Alternately, Morris *et al.*

(2010) found northern long-eared and southeastern bats (*Myotis austroriparius*) foraging in stand interiors and avoiding edges in North Carolina. Though studies have documented increased bat use of harvest edges, results differ among studies and the extent of edge influence on bat activity in adjacent forest is not well understood. Jantzen and Fenton (2013) examined bat activity along a continuum across the agriculture-forest interface in Ontario, Canada, and found hoary bats, big brown/silver-haired bats (*Lasiorycteris noctivagans*), northern long-eared bats, and little brown bats to show maximum activity along the edge. However, similar studies in a managed forest landscape are lacking (but see Menzel *et al.*, 2002; Morris *et al.*, 2010).

Acoustic technology has been widely used in bat forest management studies and can yield stronger comparisons between treatments using statistical analyses that account for imperfect detection probability ( $P < 1$ ) (Duchamp *et al.*, 2006). Recent studies have used occupancy modeling to compare bat use of differing habitat types taking into account imperfect detection (Yates and Muzika, 2006; Hein *et al.*, 2009; Bender *et al.*, 2015); however, meeting the population closure assumption of occupancy analyses is challenging given bats are able to fly great distances in a short time frame. Estimating bat call abundance using  $N$ -mixture models for open populations that account for imperfect detection may be more suitable for studies that cannot ensure population closure between sites (Dail and Madsen, 2011).

To examine the effect of timber harvest on bat activity at multiple scales, we conducted this study on Morgan-Monroe and Yellowwood State Forests, Indiana. Our study focused on several silvicultural treatments designed to regenerate oak (*Quercus spp.*) and hickory (*Carya spp.*) within the larger intact forests. Our objectives were: (1) to compare bat activity relative to forest treatment areas for common species on our study site and (2) to compare bat activity across the harvest-forest gradient. We hypothesized: (1) larger-bodied bats (big brown bat, hoary bat, and eastern red bat) would be more active in harvest treatments than in control treatments based on previous studies and smaller-bodied bats [northern long-eared bat, Indiana bat (*Myotis sodalis*), little brown bat, and tri-colored bat] would be more active in control treatments than in harvest treatments; and (2) larger-bodied bats would be more active at the harvest edge based on previous research (Menzel *et al.*, 2002; Morris *et al.*, 2010) and smaller-bodied bats would be more active in interior forest due to their clutter tolerance.

## METHODS

### STUDY AREA

This study was part of the Hardwood Ecosystems Experiment (HEE), a long-term, multi-disciplinary forest management study implemented by the Indiana Department of Natural Resources Division of Forestry (INDNR DoF) in 2006 (Kalb and Mycroft, 2013). The HEE is located on Morgan-Monroe (39°19'16"N 86°24'48"W/39.32111°N 86.41333°W) and Yellowwood State Forests (39°19'55"N 86°33'26"W/39.33194°N 86.55722°W) in Morgan, Monroe, and Brown counties in south-central Indiana. These forests are characterized by upland oak-hickory forests with a history of group and single-tree selection harvest (Kalb and Mycroft, 2013). European settlers cleared these forests during the mid-1800s (Parker and Ruffner, 2004), but forests regenerated after the lands were acquired by the state during the early to mid-1900s (Carman, 2013).

The 3603 ha HEE study site consists of nine management units, each containing an experimental core and a surrounding buffer area. Management cores received one of three

types of forest management: even-aged, uneven-aged, and control (uneven aged units: 1088 ha; even-aged units: 1294 ha; control units: 1221 ha). Uneven-aged cores were comprised of four 0.4 ha patch cuts, two 1.2 ha patch cuts, and two 2 ha patch cuts, with surrounding forest managed using single-tree selection harvest. Even-aged cores contained two 4 ha clear cuts and two 4 ha shelterwood cuts. Clear cuts were established by coppicing oak (*Quercus spp.*), hickory (*Carya spp.*), ash (*Fraxinus spp.*), tulip poplar (*Liriodendron tulipifera*), and black walnut trees (*Juglans nigra*) between 2.5 and 35.6 cm diameter at breast height (dbh) to within 15.2 cm from the ground and felling, chemically treating, or girdling all other woody stems (Kalb and Mycroft, 2013). Shelterwoods were established using a three-stage plan that will require three treatments over a 10 to 20 y period (Smith *et al.*, 1997) and were in the first stage at the time of our study. Midstory and understory non-oak stems  $\leq 25.4$  cm dbh were removed during the first stage of the shelterwood treatment. Control units were typical of forests in the region and were comprised of intact forest with a history of single-tree selection prior to the initiation of this study (2006) and will remain unharvested for the duration of the HEE study (Kalb and Mycroft, 2013). Buffer areas around each management core were managed using existing INDNR DoF management practices, which consists of using single-tree selection harvest to maintain stocking levels between 70 and 75 % and a limited use of group selection harvest (Kalb and Mycroft, 2013).

#### FIELD SAMPLING

From May 15 to July 27, 2013 and 2014, we used acoustic detectors to sample 12 control and 24 harvest treatments (12 patch cuts, six clear cuts, and six shelterwood cuts). We recorded bat calls using Song Meter SM2BAT+ detectors, which record in full-spectrum, and SMX-US microphones (Wildlife Acoustics, Inc.; Concord, Massachusetts, U.S.A.). We simultaneously deployed five detectors per treatment, placing detectors in five locations along a gradient transect radiating from the center of the treatment following a randomly generated azimuth: harvest center, harvest edge, 15 m into adjacent forest (forest edge), 50 m into adjacent forest (forest), and 100 m into adjacent forest (deep forest). In control treatments we used a randomly-generated point as the harvest center and placed the harvest edge detector 70 m from the center, which was the average distance between center and edge detectors in harvests. Detectors recorded in triggered Waveform Audio File (WAV) format from sunset to sunrise for three consecutive nights per location. We surveyed four treatments per unit, resulting in 180 total detector locations per field season (five detectors per treatment \* four treatments per unit \* nine units = 180). We surveyed treatments in reverse order during the second season to account for higher bat activity due to volant juveniles late in the season. We conducted surveys on 54 nights per season, resulting in 108 total survey nights over both seasons.

