Original Article

Relationships Between Bat Occupancy and Habitat and Landscape Structure Along a Savanna, Woodland, Forest Gradient in the Missouri Ozarks

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ABSTRACT Many land-management agencies are restoring savannas and woodlands using prescribed fire and forest thinning, and information is needed on how wildlife species respond to these management activities. Our objectives were to evaluate support for relationships of bat site occupancy with vegetation structure and management and landscape composition and structure across a gradient of savanna to forest in the Missouri Ozark Highlands, USA. We selected study sites that were actively managed for savanna and woodland conditions and control areas on similar landforms that had succeeded to closed-canopy forest. We used Anabat detectors to survey bats during the summers of 2010, 2011, and 2012. We fit single-species site-occupancy models to estimate detection probability and site occupancy. We evaluated *a priori* hypotheses in an information theoretic approach by evaluating support for candidate models that included habitat, landscape, and management effects. Site occupancy of evening bats (*Nycticeius humeralis*) was negatively related to poletimber and sawtimber density and positively related to fire frequency, while northern long-eared bat (*Myotis septentrionalis*) site occupancy was positively related to poletimber density and negatively related to understory stem densities. Site occupancy of big brown bats (*Eptesicus fuscus*), eastern red bats (*Lasiurus borealis*), and tri-colored bats (*Perimyotis subflavus*) were mostly not related to local vegetation structure and site occupancy was high across the savanna, woodland, forest gradient. We found more consistent and larger effect sizes for landscape-scale than for habitat-scale relationships; therefore, land managers should be cognizant of large-scale patterns in land cover when making local management decisions for these species. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS big brown bat, eastern red bat, evening bat, northern long-eared bat, restoration, site occupancy, tri-colored bat.

Many bat populations have declined due to habitat degradation or loss from urbanization, deforestation, and other factors, and more recently, due to white-nose syndrome and fatalities at wind energy facilities (Arnett et al. 2008, Blehert et al. 2009, Hayes 2013). The decline of bat populations could have far-reaching impacts from the loss of the ecosystem services they provide (Boyles et al. 2011). Many bats roost and forage in forests, and the way forests are managed can affect their value as bat habitat.

Land management agencies in the Midwestern United States are restoring many forested areas to their historical structure and composition as savannas and woodlands using prescribed fire and thinning. Oak savannas and woodlands declined from approximately 13 million ha in the Midwest since European settlement (Abrams 1992). Historically, fires started by lightning and Native Americans maintained savanna and woodland ecosystems. Savannas and woodlands decreased after Europeans settled in the Midwest due to conversion to settlements or farmland or by succession to forest as a result of fire control (Abrams 1992). Savanna and woodland restoration uses prescribed fire and tree thinning to reduce tree density in the understory and midstory, and to a lesser extent the overstory, to allow increased sunlight to reach the ground (McCarty 2004, Nelson 2004). Long-term repeated fire maintains a low density of understory and

midstory shrubs and trees, an abundance of grasses and forbs, and an overstory of mature trees. Occasional periods without fire allow some fire-adapted trees (i.e., oaks [*Quercus* spp.] and pine [*Pinus* spp.]) to be recruited to the overstory. Criteria for distinguishing savanna, woodland, and forest vary regionally but in Missouri, USA, desired structure for savannas is 10%–30% canopy cover and $<6.9\,m^2/ha$ basal area; woodlands, 50%–80% canopy cover and 6.9–$18.4\,m^2/ha$ basal area; and forest, $>80\%$ canopy cover and $>18.4\,m^2/ha$ basal area (Nelson 2004, U.S. Department of Agriculture, Forest Service 2005). It is important to know how savanna and woodland restoration and prescribed fire affect bats because of the extent of these activities and concern for bat populations.

