

A COMPARISON OF BAT ACTIVITY IN A MANAGED CENTRAL HARDWOOD FOREST

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ABSTRACT

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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 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 2013 and 2014. We used Wildlife Acoustics Song Meter SM2BAT+ detectors to survey bats in relation to four treatment types: clear cut, patch cut, shelterwood 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. 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. All species were active in forests adjacent to harvests. Variables affecting detection probability differed among species and included air temperature, relative humidity, barometric pressure, dew point, cloud cover, wind speed, and forest clutter. 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 bat activity to maximize bat usage of forests.

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INTRODUCTION

Approximately 75 percent 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, yet forests are scarce and fragmented on much of the landscape (Smith et al. 2001). Silvicultural practices that alter remaining forests must be well understood in regards 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).

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 alter forest structure and number of available roosts (Jones et al. 2000, Loeb and Waldrop 2008, Adams et al. 2009).

Because species' morphological features influence selection of foraging habitat, bat activity differs by species in response to silvicultural method and harvest size (Humes et al. 1999, Menzel et al. 2002, Patriquin and Barclay 2003). Bats vary in terms of morphology and echolocation call characteristics; these traits affect how bats forage in different habitats (Aldridge and Rautenbach 1987, Norberg and Rayner 1987). 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; thus, 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 are typically categorized as clutter-adapted due to their ability to forage within forest clutter where they glean prey from vegetation surfaces in addition to capturing prey in flight (Norberg and Rayner 1987).

Previous work has shown that bats are 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 may vary by species due to differences in morphology and echolocation call structure. In particular, higher activity in cut areas has been demonstrated for big brown bats (*Eptesicus fuscus*), eastern red bats (*Lasiurus borealis*), hoary bats (*Lasiurus cinereus*), and tri-colored bats (*Perimyotis subflavus*) in the coastal plain of the Carolinas (Menzel et al. 2002, Morris et al. 2010). Higher overall bat activity has been documented in shelterwood harvests (Titchenell et al. 2011) and group selection harvests compared to unharvested forest, but timber harvest area can affect bat species differently (Menzel et al. 2002). Additionally, Patriquin and Barclay (2003) found an increase in overall bat activity in clear cuts compared to unharvested forest, but also found that clear cuts negatively affected northern long-eared bat activity (*Myotis septentrionalis*). Clearly a better 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), potentially because these boundaries act as windbreaks that collect 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 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), however a study in North Carolina found northern long-eared and southeastern bats (*Myotis austroriparius*) foraging in stand interiors and avoiding edges (Morris et al. 2010). 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) termed this change in activity across a hard edge, Depth of Edge Influence (DEI) and examined bat activity along a continuum across the agriculture-forest interface in Ontario, Canada. Hoary bats, big brown/silver-haired bats (*Lasionycteris noctivagans*), northern long-eared bats, and little brown bats showed maximum activity along the edge, but similar studies in a managed forest landscape are lacking (but see Menzel et al. 2002 and Morris et al. 2010).

Edge habitats represent the interface between open and cluttered areas, potentially serving as habitat for both large and small-bodied bats. Bat activity inside the boundaries of multiple timber harvests strategies has been compared (Patriquin and Barclay 2003, Morris et al.

2010, Dodd et al. 2012), but comparison of activity in forests adjacent to timber harvests to activity in intact forest, to our knowledge, has not been made (but see O’Keefe et al. 2013). Results from this comparison could provide information on whether harvests have a positive or negative effect on activity levels for local forest interior species.

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 while accounting for 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 because bats are able to fly great distances in a short time frame. Comparing bat call abundance using N -mixture models for open populations accounts for imperfect detection and may be more suitable for studies that cannot ensure population closure between sites (Dail and Madsen 2011). Understanding bat detection probability is imperative as detectability can vary based on various factors such as season, climate, habitat, species, and forest clutter influence (Kaiser and O’Keefe 2015, O’Keefe et al. 2014, Bender et al. 2015). Determining the effects of these variables on detection probability for each species is important for understanding variation in detection across study treatments.

We conducted this study on Morgan-Monroe and Yellowwood State Forests, Indiana. Our study was concentrated on several silvicultural treatments 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; 2) compare bat activity among forests adjacent to timber harvests and in intact control forest; 3) compare bat activity at locations across the harvest-forest gradient; and

4) to identify weather and vegetation variables affecting detectability for each species. We expected that 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 that 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; 2) bat activity would not differ among harvest-adjacent forests and control forests due to similarity in forest structure; 3) 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; and 4) larger-bodied bat detectability would be negatively related to forest clutter and smaller-bodied bat detectability would be positively related to forest clutter, and detection probabilities would be related to temperature, barometric pressure, relative humidity, and vegetation clutter because these factors affect call attenuation.

STUDY AREA

This study was part of the Indiana Department of Natural Resources Division of Forestry's Hardwood Ecosystems Experiment (HEE), a 100-year experiment (Kalb and Mycroft 2013). The HEE is located on Morgan-Monroe and Yellowwood State Forests 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 1800s (Parker and Ruffner 2004), but forests regenerated after acquired by the state during the early to mid-1900s (Carman 2013).

The 3,603-ha HEE study site consisted of nine management units, each containing an experimental core and a surrounding buffer area. Management units received one of three types

of forest management: even-aged, uneven-aged, and control (uneven aged units: 1,088-ha; even-aged units: 1,294-ha; control units: 1,221-ha). Uneven-aged units 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. Trees with basal areas of 16.1-22.9m²/ha were targeted for single-tree selection harvest. Even-aged units contained two 4-ha clear cuts and two 4-ha shelterwood cuts. Clear cuts were established by coppicing oak, hickory, ash, tulip poplar, and black walnut trees 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 harvests over a 10 to 20-year 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 shelterwood stage. Control units 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 were managed using group selection harvests of sizes between 0.4-ha and 1.2-ha occurring at least 100 m from experimental cores and using single-tree selection harvest to maintain stocking levels between 70 and 75 percent (Kalb and Mycroft 2013).

METHODS

Field Sampling

From May to July, 2013 and 2014, we used acoustic detectors to sample 12 control treatments and 24 harvest treatments (12 patch cuts, 6 clear cuts, and 6 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, USA). We simultaneously deployed five detectors per treatment, placing detectors in five locations along a 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 WAV format from sunset to sunrise for three consecutive nights per location (sampling rate: 192 kHz, gain: 36 dB, dig HPF: fs/12, dig LPF: Off, trigger level: 18 SNR, trigger win: 2.0 s, div ratio: 16). 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 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, IN and KINMARTI13, Martinsville, IN; 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, USA). 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: 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 percent 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 with a negative binomial distribution to estimate call abundance (λ) and detection probability (p) (Dail and Madsen 2011). 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 because 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. The model can also estimate apparent survival and recruitment, which were not used for this study. We implemented the model 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. A negative binomial distribution best fit our data, though we tested normal, Poisson, and zero-inflated distributions. 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).

We used the Dail-Madsen model to compare activity at three scales corresponding to our study objectives, which we have titled from most broad to most fine scale: Treatment Comparison, Harvest Periphery Comparison, and Harvest-Forest Gradient Comparison. Sixteen candidate models were evaluated for 2013 data and eight candidate models were evaluated for modeling 2014 activity. Models with lowest AIC value and models with $\Delta AIC \leq 2$ of the lowest model were considered equally plausible (Tables 1-3).

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). Forest management treatment type was used as a categorical variable for comparison among treatments

in the Treatment Comparison Model and the Harvest Peripheries Model. Detector location was used as a categorical variable in the Harvest-Forest Gradient Model for comparison among detector locations.

For the Treatment Comparison, we combined call counts for the five detector locations per treatment to reflect bat use of areas within and surrounding treatments. This decision was based on three considerations: 1) bat foraging ranges are larger than our harvests so incorporating the surrounding forest in the analysis encompasses a larger portion of a bat's range, 2) these harvests are dominated by early successional vegetation making them more structurally complex than a fresh harvest, thus differences in activity are more subtle from the harvest interior to the surrounding forest, so clearer inferences can be made using a more coarse focus, and 3) differences in species' foraging habitats could bias our interpretation of activity if we ignored bat activity in forests surrounding harvests. For the Harvest Peripheries model, we used calls collected by the three detectors in forests adjacent to harvests and all calls collected in controls. For the Harvest-Forest Gradient Model, we used all calls collected in harvests and adjacent forests, but did not use calls collected in controls.

RESULTS

We sampled a total of 180 sites from 12 control treatments and 24 harvest treatments (12 patch cuts, 6 clear cuts, and 6 shelterwood cuts) over 108 nights. In 2013 we recorded 24,750 acoustic files and classified 7,083 call files to species. In 2014 we recorded 18,092 acoustic files and classified 5,656 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 4). 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 4). The vegetation PCA resulted in a single principal component that explained the number of trees per plot, distance to nearest tree, and percent canopy closure for 2013 and 2014 (Table 5).

Treatment Comparison

Large-Bodied Bats— Activity varied for species and by years (Figure 1). For big brown bats, there were two plausible models predicting activity. Harvest type was not included in best models, indicating activity in and around harvests was similar across treatment types (Table 1). Eastern red bat activity was modeled using all weather, vegetation, and harvest treatment variables in both seasons. Activity was higher in patch cuts than in control treatments in both seasons and was higher in clear cuts and shelterwood cuts than in control treatments in 2014 (Table 1, Figure 1). Hoary bats were modeled using all weather, vegetation, and harvest treatment covariates in both seasons. Shelterwood 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 1, Figure 1).

Small-Bodied Bats— Indiana/little brown bat activity was modeled using the first weather principal component for both seasons, with several equally plausible models (Table 1). Harvest treatment was not included in any top models. Northern long-eared bat activity was modeled using all weather covariates in 2013 and using all weather, vegetation, and harvest

covariates in 2014 (Table 1). Though harvest was included in top models in 2014, confidence intervals overlapped zero suggesting activity in and around harvests did not differ among treatments (Figure 2). Tri-colored bat activity was modeled using all weather and vegetation covariates for both seasons and harvest was not included in any top models (Table 1).

Harvest Peripheries Comparison

Large-bodied Bats— Best models for big brown bat activity used all weather and vegetation covariates in both seasons (Table 2). Harvest treatment was only included to model 2014 big brown bat activity, but activity did not differ among treatments in either year (Table 2, Figure 3). Eastern red bats were best modeled using all weather and vegetation covariates in both years with harvest treatment included in 2014 models (Table 2). In 2014, eastern red bat activity was higher in forests adjacent to shelterwoods than in controls (Figure 3). Hoary bat activity was best modeled using all weather and vegetation covariates in 2013 and using vegetation covariates and principal component two in 2014 (Tables 2 and 4). While harvest treatment was included in best models for both seasons, hoary bat activity did not differ among treatments (Figure 3).

Small-bodied Bats— Best models for Indiana/little brown bat activity included all weather and vegetation covariates in both seasons and harvest treatments in 2014 (Table 2). Indiana/little brown bat activity did not differ among treatments (Figure 4). Northern long-eared bats were best modeled using harvest treatments, vegetation covariates, and principal components one and two in both seasons (Tables 2 and 4). Activity was highest in forests adjacent to clear cuts, shelterwood cuts, and in control treatments in 2013. In 2014, activity was highest in forests adjacent to clear cuts and patch cuts (Figure 4). Tri-colored bat activity was

best modeled using all weather and vegetation covariates in both years and 2013 models included harvest treatments (Table 2). Activity did not differ among treatments in either year (Figure 4).