The detector apparatus consisted of two 3 m polyvinyl chloride (PVC) conduit pipes stacked vertically and held upright by three supporting ropes. A 10 m microphone cable connected the detector unit on the ground to the microphone, which was suspended from a 1.2 m wooden dowel rod inserted perpendicularly through the top of the uppermost PVC pipe. The microphone faced downward to prevent waterlogging and hung approximately 1 m out from the PVC pipe, minimizing sound wave reverberation off of the PVC apparatus.

We measured vegetation characteristics at all detector locations to indicate amount of forest clutter to be used as detection covariates. We took measurements within a 30-m diameter circular plot with the detector at the center (Weller and Zabel, 2002; Kaiser and O'Keefe, 2015). We measured three plot characteristics: number of trees at least microphone height (6 m), distance of nearest tree to detector, and canopy closure. We

visually estimated canopy closure as percentage of sky (0%, 25%, 50%, 75%, or 100%) blocked by canopy at the center of both the plot and in four equally-sized quadrants of the plot.

We collected climate measurements from local weather stations within close proximity to the study sites to use as detection covariates (KINNASHV4, Nashville, Indiana, and KINMARTI13, Martinsville, Indiana; Weather Underground, 1995). We gathered data on 16 weather variables for each survey night: cloud cover, minimum and maximum wind speed, precipitation, and minimum, mean, and maximum air temperature, relative humidity, barometric pressure, and dew point.

#### ANALYSES

We automatically classified bat echolocation calls to species using Wildlife Acoustics Kaleidoscope Pro 2.0.7 bat call analysis software (Wildlife Acoustics, Inc; Concord, Massachusetts, U.S.A). We classified calls to seven common species based on historic mist-net surveys on HEE sites (Sheets *et al.*, 2013) using The Bats of North America 2.0.5 filter with the default setting and a minimum of two pulses in agreement. Species included: hoary bat, big brown bat, eastern red bat, tri-colored bat, Indiana bat, little brown bat, and northern long-eared bat. Indiana bat and little brown bat calls were grouped due to the similarity of these calls (O'Farrell, 1999; Robbins and Britzke, 1999).

We used principal components analysis (PCA) to reduce dimensionality of vegetation and weather data and considered only principal components that explained 10 % or more variation and factor loadings of  $>[0.3]$ . These cutoff values were chosen after considering the factor loadings of PCA results.

We used a Dail-Madsen  $N$ -mixture model to estimate call abundance ( $\lambda$ ) and detection probability ( $P$ ) (Dail and Madsen, 2011) for each season and each species. Therefore, we fit a total of 12 models, one for each of the six species for 2013 and 2014. This model is an extension to the Royle (2004)  $N$ -mixture model, but allows for estimation of abundance for an open population. This model estimates species abundance, which is not reliable for bat acoustic studies given individual bats cannot be identified by call; however, we used the model to predict bat call abundance, using this as a proxy for bat activity. We modeled bat activity using a negative binomial distribution. The general Dail-Madsen  $N$ -mixture model used is as follows:

$$N_{it} \sim \text{Negative - Binomial}(\lambda, \alpha)$$

$$G_{it} | N_{it-1} \sim \text{Poisson}(\gamma * N_{it-1})$$

$$S_{it} | N_{it-1} \sim \text{Binomial}(N_{it-1}, \omega)$$

$$N_{it+1} = G_{it} + S_{it}$$

$$y_{it} \sim \text{Binomial}(N_{it}, P)$$

where  $N_{it}$  is the unobserved abundance (or bat activity) at site  $i$  at time  $t$ ,  $\lambda$  is the expected abundance,  $\alpha$  is the dispersion parameter,  $G_{it}$  is the number of individuals gained (by immigration during one night) at site  $i$  at time  $t$ ,  $\gamma$  is the arrival rate of individuals,  $\omega$  is the apparent survival probability of individuals,  $P$  is detection probability, and  $y_{it}$  is the observed number of bat calls at site  $i$  and time  $t$ . We used the three repeated nightly recording for our

repeated counts across season. A similar approach with three repeated counts were used with estimating abundance of flying squirrels *Glaucomys sabrinus* (Priol *et al.*, 2014). We additionally evaluated normal, Poisson, and zero-inflated distributions to describe expected abundance,  $\lambda$ , but they did not provide an improved fit based on model selection criteria and therefore not reported here. Covariates of abundance and detection were estimated using the log and logit link.

We used the Dail-Madsen model to compare activity at two scales corresponding to our study objectives, which we have titled from most broad to most fine scale: Treatment Comparison and Harvest-Forest Gradient Comparison. Forest management treatment type was used as a covariate of abundance for comparison among treatments in the Treatment Comparison Model. Detector location was used as a covariate of abundance in the Harvest-Forest Gradient Model for comparison among detector locations. Covariates used for estimating P included results from vegetation PCAs (canopy closure, number of trees per plot, distance to closest tree) and results from weather PCAs (air temperature, relative humidity, barometric pressure, cloud cover, and precipitation).

For the Treatment Comparison, we combined call counts from the five detector locations per treatment to reflect bat use of the entire treatment area (within and adjacent to the treatment). This allowed us to compare bat activity by treatment. This decision was based on three considerations: (1) given bat foraging ranges are larger than our harvests, incorporating the surrounding forest in the analysis encompasses a larger portion of a bat's range; (2) given these harvests are dominated by early successional vegetation making them more structurally complex than a fresh harvest, differences in activity are more subtle from the harvest interior to the surrounding forest and clearer inferences can be made using a more coarse focus; and (3) because differences in species' foraging habitats could bias our interpretation of activity if we ignored bat activity in forests surrounding harvests, including a wider sampling region would help minimize edge effects in our treatment analysis. In contrast, for the Harvest-Forest Gradient Model, we did not combine call counts, but instead compared activity at individual detector sites across the harvest-forest interface in order to look for finer scale differences. We did not use calls collected in controls for the gradient analysis.

Models were fit in R version 3.1.1 (R Core Team, 2013) using the unmarked package (Fiske and Chandler, 2011). We compared 95% confidence intervals of call abundance between treatments for all species over both seasons. All possible permutations of model covariates were evaluated and the most parsimonious model was selected using Akaike's Information Criterion (AIC) (Burnham and Anderson, 2001).