Bat use of savanna, woodland, and forest likely varies among species due to differences in wing morphology and echolocation characteristics. Species' wing morphology affects whether a species is adapted for cluttered habitats, such as dense forest, or open habitats, such as savannas (Norberg 1994). Larger species of bats with high wing loading and high aspect ratio often use forests that have been managed by either fire or thinning, whereas smaller bats with low wing loading and low aspect ratio are influenced less by tree density (Patriquin and Barclay 2003, Elmore et al. 2005, Loeb and O'Keefe 2006, Loeb and Waldrop 2008, Armitage and Ober 2012). Landscape composition and structure affect habitat use by bats in addition to vegetative structure within patches. The amount and distribution of urban and agricultural areas interact with the composition and distribution of forests. Some bats fly long distances each night from roosts to foraging sites, so landscape-scale factors may affect these species either positively or negatively (Gorresen and Willig 2004, Yates and Muzika 2006).

Our goal was to better understand how bats respond to savanna and woodland restoration. To accomplish this, we studied site occupancy of big brown bats (*Eptesicus fuscus*), northern long-eared bats (*Myotis septentrionalis*), evening bats (*Nycticeius humeralis*), tri-colored bats (*Perimyotis subflavus*), and eastern red bats (*Lasiurus borealis*) across an existing gradient of savanna, woodland, and forest in the Missouri Ozark Highlands because controlled experiments were not feasible at this scale. Our specific objectives were to evaluate support for relationships between site occupancy and 1) vegetation structure at a site and 2) landscape composition and structure. We evaluated continuous measures of vegetation structure across managed savannas and woodlands and non-managed forest because these communities represent a gradient from low to high tree densities, rather than discrete habitat types. We also considered landscape-level characteristics because these can constrain local-scale habitat use. We hypothesized that site occupancy would vary by species because of differences in wing morphology and echolocation characteristics and be affected by tree density, distance to water, distance to roads, vegetative composition, and percent forest and urban land cover. We hypothesized that vegetative structural conditions created by savanna and woodland restoration and management would result in a greater site occupancy for the big brown bat, eastern red bat, evening bat, and tri-colored bat than in mature, unmanaged forest and that these conditions would have less of an effect on site occupancy of northern long-eared bats.

STUDY AREA

We conducted our study in the Ozark Highlands of southern Missouri. The Ozark Highlands were characterized by carbonate bedrock with many karst features and consisted of plains, gently rolling hills, and rugged uplands with elevations of 762 m (Nigh and Schroeder 2002, Ethridge 2009). Soils were typically rocky and historically supported oak and oak–pine savannas, woodlands, and forests. Most streams in the area were spring-fed and clear. Common trees in upland forest were black oak (*Quercus velutina*), scarlet oak (*Q. coccinea*), white oak (*Q. alba*), post oak (*Q. stellata*), blackjack oak (*Q. marilandica*), black hickory (*Carya texana*), and shortleaf pine (*Pinus echinata*). White oak, red oak (*Q. rubra*), bitternut hickory (*C. cordiformis*), and flowering dogwood (*Cornus florida*) were more prevalent on mesic slopes. River birch (*Betula nigra*), silver maple (*Acer saccharinum*), eastern cottonwood (*Populus deltoides*), American sycamore (*Platanus occidentalis*), black willow (*Salix nigra*), and box elder (*A. negundo*) were common in riparian areas. Openlands consisted of bluestem (*Andropogon gerardii*, *Schizachyrium scoparium*) prairies, eastern red cedar (*Juniperus virginiana*) glades (McNab and Avers 1994), and improved cool-season (*Festuca* spp.) pasturelands.

METHODS

Locations of Sites and Survey Points

We consulted with land managers from the Missouri Department of Conservation, Department of Natural Resources, The Nature Conservancy, and Mark Twain National Forest to select study areas that included sites with a history of management (predominantly prescribed fire and thinning) to restore savannas or woodlands and that had achieved or demonstrated substantial progress toward the desired structure and composition (Table 1). Because this was a limited pool of study areas, we used all areas identified ($N = 26$) rather than a random sample. We identified sites actively managed for savanna and woodland conditions and control sites with no recent management at each study area. Within each site, we randomly located bat survey points using 1 of 2 protocols. Some points were part of a bird study and located on transects. Transects were established by randomly placing a 250-m grid over a site and mapping a transect of 10–20 points spaced 250 m apart and ≥ 50 m from the edge of the managed site. We selected every second or third point along the bird transects for the bat surveys to get ≤ 6 points/transect. We did not select every point on the bird transect because we wanted the bat detectors to be >250 m apart. Additional points were located consistent with an earlier bat study (Amelon 2007) by randomly locating points in a site using a Geographic Information System such that points were >250 m apart.