Harvest-Forest Gradient Comparison

Large-bodied Bats— 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 3). 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 (Figure 5). 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 3). Activity was highest at harvest edges and harvest centers of patch cuts and clear cuts (Figure 5).

Best models for hoary bat activity included detector location for all harvest types in 2013 (Table 3). Hoary bat activity was highest at harvest center in clear cuts followed by harvest edge (Figure 5). In patch cuts activity was equally high at harvest center and harvest edge. Hoary bat activity did not differ among detector locations in shelterwood cuts.

Small-bodied Bats— Indiana/little brown bat activity was best modeled using detector location for patch cuts and shelterwood cuts in 2013 and for clear cuts in 2014 (Table 3). Activity was highest at harvest edge in patch cuts and at harvest center in shelterwood cuts (Figure 6). In clear cuts, Indiana/little brown bat activity was highest at harvest center, harvest edge, and 100 m into adjacent forest.

Activity of northern long-eared bats was best modeled using detector location for patch cuts in 2013 and for shelterwood cuts in 2014, suggesting activity did not differ across clear cuts. (Table 3). In patch cuts, activity was highest at harvest and forest edges (Figure 6). Northern long-eared bat activity did not differ across locations in shelterwood cuts.

Tri-colored bat activity was best modeled using detector location for patch cuts in 2013 (Table 3). Activity was highest at harvest edge and harvest center in patch cuts (Figure 6).

Detection

Large-bodied Bats— Detection varied for species and by years (Tables 1 and 6). All weather and vegetation covariates were included in big brown bat models, but temperature and clutter variables had the largest effects on detection (Table 6). Big brown bat detection probability was positively influenced by temperature and dew point (Figure 7) and temperature and cloud cover (Figure 12), but was negatively related to clutter (Figures 10 and 13).

Eastern red bat detectability was related to all weather and vegetation covariates, but temperature and barometric pressure variables had the greatest influence on detection (Tables 1 and 6). In 2013 temperature, dew point (Figure 7), and barometric pressure were positively related to detection (Figure 8) and cloud cover and wind speed were negatively related to detection (Figure 8). In 2014, temperature was negatively related to detection and cloud cover was positively related to detection (Figure 12).

Hoary bat detection was related to all weather and vegetation variables, but was more highly influenced by temperature and clutter (Tables 1 and 6). Detection was positively related to temperature (Figures 7 and 12) and dew point (Figure 7) and was negatively related to clutter (Figure 10) and cloud cover (Figure 12).

Small-Bodied Bats— Models for Indiana/little brown bat detection included all weather and vegetation variables in both seasons (Tables 1 and 6). Detection was negatively related to relative humidity (Figure 9) and temperature and dew point (Figure 11) and was positively related to wind speed (Figure 9).

Northern long-eared bat detection was related to all weather variables in 2013 and all weather and vegetation variables in 2014 (Tables 1 and 6). Detection was negatively related to temperature and dew point in both seasons (Figures 7 and 11) and clutter (Figure 13) and was positively related to cloud cover (Figure 12).

Tri-colored bat detection probability was related to all weather and vegetation variables (Tables 1 and 6). Detection was negatively related to clutter in both seasons (Figures 10 and 13) and cloud cover (Figure 12) and was positively related to temperature (Figure 12).

DISCUSSION

Treatment Comparison

We expected that larger-bodied bats would show greater activity relative to harvest treatments than in control treatments and that smaller-bodied bats would use control treatments more than harvest treatments. 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. 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 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 northern long-eared bat or Indiana/little brown bat activity was 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 (Erickson and West 1996, 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 five years post-harvest, with tall vegetation that could be used for gleaning 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. It is also important to note that 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. Species with small home ranges, like the northern long-eared bat, may not show activity level differences at this scale of analysis (Sasse and Pekins 1996, Broders et al. 2006).

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 Peripheries Comparison

We predicted bat activity would not differ among forests adjacent to timber harvests and in control treatments. In contrast to our predictions, activity levels differed among forests adjacent to harvests and control treatments for eastern red bats and northern long-eared bats. Eastern red bats were more active in forests adjacent to shelterwood cuts than in control treatments, which is supported by findings of Titchenell et al. (2011), which noted higher eastern red bat activity in shelterwood cuts than intact forest. Northern long-eared bats were active in all treatments, but showed greatest activity in forests adjacent to clear cuts. *Myotis* species are often considered forest interior species (Patriquin and Barclay 2003, Ford et al. 2005), but our results suggest proximity to harvest may be beneficial in addition to contiguous intact forest for these species.

Though forest structure was similar, bats showed greater activity in forests adjacent to harvests than in control treatments, suggesting forests bordering timber harvests offer alternate benefits to intact contiguous forest. Forest on harvest peripheries may provide closer proximity of roost sites to harvest areas, different insect communities or abundance than open areas (Loeb and O'Keefe 2006), or greater solar radiation for roosts on edges (Barclay and Kurta 2007, Carter and Menzel 2007). Alternatively, bats could have been detected above the canopy while commuting to and from harvests, as hoary bats and big brown bats have been found to be more active above the canopy (Menzel et al. 2005).

Harvest-Forest Gradient Comparison

We also predicted bat activity would be greatest along harvest edges for larger-bodied species and in the forest interior for smaller-bodied species. 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 others (Morris et al. 2010).

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).

Detection

The detection of bat echolocation calls can be influenced by factors that alter bat behavior or affect detection of bat calls by acoustic equipment. We hypothesized detection probability would differ by bat species and that it would be influenced by temperature, barometric pressure, relative humidity, and forest clutter measurements. We found detection probability was related to temperature, dew point, barometric pressure, cloud cover, relative humidity, and forest clutter measurements.

Positive Effects— Temperature positively influenced detection for big brown, hoary, and eastern red bats, similar to other study findings (Yates and Muzika 2006, O’Keefe 2015) and to studies that noted higher bat activity with higher temperature (Erickson and West 2002, Schirmacher et al. 2007, Weller and Baldwin 2012). Barometric pressure positively influenced detection probability for eastern red bats, which is consistent with studies noting higher bat activity during high barometric pressure conditions (Kerns et al. 2005, Arnett et al. 2008, Wolcott and Vulinec 2012). Northern long-eared bats were the only species to show a positive relationship between detection and relative humidity, findings consistent with results from studies showing increasing activity of little brown bats (Lacki 1984) and Virginia big-eared bats

(Adam et al. 1994) with increasing relative humidity, which could potentially prevent water loss during flight.

Negative Effects— Northern long-eared and Indiana/little brown bats showed greater detection at lower temperatures, which is the same trend noted by Amelon (2007) in northern long-eared bat detection in Missouri and Hein et al. (2009) in *Nycticeius humeralis* detection in South Carolina, but contrasts others (Kaiser and O’Keefe 2015). Sound attenuation increases at higher temperatures (Denny 2004), which may result in poor detection of lower intensities calls like those produced by bats that forage in clutter (Waters and Jones 1995). Eastern red bats showed a conflicting influence of temperature and dew point on detection across years. Detection was negatively related to forest clutter for most species, which is similar to findings of others (Starbuck 2013, O’Keefe et al. 2014). We did not find similar results to Kaiser and O’Keefe (2015) who noted greater detection of Indiana bats in areas of higher clutter, perhaps because this species was not abundant on our study site (Sheets et al. 2013).

Cloud cover negatively influenced detection of big brown, hoary, and tri-colored bats, and showed conflicting results between seasons for eastern red bats. These results agree with studies reporting conflicting results regarding effects of cloud cover on bat activity (Elangovan and Marimuthu 2001, Russo and Jones 2003) or no relationship between cloud cover and activity (Negraeff and Brigham 1995). Indiana/little brown and northern long-eared bats showed a negative relationship between detection and relative humidity levels, which can increase attenuation of echolocation calls (Griffin 1971, Livengood 2003). These results are in contrast to findings of Starbuck (2013).

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 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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FIGURES

Treatment Comparison: Large-bodied Bats

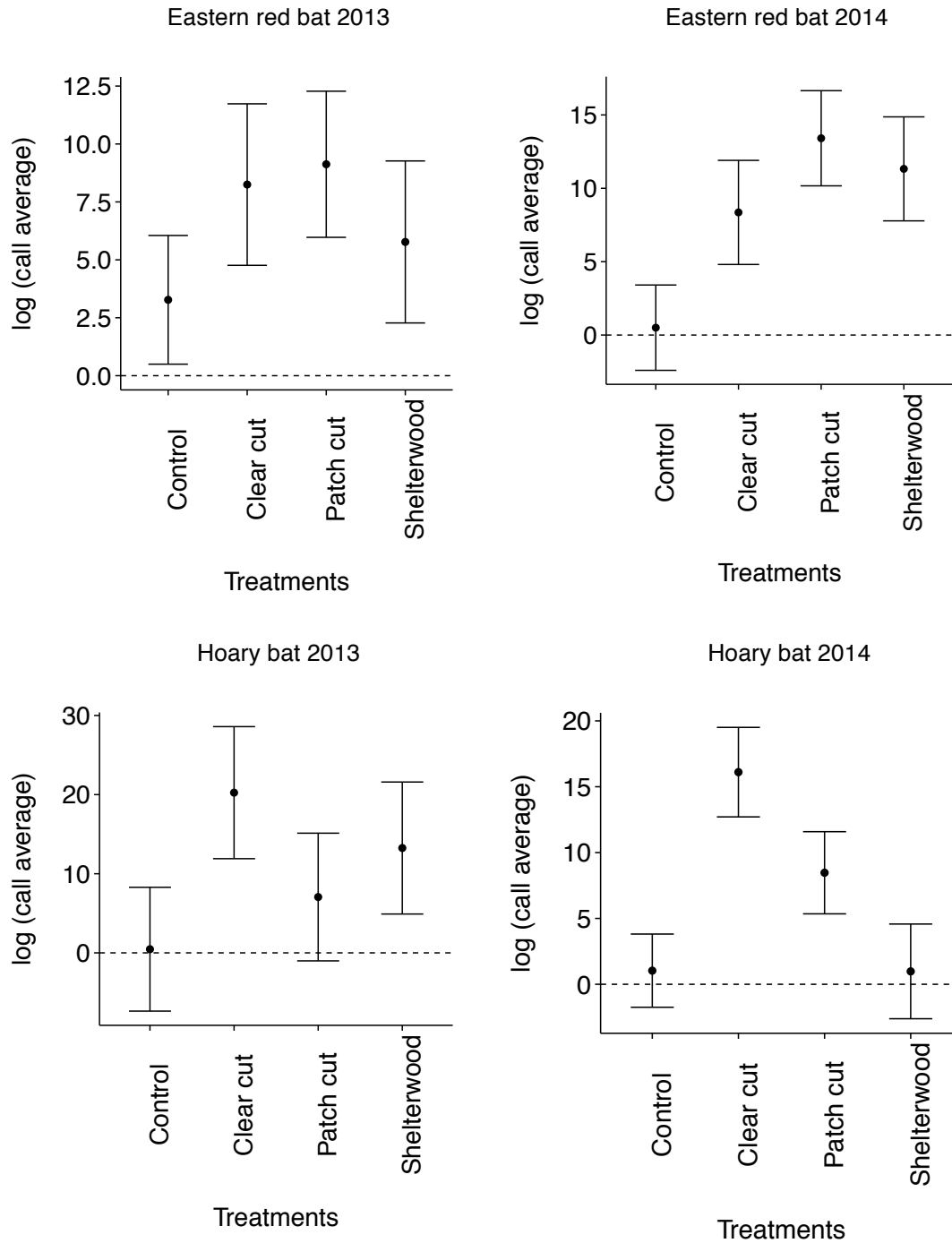


Figure 1. Log call average per harvest treatment of eastern red bats and hoary bats on Morgan-Monroe and Yellowwood State Forests, IN during May-July, 2013 and 2014 calculated using Dail and Madsen 2011 *N*-mixture abundance model.