## RESULTS

We sampled 180 sites from 12 control treatments and 24 harvest treatments (12 patch cuts, six clear cuts, and six shelterwood preparatory cuts) over 108 nights. In 2013 we classified 7083 call files to species, and in 2014 we classified 5656 call files to species.

Principal components analysis yielded three principal components explaining variation in 2013 weather data: air temperature and dew point explained the highest variation on the first principal component; wind, cloud cover, and barometric pressure explained the highest variation on the second principal component; and relative humidity and wind speed explained the highest variation on the third principal component (Table 1). Two principal components explained the highest variation in 2014 weather data: air temperature and dew point on the first principal component, and air temperature and cloud cover on the second principal component (Table 1). The vegetation PCA resulted in a single principal component that explained the number of trees per plot, distance to nearest tree, and

TABLE 1.—Factor loadings of greater than |0.3| for principal components analysis (PCA) of weather data collected on Morgan-Monroe and Yellowwood State Forests, Indiana, during May–July 2013 and 2014

Weather variables	PC1	PC2	PC3
2013			
Mean temperature	−0.36		
Min temperature	−0.38		
Max dew point	−0.37		
Mean dew point	−0.39		
Min dew point	−0.38		
Max humidity			−0.42
Mean humidity			−0.51
Min humidity			−0.40
Mean wind speed		−0.32	0.31
Cloud cover		−0.32	
Max pressure		0.36	
Mean pressure		0.39	
Min pressure		0.40	
2014			
Max temperature		0.44	
Mean temperature		0.33	
Min temperature	−0.32		
Max dew point	−0.30		
Mean dew point	−0.32		
Min dew point	−0.31		
Cloud cover		−0.41	

percent canopy closure for 2013 and 2014 (Table 2). Sixteen candidate models were evaluated for 2013 data and eight candidate models were evaluated for modeling 2014 activity.

#### TREATMENT COMPARISON

*Large-bodied bats.*—Bat use of management units varied for species and by years (Fig. 1). For big brown bats, there were two plausible models predicting activity. Harvest type was not

TABLE 2.—Factor loadings greater than |0.3| for principal components analysis (PCA) of vegetation data collected on Morgan-Monroe and Yellowwood State Forests, Indiana, during May–July 2013 and 2014

Vegetation variables	2013	2014
Canopy Closure Center	−0.400	−0.407
Canopy Closure Quad 1	−0.399	−0.401
Canopy Closure Quad 2	−0.402	−0.403
Canopy Closure Quad 3	−0.400	−0.398
Canopy Closure Quad 4	−0.398	−0.397
Number trees	−0.333	−0.327
Distance to tree	0.300	0.296

TREATMENT COMPARISON : LARGE-BODIED BATS

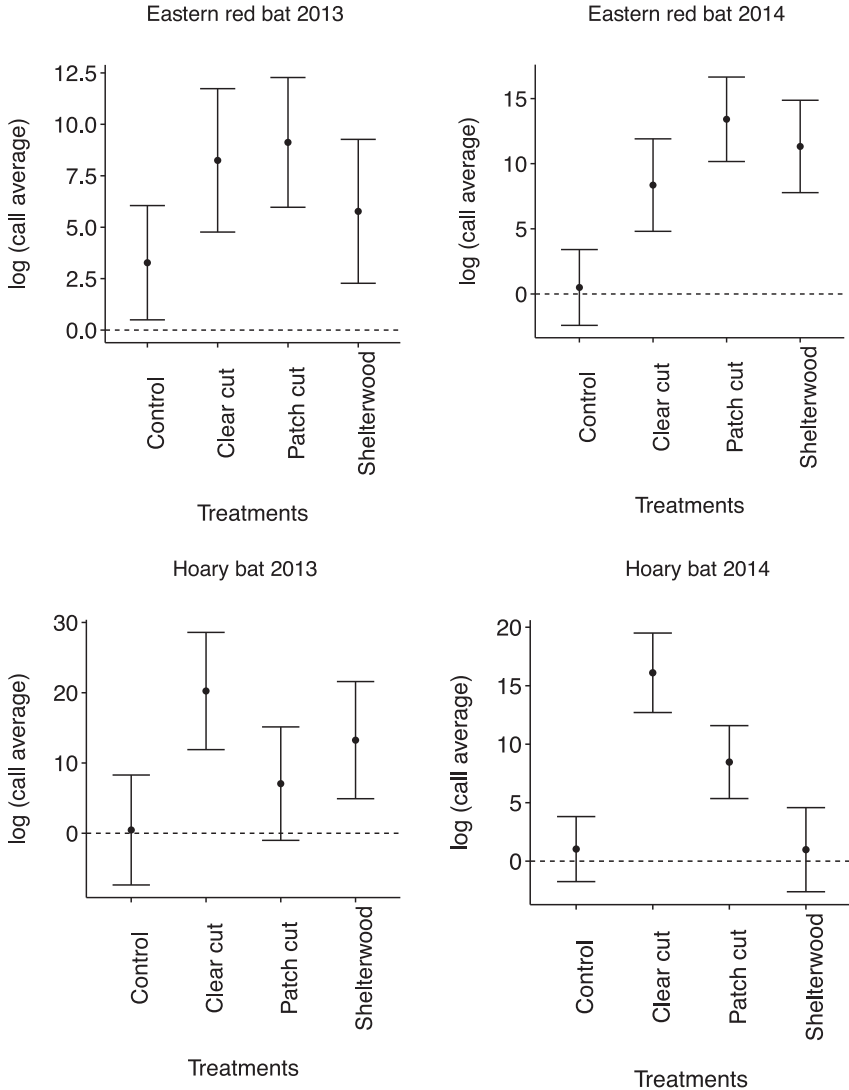


FIG. 1.—Log call average per harvest treatment of eastern red bats (*Lasiurus borealis*) and hoary bats (*Lasiurus cinereus*) on Morgan-Monroe and Yellowwood State Forests, Indiana, during May–July 2013 and 2014, calculated using the most parsimonious Dail and Madsen (2011) *N*-mixture abundance model

included in the best models, indicating activity in and around harvests was similar across treatment types (Table 3). Eastern red bat activity was modeled using all weather and vegetation covariates of detection, and all harvest treatment variables in both seasons. Activity was higher in patch cuts than in control treatments in both seasons and was higher