Treatment Comparison: Small-bodied Bats

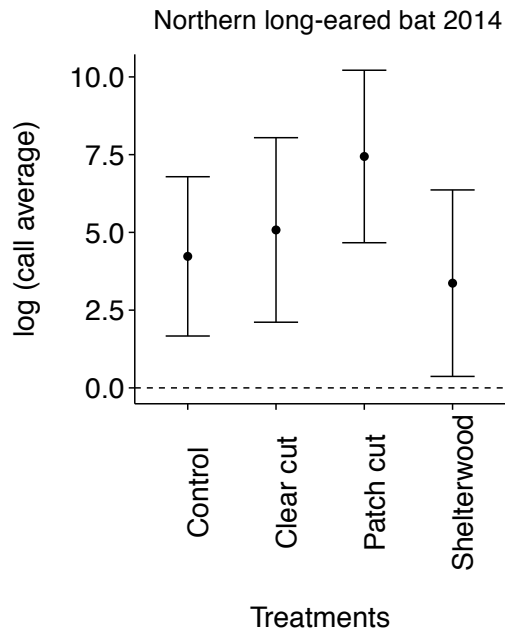


Figure 2. Log call average per harvest treatment of northern long-eared bats on Morgan-Monroe and Yellowwood State Forests, IN during May-July, 2014 calculated using Dail and Madsen 2011 *N*-mixture abundance model.

Harvest Peripheries Comparison: Large-bodied Bats

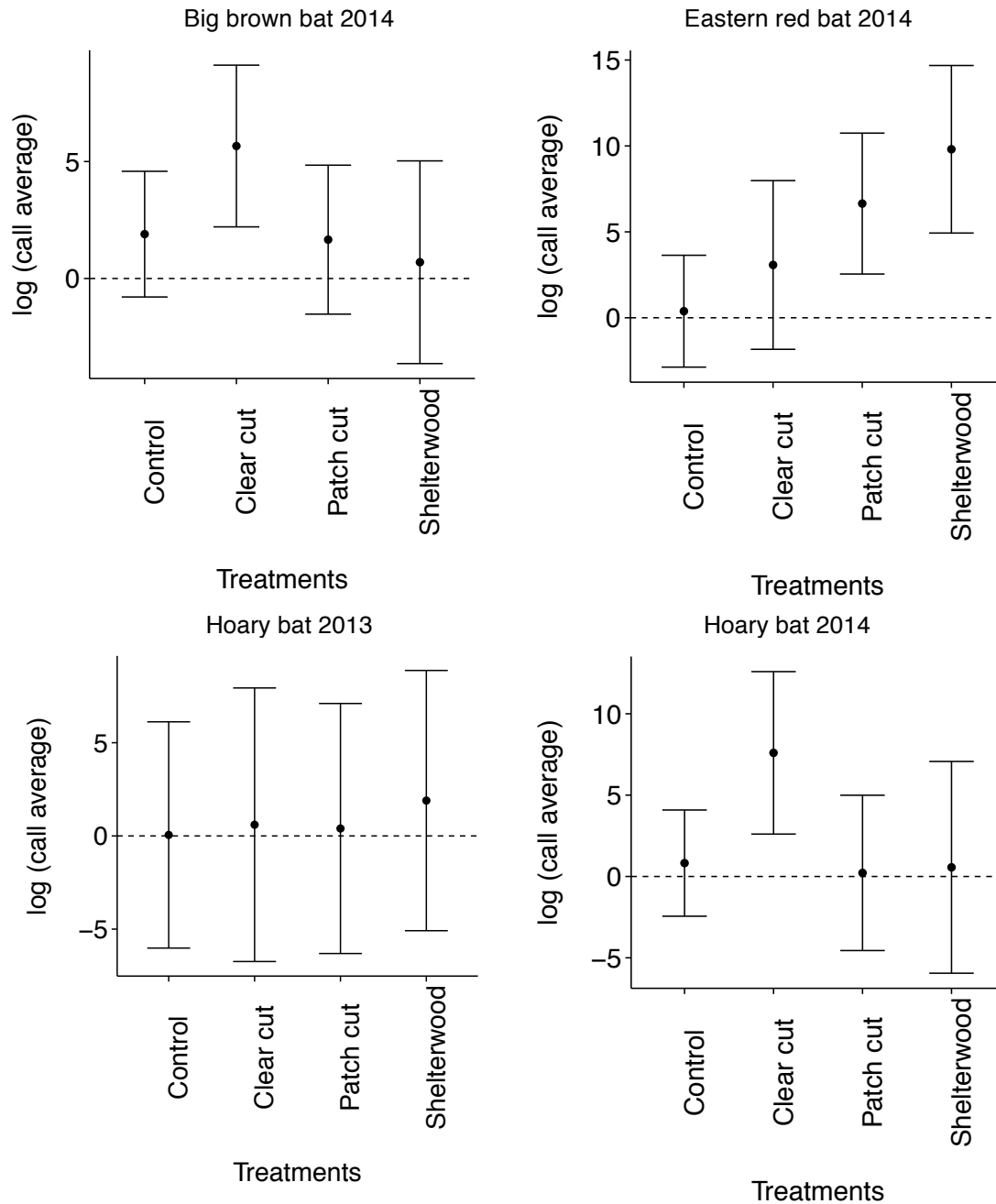


Figure 3. Log call averages of big brown, eastern red, and hoary bats in control treatments and in forests adjacent to harvest treatments on Morgan-Monroe and Yellowwood State Forests, IN during May-July, 2013 and 2014 calculated using Dail and Madsen 2011 *N*-mixture abundance model.

Harvest Peripheries Comparison: Small-bodied Bats

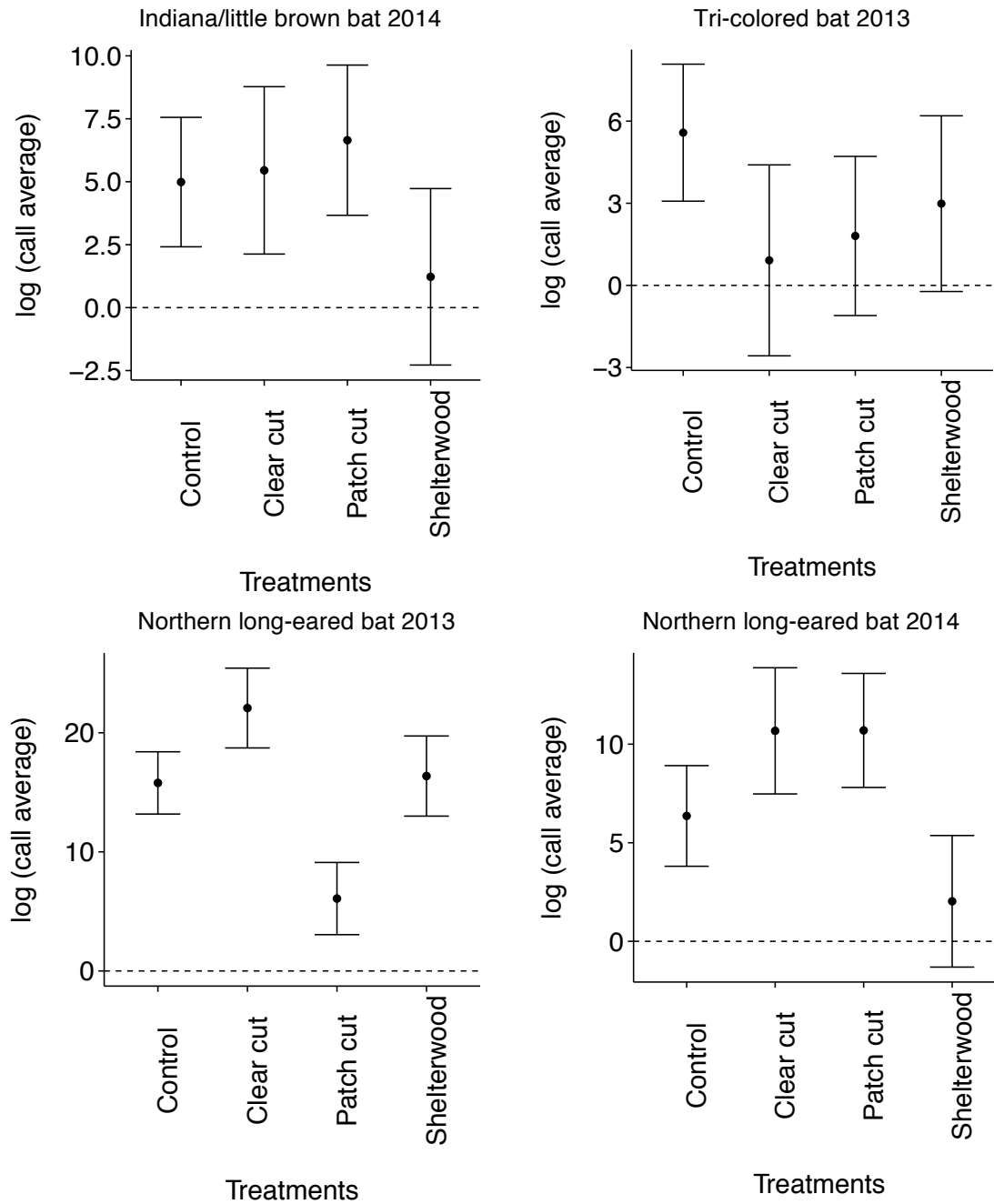


Figure 4. Log call averages of Indiana/little brown bats, tri-colored bats, and northern long-eared bats in control treatments and in forests adjacent to harvest treatments on Morgan-Monroe and Yellowwood State Forests, IN during May-July, 2013 and 2014 calculated using Dail and Madsen 2011 *N*-mixture abundance model.