TABLE 3.—Dail-Madsen model results for the Treatment Comparison Model with lowest Akaike’s Information Criterion value. Abundance ( $\lambda$ ), recruitment ( $\gamma$ ), survivorship ( $\omega$ ), and detection probability ( $p$ ) are included in model descriptions along with covariates: H: Harvest treatments; PC1: principal component 1; PC2: principal component 2; PC3: principal component 3; VPC: vegetation principal component; and a period for no covariate effects. Species names are big brown bat (*Eptesicus fuscus*), eastern red bat (*Lasiurus borealis*), hoary bat (*Lasiurus cinereus*), Indiana/little brown bat (*Myotis sodalis/lucifugus*), northern long-eared bat (*Myotis septentrionalis*), and tri-colored bat (*Perimyotis subflavus*). Echolocation calls collected during May-July 2013 and 2014 on forest management treatments in Morgan-Monroe and Yellowwood States Forests, Indiana, were used for model creation

Year	Species	Model	$\Delta AIC^a$	$\Omega^b$	$K^c$
2013	Big brown	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+pc3+vpc)$	0.00	0.52	9
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc3+vpc)$	0.95	0.32	8
	Eastern red	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+pc3+vpc)$	0.00	0.42	9
		$\lambda(H)\gamma(.)\omega(.)p(pc1+pc2+pc3+vpc)$	1.04	0.25	13
	Hoary	$\lambda(H)\gamma(.)\omega(.)p(pc1+pc2+pc3+vpc)$	0.00	0.93	13
	Indiana/Little brown	$\lambda(.)\gamma(.)\omega(.)p(pc1)$	0.00	0.23	6
		$\lambda(.)\gamma(.)\omega(.)p(pc1+vpc)$	1.46	0.11	7
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2)$	1.61	0.10	7
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc3)$	1.61	0.10	7
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+pc3)$	0.00	0.75	8
	Northern long-eared	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+pc3+vpc)$	0.00	0.50	9
	Tri-colored	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	1.01	0.30	8
2014	Big brown	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	0.00	0.66	8
	Eastern red	$\lambda(H)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	0.00	0.65	12
		$\lambda(H)\gamma(.)\omega(.)p(pc1+pc2)$	0.00	0.53	10
	Hoary	$\lambda(H)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	0.32	0.45	11
		$\lambda(.)\gamma(.)\omega(.)p(pc1)$	0.00	0.44	6
		$\lambda(.)\gamma(.)\omega(.)p(pc1+vpc)$	1.73	0.19	7
	Indiana/little brown	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2)$	1.99	0.16	7
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	0.00	0.39	8
		$\lambda(H)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	1.09	0.22	11
		$\lambda(H)\gamma(.)\omega(.)p(pc1+pc2)$	1.20	0.21	10
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2)$	1.55	0.18	7
	Tri-colored	$\lambda(.)\gamma(.)\omega(.)p(pc2+vpc)$	0.00	0.59	7
$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$		1.74	0.25	8	

<sup>a</sup> Difference between model’s Akaike’s Information Criterion and the lowest AIC value

<sup>b</sup> AIC model weight

<sup>c</sup> Number of parameters estimated by the model

in clear cuts and shelterwood preparatory cuts than in control treatments in 2014 (Table 3, Fig. 1). The best model for hoary bats included all weather and vegetation covariates of detection and harvest treatment covariates in both seasons. Shelterwood preparatory cuts showed greater hoary bat activity compared to control treatments in 2013. In 2014 activity was greater in clear cuts and patch cuts than in control treatments (Table 3, Fig. 1).

*Small-bodied bats.*—The best model for Indiana/little brown bat activity included the first weather principal component for both seasons, with several equally plausible models (Table 3). Harvest treatment was not included in any top models. Northern long-eared bat activity was modeled using all weather covariates of detection in 2013 and using all weather and vegetation covariates of detection and harvest covariates in 2014 (Table 3). Though harvest

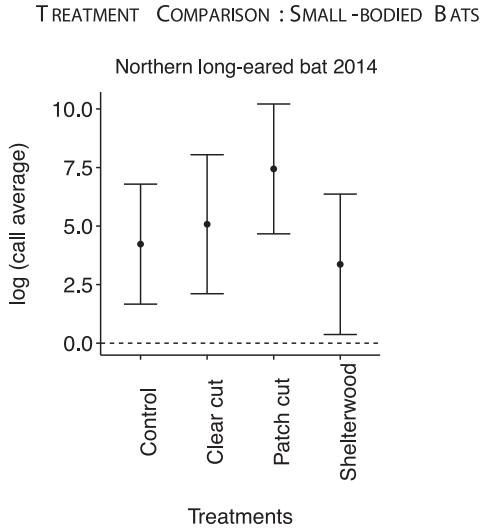


FIG. 2.—Log call average per harvest treatment of northern long-eared bats (*Myotis septentrionalis*) on Morgan-Monroe and Yellowwood State Forests, Indiana, during May–July 2014, calculated using the most parsimonious Dail and Madsen (2011)  $N$ -mixture abundance model

was included in top models in 2014, confidence intervals overlapped zero suggesting activity in and around harvests did not differ among treatments (Fig. 2). The best model for tri-colored bat activity included all weather and vegetation covariates of detection for both seasons and harvest was not included in any top models (Table 3).

#### HARVEST-FOREST GRADIENT COMPARISON

*Large-bodied bats.*—Bat activity across the harvest-forest interface varied by species and year. Big brown bat activity across the harvest-forest gradient was best modeled using detector location for all harvest treatments except in clear cuts and patch cuts in 2014 (Table 4). In 2013 big brown bat activity was highest at harvest edges of patch and clear cuts, but was also high 100 m into forest adjacent to patch cuts (Deep Forest; Fig. 3). Activity did not differ among shelterwood treatment detector locations.

Eastern red bat activity was best modeled using detector location in patch cuts and clear cuts in 2013, suggesting activity did not differ among detector locations in other harvests or in other seasons (Table 4). Activity was highest at harvest edges and harvest centers of patch cuts and clear cuts (Fig. 3).

Best models for hoary bat activity included detector location for all harvest types in 2013 (Table 2). Hoary bat activity was highest at harvest center in clear cuts followed by harvest edge (Fig. 3). In patch cuts activity was equally high at harvest center and harvest edge. Hoary bat activity did not differ among detector locations in shelterwood preparatory cuts.

*Small-bodied bats.*—Indiana/little brown bat activity was best modeled using detector location for patch cuts and shelterwood preparatory cuts in 2013 and for clear cuts in 2014 (Table 4). Activity was highest at harvest edge in patch cuts and at harvest center in shelterwood preparatory cuts (Fig. 4). In clear cuts Indiana/little brown bat activity was highest at harvest center, harvest edge, and 100 m into adjacent forest.

TABLE 4.—Dail-Madsen model results for the Harvest-Forest Gradient Model with lowest Akaike's Information Criterion value. Abundance ( $\lambda$ ), recruitment ( $\gamma$ ), survivorship ( $\omega$ ), and detection probability (P) are included in model descriptions along with covariates: L: Detector location; PC1: principal component 1; PC2: principal component 2; PC3: principal component 3; VPC: vegetation principal component; and a period for no covariate effects. Species names are big brown bat (*Eptesicus fuscus*), eastern red bat (*Lasiurus borealis*), hoary bat (*Lasiurus cinereus*), Indiana/little brown bat (*Myotis sodalis/lucifugus*), northern long-eared bat (*Myotis septentrionalis*), and tri-colored bat (*Perimyotis subflavus*). Echolocation calls collected during May-July 2013 and 2014 on forest management treatments in Morgan-Monroe and Yellowwood States Forests, Indiana, were used for model creation

Year	Species	Harvest	Model	$\Delta AIC^a$	$\Omega^b$	$K^c$
2013	Big brown	Patch	$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+pc3+vpc)$	0.00	0.65	13
			$\lambda(.)\gamma(.)\omega(.)p(pc1+pc3)$	0.00	0.15	7
		Shelterwood	$\lambda(L)\gamma(.)\omega(.)p(pc1+pc3)$	0.18	0.14	11
			$\lambda(.)\gamma(.)\omega(.)p(pc1+vpc)$	0.38	0.13	7
			$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+pc3)$	1.01	0.09	8
			$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+pc3)$	1.62	0.07	12
	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc3+vpc)$		1.84	0.06	8	
	$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+vpc)$		0.00	0.55	12	
	Clear cut	$\lambda(L)\gamma(.)\omega(.)p(pc1+pc3+vpc)$	0.37	0.45	12	
		Patch	$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	0.00	0.40	12
			$\lambda(L)\gamma(.)\omega(.)p(pc1+vpc)$	0.33	0.34	11
		Shelterwood	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	0.00	0.52	8
			$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+pc3+vpc)$	0.53	0.40	9
		Clear cut	$\lambda(L)\gamma(.)\omega(.)p(pc2+vpc)$	0.00	0.46	11
	$\lambda(L)\gamma(.)\omega(.)p(pc2+pc3+vpc)$		1.74	0.19	12	
	Eastern red	Patch	$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	1.75	0.19	12
			$\lambda(L)\gamma(.)\omega(.)p(pc1+pc3)$	0.00	0.24	11
		Shelterwood	$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+pc3)$	0.16	0.22	12
			$\lambda(L)\gamma(.)\omega(.)p(pc3)$	0.56	0.18	10
		Clear cut	$\lambda(L)\gamma(.)\omega(.)p(pc2+pc3)$	0.58	0.18	11
			$\lambda(.)\gamma(.)\omega(.)p(pc1)$	0.00	0.11	6
	Hoary	Patch	$\lambda(.)\gamma(.)\omega(.)p(.)$	0.64	0.08	5
			$\lambda(.)\gamma(.)\omega(.)p(pc1+pc3)$	1.00	0.07	7
		Shelterwood	$\lambda(L)\gamma(.)\omega(.)p(pc1)$	1.15	0.06	10
			$\lambda(.)\gamma(.)\omega(.)p(pc3)$	1.33	0.06	6
		Clear cut	$\lambda(L)\gamma(.)\omega(.)p(.)$	1.50	0.05	9
			$\lambda(.)\gamma(.)\omega(.)p(pc1+vpc)$	1.75	0.05	7
	Indiana/little brown	Patch	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2)$	1.99	0.04	7
			$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+pc3)$	0.00	0.70	12
		Shelterwood	$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+pc3+vpc)$	1.99	0.26	13
$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2)$			0.00	0.32	11	
Clear cut		$\lambda(L)\gamma(.)\omega(.)p(pc2)$	1.67	0.14	10	
		$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	1.83	0.13	12	
Shelterwood	$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+pc3)$	2.00	0.12	12		
	$\lambda(.)\gamma(.)\omega(.)p(pc2)$	0.00	0.15	6		
	$\lambda(L)\gamma(.)\omega(.)p(pc2)$	0.33	0.13	10		
	$\lambda(.)\gamma(.)\omega(.)p(pc2+pc3)$	1.44	0.08	7		
	$\lambda(L)\gamma(.)\omega(.)p(pc2+vpc)$	1.51	0.07	11		
	$\lambda(.)\gamma(.)\omega(.)p(pc2+vpc)$	1.55	0.07	7		
Clear cut	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2)$	1.70	0.07	7		
	$\lambda(L)\gamma(.)\omega(.)p(pc2+pc3)$	1.72	0.07	11		