Harvest-Forest Gradient Comparison: Large-bodied Bats

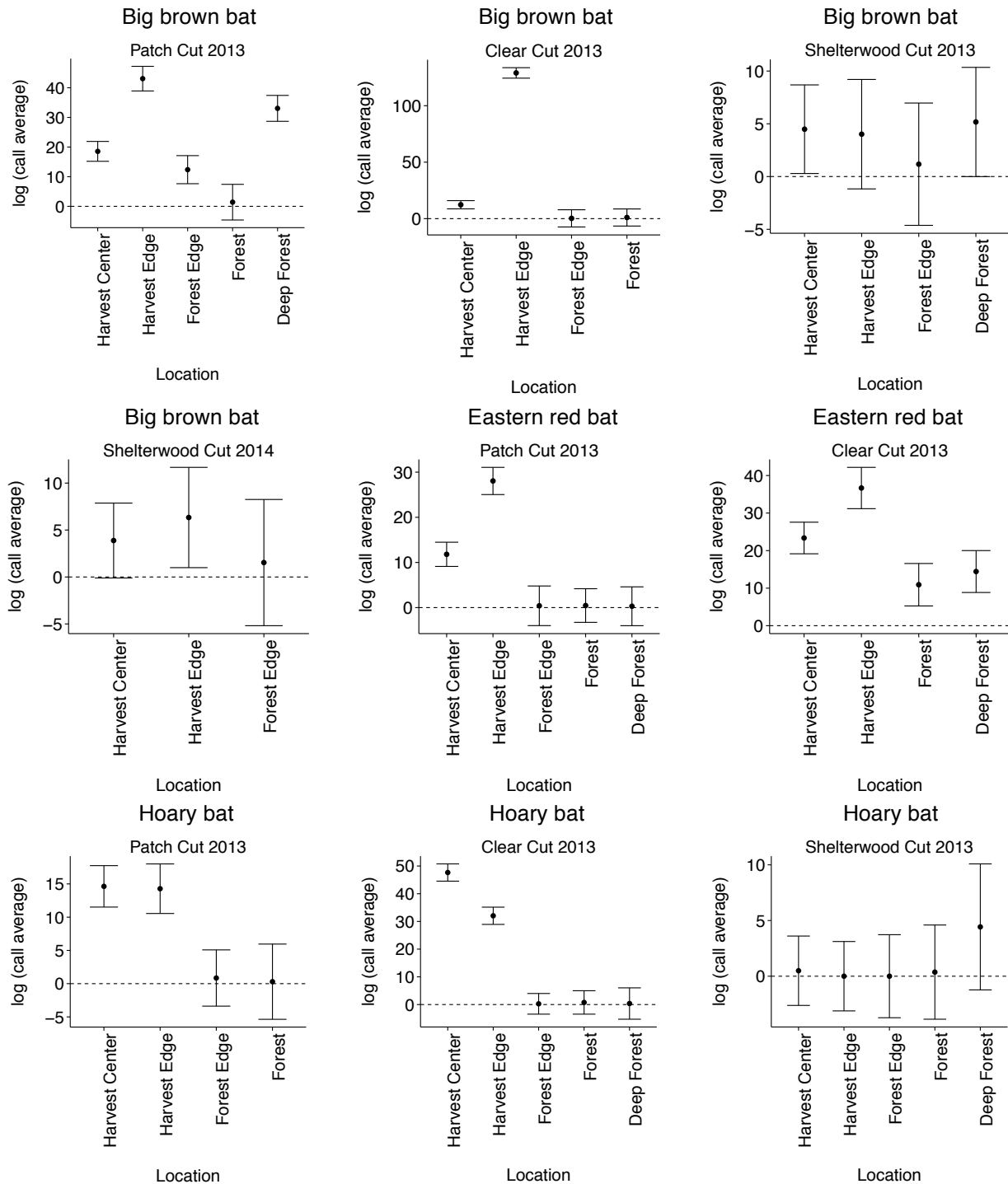


Figure 5. Log call averages of big brown bats, eastern red bats, and hoary bats at locations across the harvest-forest gradient in harvest treatments on Morgan-Monroe and Yellowwood State Forests, IN during May-July, 2013 and 2014 calculated using Dail and Madsen 2011 *N*-mixture abundance model.

Harvest-Forest Gradient Comparison: Small-bodied Bats

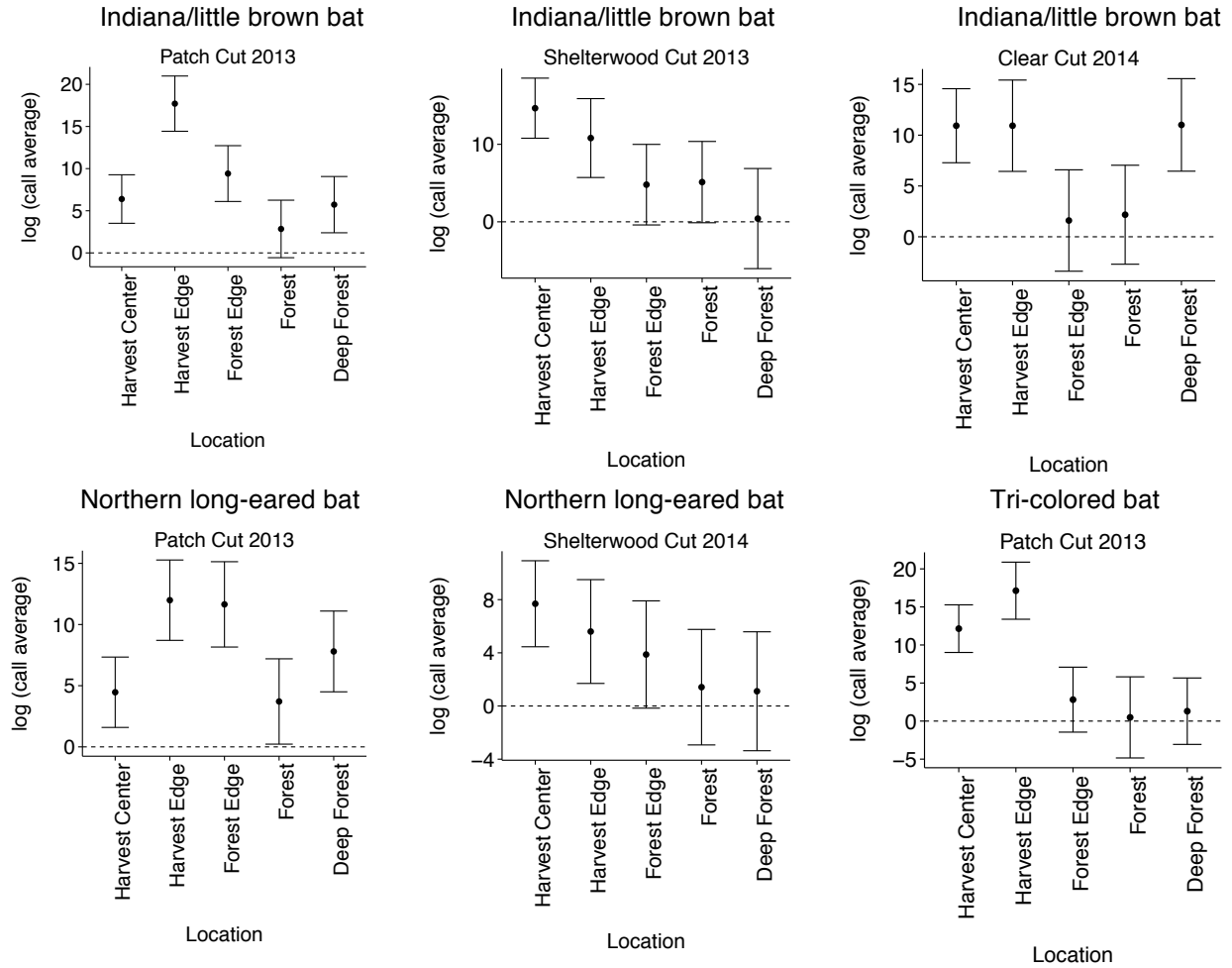


Figure 6. Log call averages of Indiana/little brown bats, northern long-eared bats, and tri-colored bats at locations across the harvest-forest gradient in harvest treatments on Morgan-Monroe and Yellowwood State Forests, IN during May-July, 2013 and 2014 calculated using Dail and Madsen 2011 *N*-mixture abundance model.

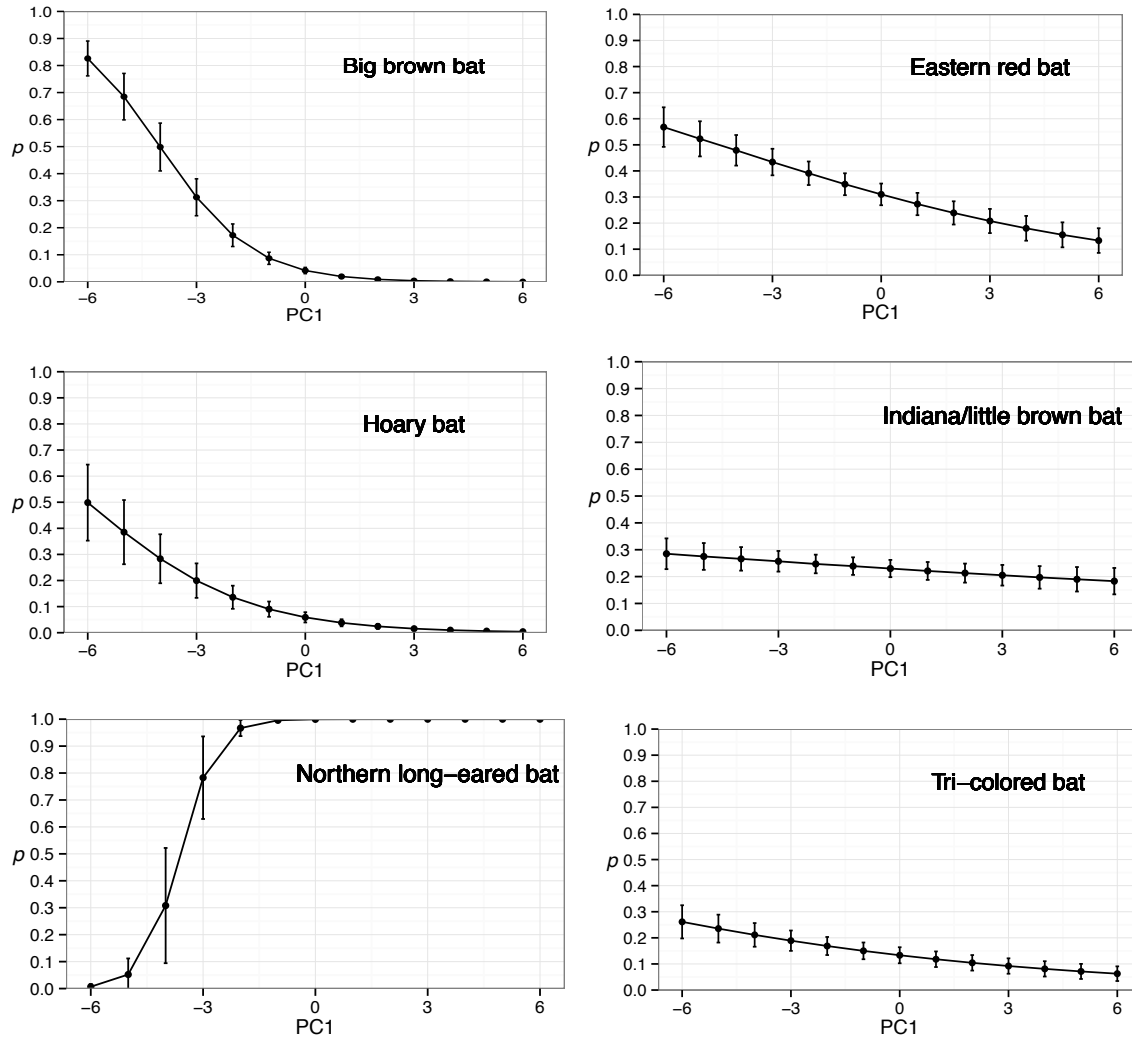


Figure 7. Change in detection probability of bats with changes in PC1 values calculated from echolocation calls collected on Morgan-Monroe and Yellowwood State Forests during May-July, 2013. PC1 was comprised of five variables: mean temperature(-), minimum temperature(-), maximum dew point(-), minimum dew point(-), and mean dew point(-).