TABLE 4.—Continued

Year	Species	Harvest	Model	$\Delta AIC^a$	$\Omega^b$	$K^c$	
2014	Northern long-eared	Clear cut	$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+pc3+vpc)$	0.00	0.29	8	
			$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc3+vpc)$	0.97	0.18	7	
			$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+pc2+pc3+vpc)$	1.62	0.13	9	
		Patch	$\lambda(.)\gamma(.)\omega(.)\hat{p}(.)$	0.00	0.1342	5	
			$\lambda(L)\gamma(.)\omega(.)\hat{p}(.)$	0.22	0.1205	9	
			$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc3)$	1.56	0.0614	6	
			$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc2)$	1.81	0.0542	6	
			$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1)$	1.83	0.0539	6	
			$\lambda(L)\gamma(.)\omega(.)\hat{p}(pc3)$	1.85	0.0531	10	
		Shelterwood	$\lambda(L)\gamma(.)\omega(.)\hat{p}(pc2)$	1.94	0.0508	10	
			$\lambda(.)\gamma(.)\omega(.)\hat{p}(vpc)$	2.00	0.0494	6	
			Clear cut	$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+pc3+vpc)$	0.00	0.45	8
	$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+pc2+pc3+vpc)$			0.35	0.38	9	
	Patch		$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+pc2+vpc)$	0.00	0.54	8	
			$\lambda(L)\gamma(.)\omega(.)\hat{p}(pc1+pc2+pc3+vpc)$	0.00	0.43	13	
	Tri-colored	Shelterwood	$\lambda(L)\gamma(.)\omega(.)\hat{p}(pc1+pc2+pc3)$	0.17	0.40	12	
			$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+pc2+pc3+vpc)$	0.00	0.56	9	
		Clear cut	$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+pc2+vpc)$	0.96	0.34	8	
			$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+pc2+pc3+vpc)$	0.00	0.58	9	
		Patch	$\lambda(L)\gamma(.)\omega(.)\hat{p}(pc1+pc2+vpc)$	0.00	0.53	12	
			$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+pc2+vpc)$	0.20	0.47	8	
		Shelterwood	$\lambda(L)\gamma(.)\omega(.)\hat{p}(pc1+vpc)$	0.00	0.98	11	
			$\lambda(.)\gamma(.)\omega(.)\hat{p}(vpc)$	0.00	0.47	6	
		Big brown	Clear cut	$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+vpc)$	1.69	0.20	7
				$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc2+vpc)$	1.92	0.18	7
				$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc2+vpc)$	0.00	0.63	7
			Patch	$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+pc2+vpc)$	1.90	0.25	8
	$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+pc2)$			0.00	0.62	7	
	$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+pc2+vpc)$			1.96	0.23	8	
	Eastern red	Clear cut	$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc2+vpc)$	0.00	0.89	7	
			$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc2+vpc)$	0.00	0.45	7	
		Patch	$\lambda(.)\gamma(.)\omega(.)\hat{p}(vpc)$	1.65	0.20	6	
			$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+pc2+vpc)$	1.66	0.20	8	
		Shelterwood	$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+pc2)$	0.00	0.27	7	
			$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+vpc)$	0.38	0.23	7	
	Hoary	Clear cut	$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1)$	0.40	0.22	6	
			$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+pc2+vpc)$	0.63	0.20	8	
			$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+pc2+vpc)$	0.00	0.75	8	
		Patch	$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+pc2+vpc)$	0.00	0.46	8	
			$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+pc2)$	0.02	0.46	7	
		Shelterwood	$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+vpc)$	0.00	0.59	7	
			$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+pc2+vpc)$	1.92	0.23	8	
Indiana/little brown		Clear cut	$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+vpc)$	0.00	0.27	7	
			$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+pc2)$	0.49	0.21	7	
		Patch	$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc2+vpc)$	1.89	0.11	7	
			$\lambda(L)\gamma(.)\omega(.)\hat{p}(pc1+vpc)$	1.92	0.10	11	
		Shelterwood	$\lambda(.)\gamma(.)\omega(.)\hat{p}(pc1+pc2+vpc)$	2.00	0.10	8	

TABLE 4.—Continued

Year	Species	Harvest	Model	$\Delta AIC^a$	$\Omega^b$	$K^c$
	Northern long-eared	Patch	$\lambda(.)\gamma(.)\omega(.)p(pc2+vpc)$	0.00	0.28	7
			$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2)$	0.37	0.24	7
			$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	0.45	0.23	8
		Shelterwood	$\lambda(.)\gamma(.)\omega(.)p(pc2)$	1.27	0.15	6
			$\lambda(.)\gamma(.)\omega(.)p(pc1+vpc)$	0.00	0.25	7
			$\lambda(.)\gamma(.)\omega(.)p(pc1)$	1.31	0.13	6
	Clear cut	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	1.72	0.11	8	
		$\lambda(L)\gamma(.)\omega(.)p(pc1)$	1.77	0.10	10	
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2)$	1.36	0.31	7	
	Tri-colored	Patch	$\lambda(.)\gamma(.)\omega(.)p(pc2)$	0.00	0.28	6
			$\lambda(.)\gamma(.)\omega(.)p(.)$	0.50	0.21	5
			$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2)$	1.55	0.13	7
Shelterwood		$\lambda(.)\gamma(.)\omega(.)p(pc2+vpc)$	1.98	0.10	7	
		$\lambda(.)\gamma(.)\omega(.)p(pc2+vpc)$	0.00	0.43	7	
		$\lambda(.)\gamma(.)\omega(.)p(pc1+vpc)$	1.84	0.17	7	
Clear cut		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	0.00	0.59	8	
		$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	1.58	0.27	12	

<sup>a</sup> Difference between model's Akaike's Information Criterion and the lowest AIC value

<sup>b</sup> AIC model weight

<sup>c</sup> Number of parameters estimated by the model

Activity of northern long-eared bats was best modeled using detector location for patch cuts in 2013 and for shelterwood preparatory cuts in 2014, suggesting activity did not differ across clear cuts. (Table 4). In patch cuts activity was highest at harvest and forest edges (Fig. 4). Northern long-eared bat activity did not differ across locations in shelterwood preparatory cuts. Tri-colored bat activity was best modeled using detector location for patch cuts in 2013 (Table 4). Activity was highest at harvest edge and harvest center in patch cuts (Fig. 4).

## DISCUSSION

### TREATMENT COMPARISON

Although we expected larger-bodied bats would show greater activity relative to harvest treatments than control treatments and smaller-bodied bats would use control treatments more than harvest treatments, we did not find many differences in activity among treatments for either bat group. The greater activity of *Lasiurus* species in harvest stands supports our hypothesis and is in agreement with findings of previous studies (Owen *et al.*, 2004; Morris *et al.*, 2010; Titchenell *et al.*, 2011). Menzel *et al.* (2002) found greater *Lasiurus* activity in small gaps compared to large gaps, which is consistent with our results of greatest eastern red bat activity in patch cuts. This suggests eastern red bats may prefer smaller scale disturbance events over larger clear cuts. The similarity of big brown bat activity across all treatments did not support our initial hypothesis but was in agreement with others (Owen *et al.*, 2004; Morris *et al.*, 2010). The trend we noted of greater big brown bat activity in and around clear cuts was similar to others (Menzel *et al.*, 2002), but the general similarity in activity between

HARVEST-FOREST GRADIENT COMPARISON: LARGE-BODIED BATS

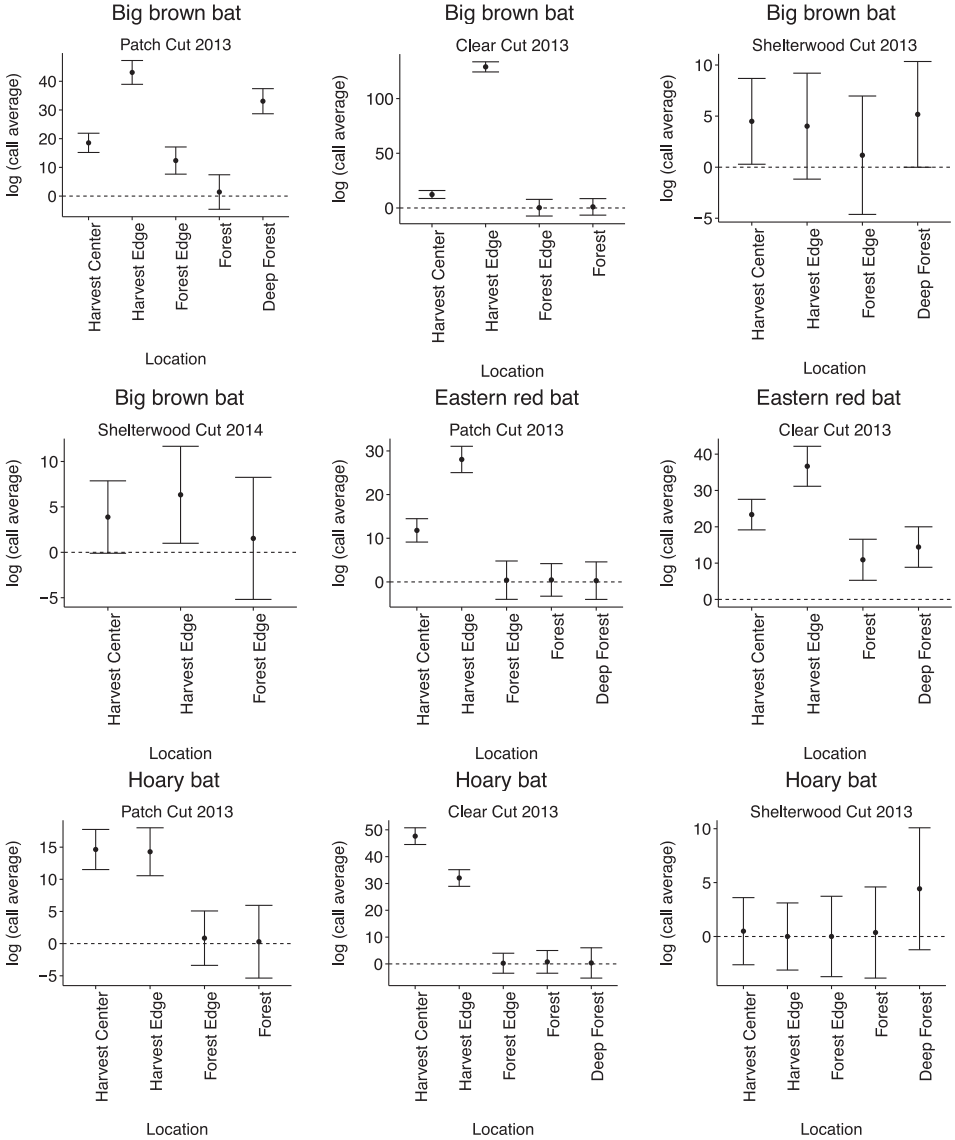


FIG. 3.—Log call averages of big brown bat (*Eptesicus fuscus*), eastern red bat (*Lasiurus borealis*), hoary bat (*Lasiurus cinereus*) at locations across the harvest-forest gradient in harvest treatments on Morgan-Monroe and Yellowwood State Forests, Indiana, during May–July 2013 and 2014, calculated using the most parsimonious Dail and Madsen (2011) *N*-mixture abundance model