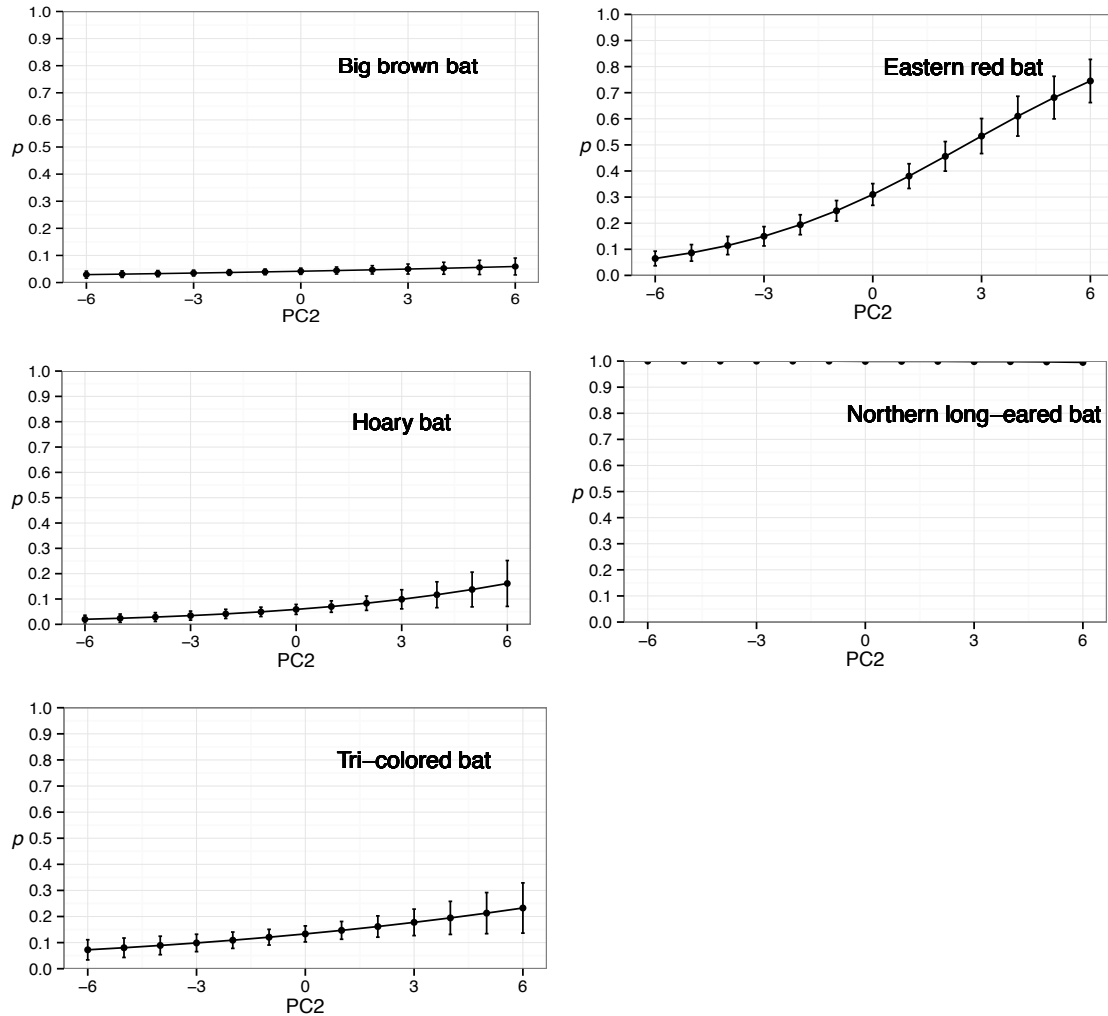


Figure 8. Change in detection probability of bats with changes in PC2 values calculated from echolocation calls collected on Morgan-Monroe and Yellowwood State Forests during May-July, 2013. PC2 was comprised of five variables: maximum barometric pressure(+), mean barometric pressure(+), minimum barometric pressure(+), mean wind speed(-), and cloud cover(-).

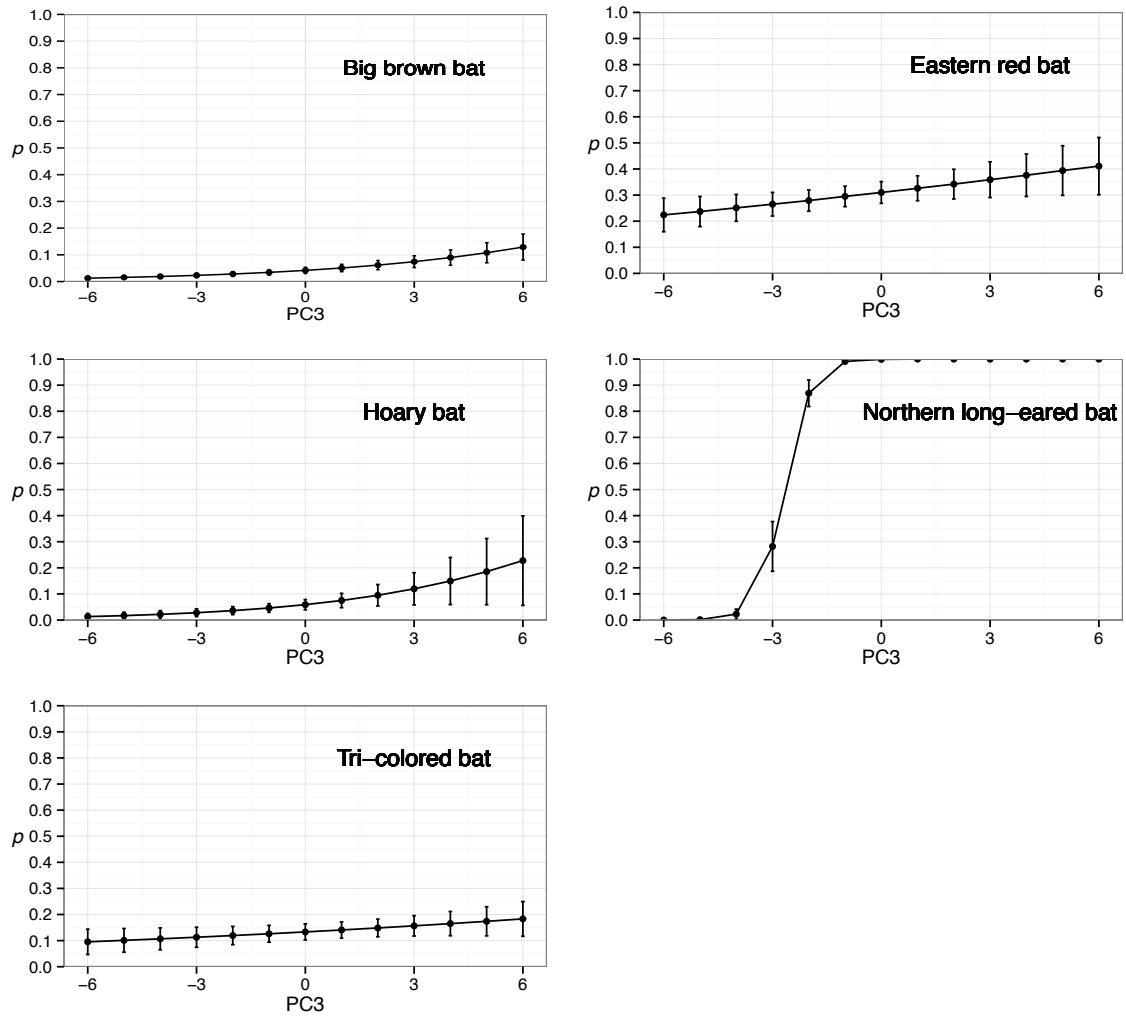


Figure 9. Change in detection probability of bats with changes in PC3 values calculated from echolocation calls collected on Morgan-Monroe and Yellowwood State Forests during May-July, 2013. PC3 was comprised of four variables: mean wind speed(+), maximum humidity(-), mean humidity(-), and minimum humidity(-).

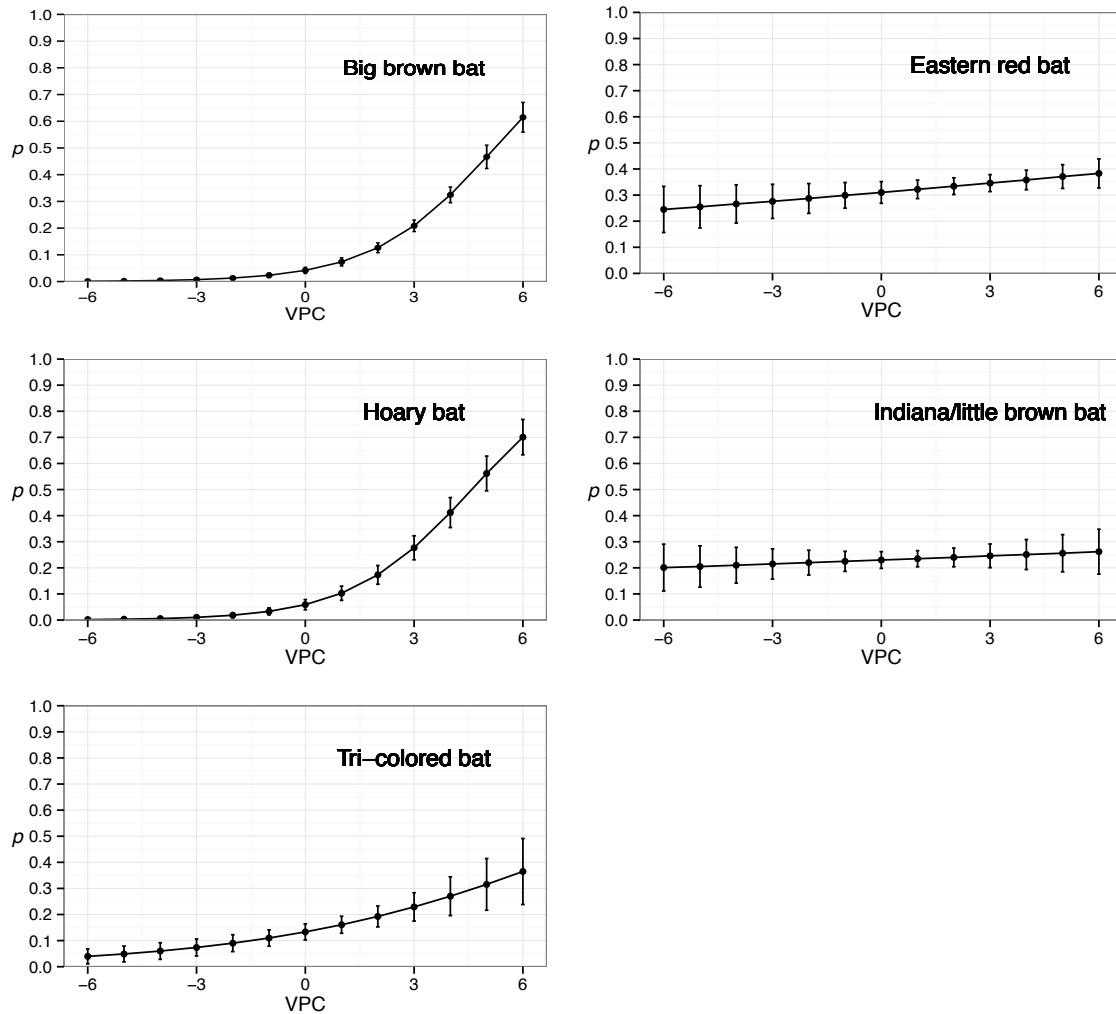


Figure 10. Change in detection probability of bats with changes in VPC values calculated from echolocation calls collected on Morgan-Monroe and Yellowwood State Forests during May-July, 2013. VPC was comprised of three variables: distance to nearest tree(+), number of trees per plot(-), and canopy closure(-).

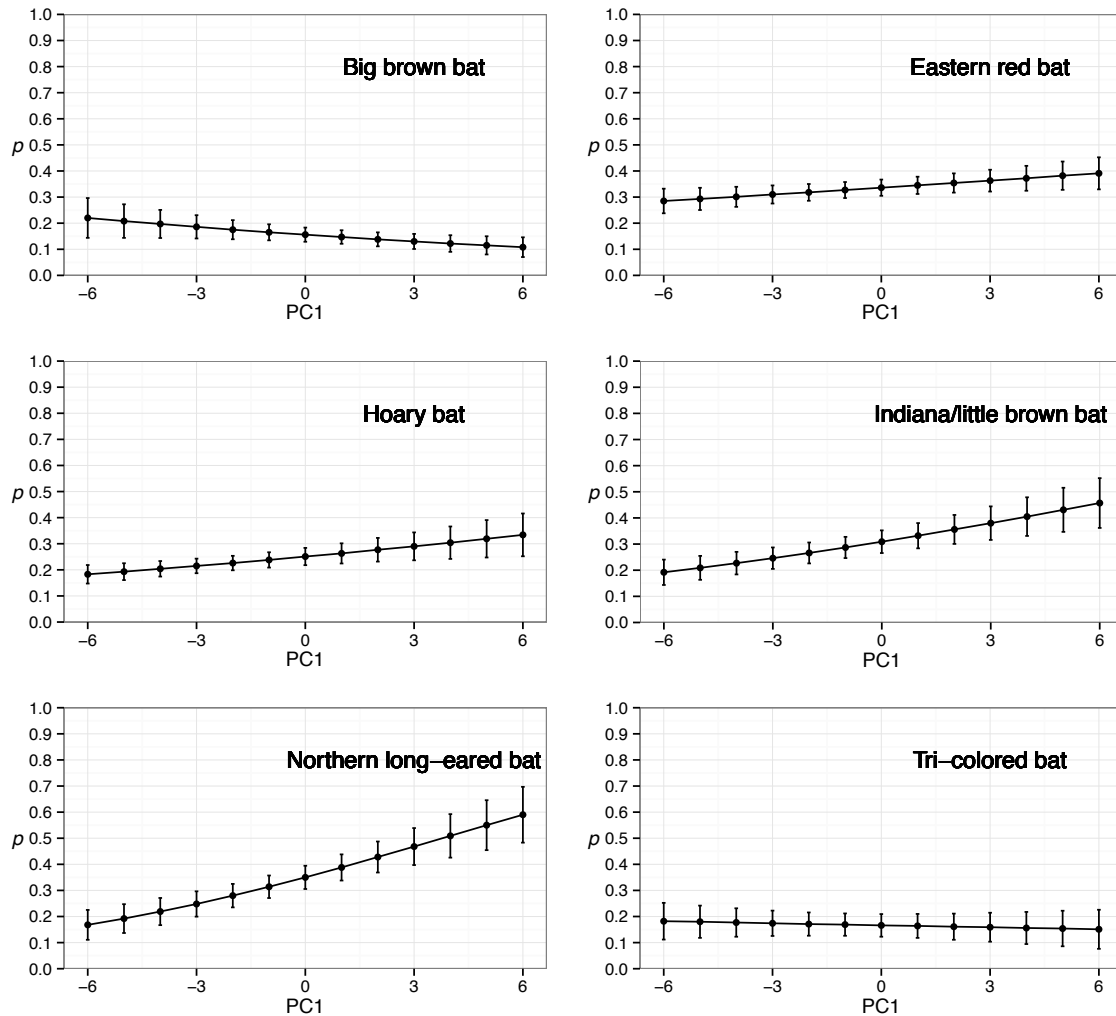


Figure 11. Change in detection probability of bats with changes in PC1 values calculated from echolocation calls collected on Morgan-Monroe and Yellowwood State Forests during May-July, 2014. PC1 was comprised of four variables: minimum temperature(-), and maximum dew point(-), minimum dew point(-), and mean dew point(-).

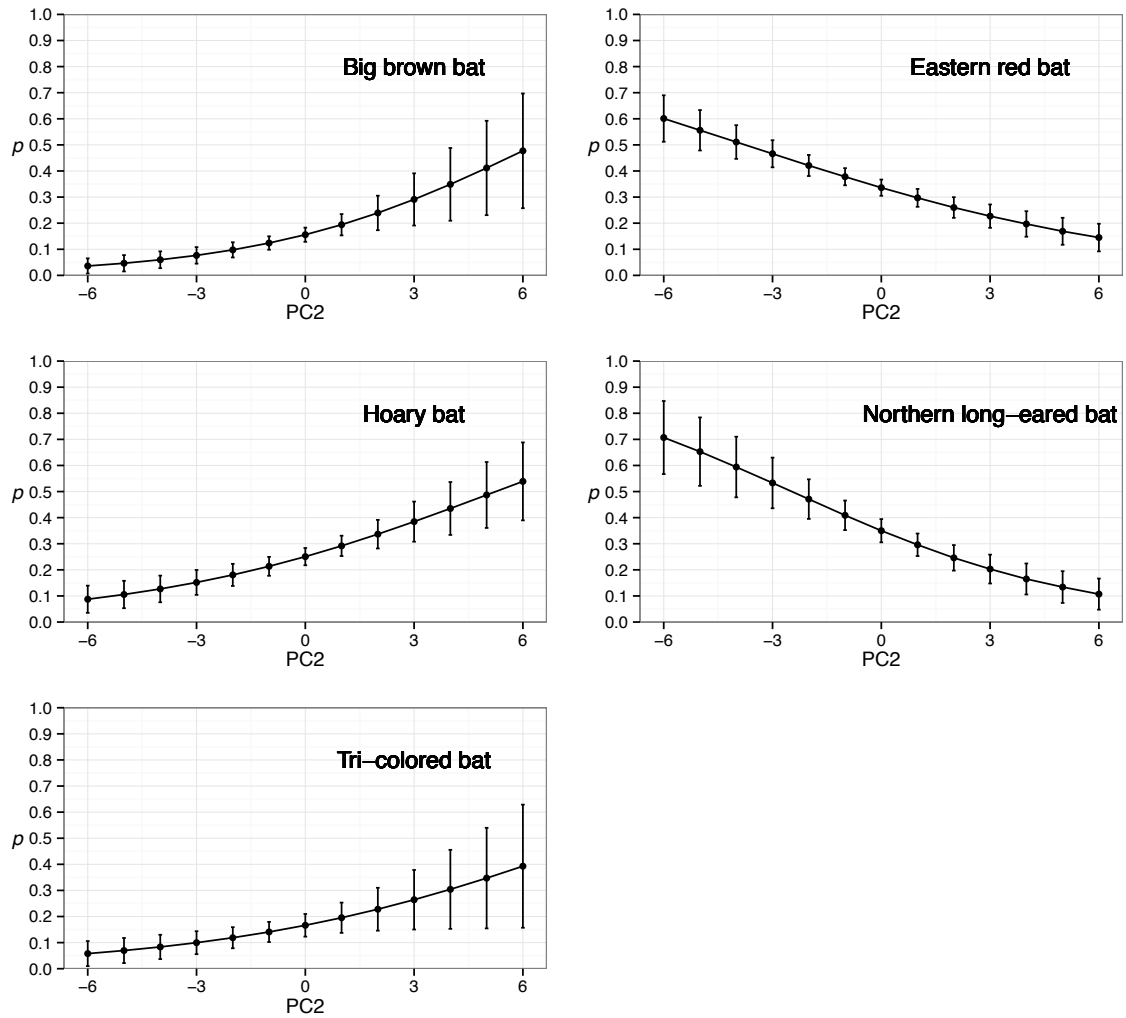


Figure 12. Change in detection probability of bats with changes in PC2 values calculated from echolocation calls collected on Morgan-Monroe and Yellowwood State Forests during May-July, 2014. PC2 was comprised of three variables: maximum temperature(+), mean temperature(+), and cloud cover(-).

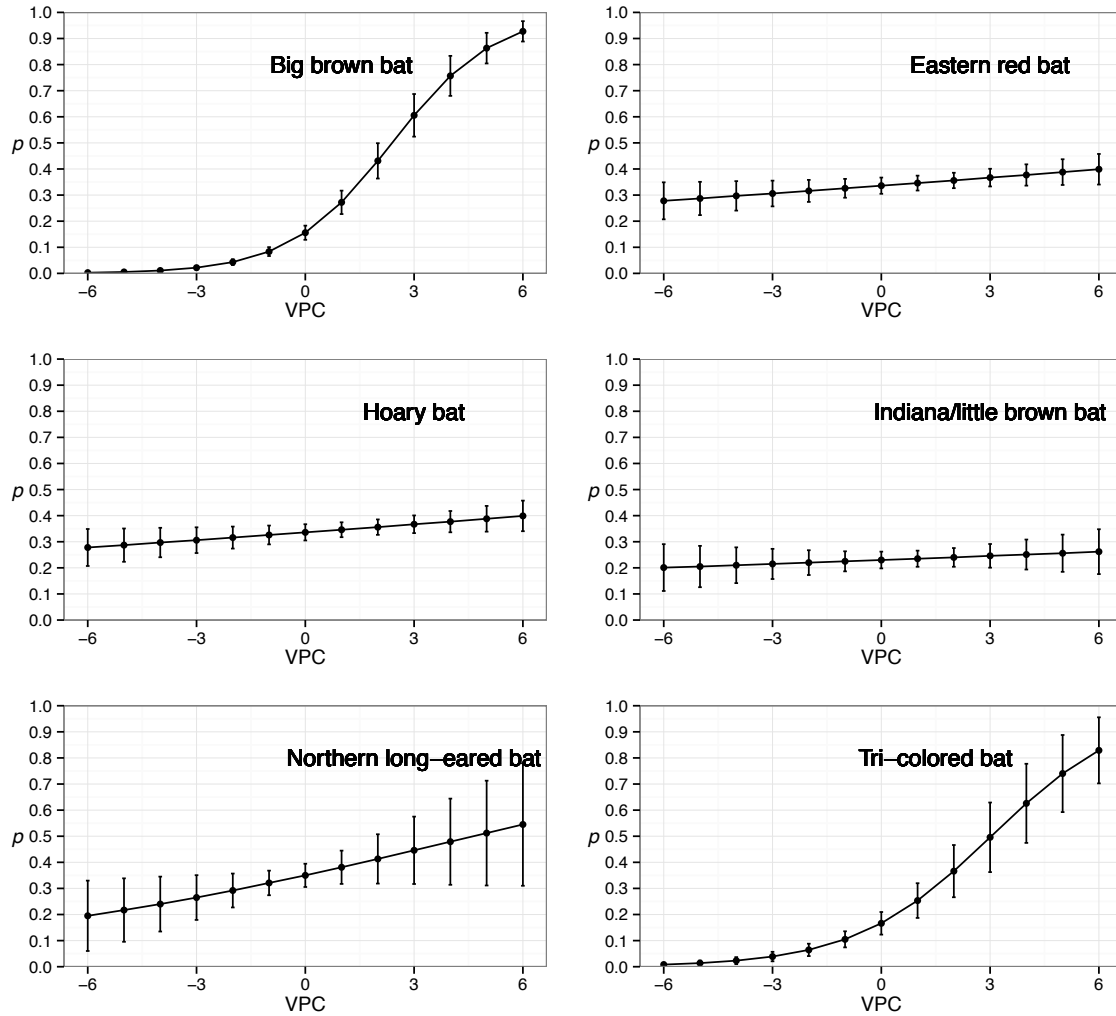


Figure 13. Change in detection probability of bats with changes in VPC values calculated from echolocation calls collected on Morgan-Monroe and Yellowwood State Forests during May-July, 2014. VPC was comprised of three variables: distance to nearest tree(+), number of trees per plot(-), and canopy closure(-).