## HARVEST-FOREST GRADIENT COMPARISON: SMALL-BODIED BATS

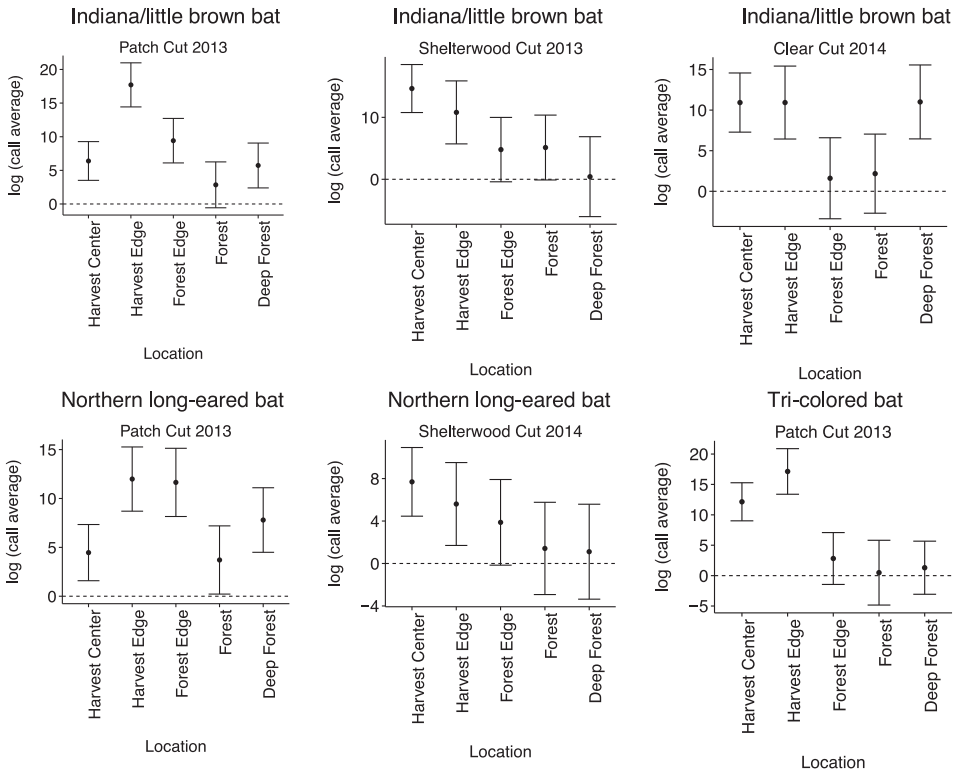


FIG. 4.—Log call averages of Indiana/little brown bat (*Myotis sodalis/lucifugus*), northern long-eared bat (*Myotis septentrionalis*), and tri-colored bat (*Perimyotis subflavus*) at locations across the harvest-forest gradient in harvest treatments on Morgan-Monroe and Yellowwood State Forests, Indiana, during May–July 2013 and 2014, calculated using the most parsimonious Dail and Madsen (2011)  $N$ -mixture abundance model

treatments suggests foraging flexibility of this species despite its morphological characteristics (Brigham, 1991).

Though *Myotis* species are considered forest-dependent (Sasse and Pekins, 1996; Foster and Kurta, 1999; Jung *et al.*, 1999) and greater *Myotis* species detection has been documented in areas of closed canopy over open canopy (Ford *et al.*, 2005) or in stand interiors over open and thinned stands (Morris *et al.*, 2010), we did not find differences in activity across treatments for these species, which was similar to other study findings (Krusic *et al.*, 1996; Patriquin and Barclay, 2003; Owen *et al.*, 2004; Titchenell *et al.*, 2011). Contrary to Patriquin and Barclay (2003), we did not find lower northern long-eared bat activity in clear cuts; however, the clear cuts in our study were approximately 5 y post-harvest, with tall vegetation that could be used for gleaned insects. It is also important to note that while timber harvests were spread across our study site, the harvests represent a very minimal portion of both state forests, which provide plentiful roosting habitat for these species. Additionally, this analysis represents a broad scale comparison as calls collected within and

adjacent to treatments were pooled, which could have masked fine scale differences in activity.

Tri-colored bats are small-bodied, but similarly to other studies, we did not find a preference for cluttered habitats for this species (Ford *et al.*, 2005; Loeb and O'Keefe, 2006). Studies have also noted that tri-colored bats are active across both open and cluttered habitats (Menzel *et al.*, 2002; Menzel *et al.*, 2005; Titchenell *et al.*, 2011), but the lack of differences in activity in our study could also possibly be attributed to the low abundance of this species on our study site.

#### HARVEST-FOREST GRADIENT COMPARISON

We predicted bat activity would be greatest along harvest edges for larger-bodied species and in the forest interior for smaller-bodied species but found activity was high along harvest edges for both bat groups. Activity of eastern red bats and big brown bats supported this prediction, but hoary bats showed higher activity levels at harvest center. Morris *et al.* (2010) also found greater big brown and eastern red bat activity along edges than in harvest or forest interiors.

Indiana/little brown bat activity was highest 100 m into adjacent forests of clear cuts, supporting our hypothesis, but was also highest at the harvest edge of patch cuts and shelterwood cuts. Activity of northern long-eared bats partially supported our hypothesis, with greatest activity in patch cuts at forest edge, but also at the harvest edge. This species also did not show a difference in activity levels among locations across clear cuts, which did not agree with our predictions. The activity of *Myotis* species at edges was consistent with results from others (Hogberg *et al.*, 2002; Patriquin and Barclay, 2003), which also noted greater activity of northern long-eared and little brown bats at edges of harvests, but was inconsistent with data suggesting *Myotis* species avoid edges (Morris *et al.*, 2010). Tri-colored bat activity also did not follow our predictions, showing greatest activity in patch cuts at harvest edge and harvest center, but was consistent with the results of Morris *et al.*, 2010, who found high tri-colored bat activity along edges.

The trend of greater bat activity at edges is similar to results from previous studies showing preferences of bats for edge habitats (Grindal and Brigham, 1999; Krusic *et al.*, 1996; Morris *et al.*, 2010; Menzel *et al.*, 2002; Patriquin and Barclay, 2003; Jantzen and Fenton, 2013). Although we did not quantify insect abundance in our study, others found correlation between insect availability and bat activity, which may explain the observed activity in our study. Studies have found greater insect abundance and diversity along forest edges than in neighboring forest interiors or open areas (Verboom and Huitema, 1997; Voller, 1998; Grindal, 1996; Grindal and Brigham, 1999), which provides support for the high bat activity levels we found at the harvest-forest interface. Studies have also found higher insect densities in cluttered versus uncluttered habitats (Kalcounis and Brigham, 1995; Grindal, 1996) and at edges of clear cuts or in intact forest compared with centers of clear cuts (Burford *et al.*, 1999), but others found higher insect abundance in small openings (Tibbels and Kurta, 2003) or clear cuts (Lunde and Harestad, 1986), which may explain discrepancies among species activity in our study. Finally, hard edges may offer protection from wind, predators, and act as orientation landmarks (Verboom and Spoelstra, 1999).

#### MANAGEMENT IMPLICATIONS

Four of the six species in our study did not differ in usage of harvest and control treatments, suggesting forest management that employs an array of silvicultural treatments

across a forested landscape provides suitable bat habitat for a variety of species. The largest harvest treatments on our site were 4 ha in size, suggesting smaller scale harvest openings are beneficial to both small and large-bodied bats. Our results also suggest eastern red bats and hoary bats could particularly benefit from the creation of harvest openings within contiguous forest stands. Maintaining forest buffers surrounding harvests could serve as important habitat since bats in our study were active in forests adjacent to harvest. Small and large-bodied species were active on edges of harvests, so providing edge habitat within a forested matrix may be suitable for a variety of species. Probability of detection was imperfect ( $P < 1$ ) for all species and differed among species in our study illustrating the importance of considering probability of detection and factors that affect detection during acoustic surveys.

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