TABLES

Table 1. Dail-Madsen model results for the Treatment Comparison Model with lowest Akaike's Information Criterion value. Abundance (λ), recruitment (γ), survivorship (ω), 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, IN were used for model creation.

Year	Species	Model	AIC ^a	Δ AIC ^b	ω^c	K^d
2013	Big brown	$\lambda(.)\gamma(.)\omega(.)p(\text{pc1+pc2+pc3+vpc})$	2186.45	0.00	0.52	9
		$\lambda(.)\gamma(.)\omega(.)p(\text{pc1+pc3+vpc})$	2187.40	0.95	0.32	8
	Eastern red	$\lambda(.)\gamma(.)\omega(.)p(\text{pc1+pc2+pc3+vpc})$	1914.76	0.00	0.42	9
		$\lambda(\text{H})\gamma(.)\omega(.)p(\text{pc1+pc2+pc3+vpc})$	1915.80	1.04	0.25	13
	Hoary	$\lambda(\text{H})\gamma(.)\omega(.)p(\text{pc1+pc2+pc3+vpc})$	1214.81	0.00	0.93	13
	Indiana/Little brown	$\lambda(.)\gamma(.)\omega(.)p(\text{pc1})$	2081.64	0.00	0.23	6
		$\lambda(.)\gamma(.)\omega(.)p(\text{pc1+vpc})$	2083.10	1.46	0.11	7
		$\lambda(.)\gamma(.)\omega(.)p(\text{pc1+pc2})$	2083.25	1.61	0.10	7
		$\lambda(.)\gamma(.)\omega(.)p(\text{pc1+pc3})$	2083.26	1.61	0.10	7
	Northern long-eared	$\lambda(.)\gamma(.)\omega(.)p(\text{pc1+pc2+pc3})$	2571.90	0.00	0.75	8
	Tri-colored	$\lambda(.)\gamma(.)\omega(.)p(\text{pc1+pc2+pc3+vpc})$	1619.59	0.00	0.50	9
		$\lambda(.)\gamma(.)\omega(.)p(\text{pc1+pc2+vpc})$	1620.60	1.01	0.30	8
2014	Big brown	$\lambda(.)\gamma(.)\omega(.)p(\text{pc1+pc2+vpc})$	1832.62	0.00	0.66	8
	Eastern red	$\lambda(\text{H})\gamma(.)\omega(.)p(\text{pc1+pc2+vpc})$	2038.56	0.00	0.65	12
	Hoary	$\lambda(\text{H})\gamma(.)\omega(.)p(\text{pc1+pc2})$	2133.41	0.00	0.53	10
		$\lambda(\text{H})\gamma(.)\omega(.)p(\text{pc1+pc2+vpc})$	2133.73	0.32	0.45	11
	Indiana/little brown	$\lambda(.)\gamma(.)\omega(.)p(\text{pc1})$	1630.19	0.00	0.44	6
		$\lambda(.)\gamma(.)\omega(.)p(\text{pc1+vpc})$	1631.93	1.73	0.19	7
		$\lambda(.)\gamma(.)\omega(.)p(\text{pc1+pc2})$	1632.18	1.99	0.16	7
	Northern long-eared	$\lambda(.)\gamma(.)\omega(.)p(\text{pc1+pc2+vpc})$	1697.58	0.00	0.39	8
		$\lambda(\text{H})\gamma(.)\omega(.)p(\text{pc1+pc2+vpc})$	1698.67	1.09	0.22	11
		$\lambda(\text{H})\gamma(.)\omega(.)p(\text{pc1+pc2})$	1698.78	1.20	0.21	10
		$\lambda(.)\gamma(.)\omega(.)p(\text{pc1+pc2})$	1699.13	1.55	0.18	7
	Tri-colored	$\lambda(.)\gamma(.)\omega(.)p(\text{pc2+vpc})$	1094.27	0.00	0.59	7
$\lambda(.)\gamma(.)\omega(.)p(\text{pc1+pc2+vpc})$		1096.01	1.74	0.25	8	

^aAkaike's Information Criterion

^bDifference between model's Akaike's Information Criterion and the lowest AIC value

^cAIC model weight

^dNumber of parameters estimated by the model

Table 2. Dail-Madsen model results for the Harvest Peripheries Model with lowest Akaike's Information Criterion value. Abundance (λ), recruitment (γ), survivorship (ω), and detection probability (p) are included in model descriptions along with covariates: H: Harvest treatment, PC1: principal component 1, PC2: principal component 2, PC3: principal component 3, VPC: vegetation principal component, and a period for no covariate effects. Species codes are EPFU: Big brown bat (*Eptesicus fuscus*), LABO: eastern red bat (*Lasiurus borealis*), LACI: hoary bat (*Lasiurus cinereus*), LU/SO: Indiana/little brown bat (*Myotis sodalis/lucifugus*), MYSE: northern long-eared bat (*Myotis septentrionalis*), and PESU: 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, IN were used for model creation.

Year	Species	Model	AIC ^a	Δ AIC ^b	ω^c	K^d
2013	Big brown	$\lambda(.)\gamma(.)\omega(.)p(pc2)$	597.34	0.00	0.21	6
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2)$	598.05	0.70	0.36	7
		$\lambda(.)\gamma(.)\omega(.)p(pc2+pc3)$	598.43	1.09	0.48	7
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+pc3)$	599.18	1.84	0.56	8
		$\lambda(.)\gamma(.)\omega(.)p(pc2+vpc)$	599.34	2.00	0.64	7
	Eastern red	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+pc3+vpc)$	617.03	0.00	0.38	9
	Hoary	$\lambda(H)\gamma(.)\omega(.)p(pc1+pc3)$	371.63	0.00	0.14	10
		$\lambda(H)\gamma(.)\omega(.)p(pc3)$	372.09	0.46	0.26	9
		$\lambda(H)\gamma(.)\omega(.)p(pc1+pc3+vpc)$	373.01	1.39	0.33	11
		$\lambda(H)\gamma(.)\omega(.)p(pc1+pc2)$	373.03	1.40	0.40	10
		$\lambda(H)\gamma(.)\omega(.)p(pc3+vpc)$	373.04	1.42	0.47	10
	Indiana/little brown	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	1181.66	0.00	0.40	8
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+pc3+vpc)$	1182.39	0.73	0.68	9
		$\lambda(.)\gamma(.)\omega(.)p(pc1+vpc)$	1183.32	1.66	0.86	7
	Northern long-eared	$\lambda(H)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	1764.20	0.00	0.47	11
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	1764.43	0.23	0.89	8
	Tri-colored	$\lambda(H)\gamma(.)\omega(.)p(pc3+vpc)$	830.19	0.00	0.29	10
		$\lambda(H)\gamma(.)\omega(.)p(pc1+pc3+vpc)$	831.25	1.06	0.47	11
$\lambda(H)\gamma(.)\omega(.)p(pc2+pc3+vpc)$		831.57	1.38	0.62	11	
2014	Big brown	$\lambda(H)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	743.03	0.00	0.66	11
	Eastern red	$\lambda(H)\gamma(.)\omega(.)p(pc1+pc2)$	944.39	0.00	0.53	10
		$\lambda(H)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	944.68	0.29	0.99	11
	Hoary	$\lambda(H)\gamma(.)\omega(.)p(pc2)$	423.81	0.00	0.47	9
		$\lambda(H)\gamma(.)\omega(.)p(pc2+vpc)$	425.72	1.90	0.65	10
	Indiana/little brown	$\lambda(H)\gamma(.)\omega(.)p(pc1+vpc)$	1102.24	0.00	0.41	10
		$\lambda(.)\gamma(.)\omega(.)p(pc1+vpc)$	1102.84	0.59	0.71	7
		$\lambda(H)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	1104.10	1.85	0.87	11
	Northern long-eared	$\lambda(H)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	1221.73	0.00	0.80	11
	Tri-colored	$\lambda(.)\gamma(.)\omega(.)p(pc2+vpc)$	676.44	0.00	0.54	7
$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$		677.80	1.36	0.82	8	

^aAkaike's Information Criterion

^bDifference between model's Akaike's Information Criterion and the lowest AIC value

^cAIC model weight

^dNumber of parameters estimated by the model

Table 3. Dail-Madsen model results for the Harvest-Forest Gradient Model with lowest Akaike's Information Criterion value. Abundance (λ), recruitment (γ), survivorship (ω), 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 codes are EPFU: Big brown bat (*Eptesicus fuscus*), LABO: eastern red bat (*Lasiurus borealis*), LACI: hoary bat (*Lasiurus cinereus*), LU/SO: Indiana/little brown bat (*Myotis sodalis/lucifugus*), MYSE: northern long-eared bat (*Myotis septentrionalis*), and PESU: 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, IN were used for model creation.

Year	Species	Harvest	Model	AIC ^a	Δ AIC ^b	ω^c	K^d
2013	Big brown	Patch	$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+pc3+vpc)$	1203.35	0.00	0.65	13
		Shelterwood	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc3)$	207.67	0.00	0.15	7
			$\lambda(L)\gamma(.)\omega(.)p(pc1+pc3)$	207.85	0.18	0.14	11
			$\lambda(.)\gamma(.)\omega(.)p(pc1+vpc)$	208.06	0.38	0.13	7
			$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+pc3)$	208.69	1.01	0.09	8
			$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+pc3)$	209.30	1.62	0.07	12
			$\lambda(.)\gamma(.)\omega(.)p(pc1+pc3+vpc)$	209.51	1.84	0.06	8
		Clear cut	$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	595.83	0.00	0.55	12
	$\lambda(L)\gamma(.)\omega(.)p(pc1+pc3+vpc)$		596.20	0.37	0.45	12	
	Eastern red	Patch	$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	829.04	0.00	0.40	12
			$\lambda(L)\gamma(.)\omega(.)p(pc1+vpc)$	829.36	0.33	0.34	11
		Shelterwood	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	290.00	0.00	0.52	8
			$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+pc3+vpc)$	290.53	0.53	0.40	9
		Clear cut	$\lambda(L)\gamma(.)\omega(.)p(pc2+vpc)$	354.13	0.00	0.46	11
			$\lambda(L)\gamma(.)\omega(.)p(pc2+pc3+vpc)$	355.86	1.74	0.19	12
	Hoary	Patch	$\lambda(L)\gamma(.)\omega(.)p(pc1+pc3)$	635.24	0.00	0.24	11
			$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+pc3)$	635.40	0.16	0.22	12
		Shelterwood	$\lambda(L)\gamma(.)\omega(.)p(pc3)$	635.79	0.56	0.18	10
			$\lambda(L)\gamma(.)\omega(.)p(pc2+pc3)$	635.82	0.58	0.18	11
			$\lambda(.)\gamma(.)\omega(.)p(pc1)$	123.07	0.00	0.11	6
			$\lambda(.)\gamma(.)\omega(.)p(.)$	123.71	0.64	0.08	5
			$\lambda(.)\gamma(.)\omega(.)p(pc1+pc3)$	124.07	1.00	0.07	7
			$\lambda(L)\gamma(.)\omega(.)p(pc1)$	124.21	1.15	0.06	10
			$\lambda(.)\gamma(.)\omega(.)p(pc3)$	124.40	1.33	0.06	6
			$\lambda(L)\gamma(.)\omega(.)p(.)$	124.57	1.50	0.05	9
			$\lambda(.)\gamma(.)\omega(.)p(pc1+vpc)$	124.82	1.75	0.05	7
			$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2)$	125.06	1.99	0.04	7
		Clear cut	$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+pc3)$	316.55	0.00	0.70	12
$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+pc3+vpc)$			318.54	1.99	0.26	13	
Indiana/little brown	Patch	$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2)$	894.12	0.00	0.32	11	
		$\lambda(L)\gamma(.)\omega(.)p(pc2)$	895.78	1.67	0.14	10	
		$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	895.94	1.83	0.13	12	
		$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+pc3)$	896.12	2.00	0.12	12	
	Shelterwood	$\lambda(.)\gamma(.)\omega(.)p(pc2)$	356.78	0.00	0.15	6	
		$\lambda(L)\gamma(.)\omega(.)p(pc2)$	357.11	0.33	0.13	10	
		$\lambda(.)\gamma(.)\omega(.)p(pc2+pc3)$	358.21	1.44	0.08	7	

		$\lambda(L)\gamma(.)\omega(.)p(pc2+vpc)$	358.29	1.51	0.07	11
		$\lambda(.)\gamma(.)\omega(.)p(pc2+vpc)$	358.33	1.55	0.07	7
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2)$	358.48	1.70	0.07	7
		$\lambda(L)\gamma(.)\omega(.)p(pc2+pc3)$	358.50	1.72	0.07	11
	Clear cut	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc3+vpc)$	281.70	0.00	0.29	8
		$\lambda(.)\gamma(.)\omega(.)p(pc3+vpc)$	282.67	0.97	0.18	7
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+pc3+vpc)$	283.32	1.62	0.13	9
Northern long-eared	Patch	$\lambda(.)\gamma(.)\omega(.)p(.)$	791.26	0.00	0.1342	5
		$\lambda(L)\gamma(.)\omega(.)p(.)$	791.48	0.22	0.1205	9
		$\lambda(.)\gamma(.)\omega(.)p(pc3)$	792.83	1.56	0.0614	6
		$\lambda(.)\gamma(.)\omega(.)p(pc2)$	793.07	1.81	0.0542	6
		$\lambda(.)\gamma(.)\omega(.)p(pc1)$	793.09	1.83	0.0539	6
		$\lambda(L)\gamma(.)\omega(.)p(pc3)$	793.12	1.85	0.0531	10
		$\lambda(L)\gamma(.)\omega(.)p(pc2)$	793.21	1.94	0.0508	10
		$\lambda(.)\gamma(.)\omega(.)p(vpc)$	793.26	2.00	0.0494	6
	Shelterwood	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc3+vpc)$	412.37	0.00	0.45	8
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+pc3+vpc)$	412.72	0.35	0.38	9
	Clear cut	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	393.14	0.00	0.54	8
Tri-colored	Patch	$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+pc3+vpc)$	631.64	0.00	0.43	13
		$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+pc3)$	631.81	0.17	0.40	12
	Shelterwood	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+pc3+vpc)$	198.59	0.00	0.56	9
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	199.56	0.96	0.34	8
	Clear cut	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+pc3+vpc)$	196.62	0.00	0.58	9
Big brown	Patch	$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	720.42	0.00	0.53	12
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	720.62	0.20	0.47	8
	Shelterwood	$\lambda(L)\gamma(.)\omega(.)p(pc1+vpc)$	185.81	0.00	0.98	11
	Clear cut	$\lambda(.)\gamma(.)\omega(.)p(vpc)$	413.70	0.00	0.47	6
		$\lambda(.)\gamma(.)\omega(.)p(pc1+vpc)$	415.40	1.69	0.20	7
		$\lambda(.)\gamma(.)\omega(.)p(pc2+vpc)$	415.63	1.92	0.18	7
Eastern red	Patch	$\lambda(.)\gamma(.)\omega(.)p(pc2+vpc)$	1131.31	0.00	0.63	7
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	1133.21	1.90	0.25	8
	Shelterwood	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2)$	420.06	0.00	0.62	7
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	422.02	1.96	0.23	8
2014	Clear cut	$\lambda(.)\gamma(.)\omega(.)p(pc2+vpc)$	302.88	0.00	0.89	7
Hoary	Patch	$\lambda(.)\gamma(.)\omega(.)p(pc2+vpc)$	1017.86	0.00	0.45	7
		$\lambda(.)\gamma(.)\omega(.)p(vpc)$	1019.51	1.65	0.20	6
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	1019.52	1.66	0.20	8
	Shelterwood	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2)$	117.58	0.00	0.27	7
		$\lambda(.)\gamma(.)\omega(.)p(pc1+vpc)$	117.97	0.38	0.23	7
		$\lambda(.)\gamma(.)\omega(.)p(pc1)$	117.99	0.40	0.22	6
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	118.21	0.63	0.20	8
	Clear cut	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	515.91	0.00	0.75	8
Indiana/little brown	Patch	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	576.19	0.00	0.46	8
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2)$	576.21	0.02	0.46	7

Northern long-eared	Shelterwood	$\lambda(.)\gamma(.)\omega(.)p(pc1+vpc)$	239.22	0.00	0.59	7
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	241.15	1.92	0.23	8
	Clear cut	$\lambda(.)\gamma(.)\omega(.)p(pc1+vpc)$	297.52	0.00	0.27	7
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2)$	298.02	0.49	0.21	7
		$\lambda(.)\gamma(.)\omega(.)p(pc2+vpc)$	299.42	1.89	0.11	7
		$\lambda(L)\gamma(.)\omega(.)p(pc1+vpc)$	299.44	1.92	0.10	11
	Patch	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	299.52	2.00	0.10	8
		$\lambda(.)\gamma(.)\omega(.)p(pc2+vpc)$	645.38	0.00	0.28	7
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2)$	645.74	0.37	0.24	7
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	645.83	0.45	0.23	8
$\lambda(.)\gamma(.)\omega(.)p(pc2)$		646.65	1.27	0.15	6	
$\lambda(L)\gamma(.)\omega(.)p(pc1)$		646.65	1.27	0.15	6	
Tri-colored	Shelterwood	$\lambda(.)\gamma(.)\omega(.)p(pc1+vpc)$	240.24	0.00	0.25	7
		$\lambda(.)\gamma(.)\omega(.)p(pc1)$	241.54	1.31	0.13	6
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	241.95	1.72	0.11	8
		$\lambda(L)\gamma(.)\omega(.)p(pc1)$	242.01	1.77	0.10	10
	Clear cut	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	318.09	0.00	0.61	8
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2)$	319.46	1.36	0.31	7
	Patch	$\lambda(.)\gamma(.)\omega(.)p(pc2)$	415.35	0.00	0.28	6
		$\lambda(.)\gamma(.)\omega(.)p(.)$	415.85	0.50	0.21	5
		$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2)$	416.91	1.55	0.13	7
		$\lambda(.)\gamma(.)\omega(.)p(pc2+vpc)$	417.33	1.98	0.10	7
Shelterwood	$\lambda(.)\gamma(.)\omega(.)p(pc2+vpc)$	168.35	0.00	0.43	7	
	$\lambda(.)\gamma(.)\omega(.)p(pc1+vpc)$	170.20	1.84	0.17	7	
	Clear cut	$\lambda(.)\gamma(.)\omega(.)p(pc1+pc2+vpc)$	199.33	0.00	0.59	8
$\lambda(L)\gamma(.)\omega(.)p(pc1+pc2+vpc)$		200.91	1.58	0.27	12	

^aAkaike's Information Criterion

^bDifference between model's Akaike's Information Criterion and the lowest AIC value

^cAIC model weight

^dNumber of parameters estimated by the model

Table 4. Factor loadings of greater than absolute value of 0.3 for principal components analysis (PCA) of weather data collected on Morgan-Monroe and Yellowwood State Forests, IN 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	

Table 5. Factor loadings greater than absolute value of 0.3 for principal components analysis (PCA) of vegetation data collected on Morgan-Monroe and Yellowwood State Forests, IN during May-July, 2013 and 2014.

Vegetation Variables	2013	2014
	VPC	
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

Table 6. Probability of detection (logit scale) and parameter estimates for six species acoustically surveyed in forest management treatments on Morgan-Monroe and Yellowwood State Forests, IN during May-July, 2013 and 2014. Parameters include detection probability intercept, PC1: principal components 1, PC2: principal components 2, PC3: principal components 3, and VPC: vegetation principal components. Species codes 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*).

Species	Parameter	Estimate	SE	z	P	Parameter	Estimate	SE	z	P
Big brown	Intercept	-3.13	0.15	-21.53	<0.01	Intercept	-1.69	0.1	-16.22	<0.01
	PC1	-0.78	0.03	-22.88	<0.01	PC1	-0.07	0.03	-2.3	0.02
	PC2	0.06	0.04	1.72	0.09	PC2	0.27	0.07	3.79	<0.01
	PC3	0.2	0.03	6.7	<0.01	VPC	0.71	0.05	15.65	<0.01
	VPC	0.6	0.04	15.62	<0.01					
Eastern red	Intercept	1.19	0.34	3.51	<0.01	Intercept	-0.68	0.07	-9.7	<0.01
	PC1	0.92	0.57	1.63	0.1	PC1	0.04	0.02	2.35	0.02
	PC2	1.03	0.47	2.2	0.03	PC2	-0.18	0.03	-5.77	<0.01
	PC3	0.57	0.57	1	0.32	VPC	0.05	0.02	1.99	0.05
	VPC	1.19	0.34	3.51	<0.01					
Hoary	Intercept	-2.77	0.18	-15.47	<0.01	Intercept	-1.1	0.09	-12.32	<0.01
	PC1	-0.46	0.04	-11.04	<0.01	PC1	0.07	0.02	3.13	<0.01
	PC2	0.19	0.06	3.39	<0.01	PC2	0.21	0.05	4.12	<0.01
	PC3	0.26	0.07	3.48	<0.01	VPC	0.03	0.02	1.29	0.2
	VPC	0.6	0.04	14.36	<0.01					
Indiana/little brown	Intercept	-1.21	0.09	-13.18	<0.01	Intercept	-0.8	0.1	-7.85	<0.01
	PC1	-0.05	0.02	-2.33	0.02	PC1	0.11	0.02	4.38	<0.01
	VPC	0.03	0.04	0.73	0.47	VPC	0.03	0.06	0.52	0.61
Northern long-eared	Intercept	7.55	0.65	11.6	<0.01	Intercept	-0.61	0.1	-6.37	<0.01
	PC1	2.09	0.18	11.9	<0.01	PC1	0.16	0.03	5	<0.01
	PC2	-0.37	0.09	-4.3	<0.01	PC2	-0.25	0.05	-4.7	<0.01
	PC3	2.83	0.25	11.2	<0.01	VPC	0.11	0.07	1.43	0.15
Tri-colored	Intercept	-1.87	0.13	-14	<0.01	Intercept	-1.61	0.16	-10.22	<0.01
	PC1	-0.14	0.03	-5.24	<0.01	PC1	-0.02	0.04	-0.52	0.61
	PC2	0.11	0.04	2.74	0.01	PC2	0.2	0.07	2.64	0.01
	PC3	0.06	0.04	1.73	0.08	VPC	0.53	0.07	7.82	<0.01
	VPC	0.22	0.05	4.36	<0.01					