Table 1. Study areas, ownership, year(s) sampled, and number of points per area surveyed for bat occupancy in the Missouri Ozark Highlands, USA, 2010–2012.

Study area	Ownership[a]	Year(s) sampled	No. of points
Lead Mine Conservation Area	MDC	2010	9
Sunklands Conservation Area	MDC	2010	9
Little Black Conservation Area	MDC	2011	8
Ha Ha Tonka State Park	DNR	2011	10
Lake of the Ozarks State Park	DNR	2011	16
Knob Noster State Park	DNR	2011	12
Rocky Creek Conservation Area	MDC	2011	4
Western Star Flatwoods	MTNF	2011	10
Caney Mountain Conservation Area	MDC	2011	15
Drury–Mincy Conservation Area	MDC	2011	11
Bluff Springs Conservation Area	MDC	2011	8
Indian Trail Conservation Area	MDC	2011	12
St. Joe State Park	DNR	2011	16
White Ranch Conservation Area	MDC	2011	7
Chilton Creek	TNC	2011	7
Cuivre River State Park	DNR	2012	19
Handy	MTNF	2012	16
Cane Ridge	MTNF	2012	14
Peck Ranch Conservation Area	MDC	2012	28
St. Francois State Park	DNR	2012	14
Mark Twain Glade Top	MTNF	2012	13
Ava	MTNF	2012	12
Big Creek	MTNF	2012	18
Three Sisters	MTNF	2012	10
Bennett Springs State Park	DNR	2010, 2012	19
Pine Knot	MTNF	2011, 2012	25

[a] MDC = Missouri Department of Conservation, DNR = Missouri Department of Natural Resources, MTNF = Mark Twain National Forest, TNC = The Nature Conservancy.

Acoustic Detection

We surveyed bats with either Anabat II bat detectors and Zero-Crossing Analysis Interference Modules with Compact Flash memory storage (CF ZCAIM) or Anabat SD1 (combined detector and storage model; Titley Electronics, Columbia, MO). The detector and a 12-V battery were housed in a waterproof Pelican™ case with the microphone pointed through a hole with a 45° polyvinyl chloride elbow attached to the side of the case to protect the microphone and direct the detection cone upward (Britzke et al. 2010). We calibrated the sensitivity of each Anabat detector to standardize the detection distance and area sampled (Larson and Hayes 2000, Livengood 2003); therefore, there should not be an effect of the detector model on detection probability.

We placed a detector at each point and recorded echolocation calls from 1800 hr to 0600 hr on each of 2 consecutive nights. By sampling on consecutive nights, we could create a detection history, during which the bat populations are assumed closed to emigration and immigration, a key assumption of our analysis approach. We placed the detector on the ground with the microphone oriented upward and toward the most open area in the vegetation to exclude as much insect noise as possible (Weller and Zabel 2002). We removed the detectors after 2 nights and downloaded data from the compact flash card to a computer. We analyzed and identified the calls with AnalookW (Corben 2007). We used digital filters to eliminate ambient noise, low-quality sequences, and sequences with <5 call pulses. We then identified the remaining sequences by having 3 individuals whose independent identification accuracy was >90% in blind tests using known call sequences. Species were identified using call characteristics, including minimum frequency (minF), duration (dur), characteristic frequency (Fc), initial slope (S1), and characteristic slope (Sc) based on data from known call libraries (S. K. Amelon, personal communication). We assigned 1 to a sampling period when a species was detected and a 0, if it was not detected to create a detection history.

Vegetation and Landscape Measurements

We measured diameter at breast height (DBH) of trees >2.5 cm with a DBH tape; we selected trees with a 10-factor prism at survey points and classified trees as coniferous or deciduous. We calculated tree stems/ha of saplings (2.5 cm–12.5 cm DBH), poletimber (12.5 cm–27.5 cm DBH), and sawtimber (>27.5 cm DBH) and basal area using the prism factor and calculated percent stocking of all trees using equations for upland oaks and hickories and shortleaf pine (Gingrich 1967, Johnson et al. 2009). We calculated small stems/ha by counting the trees with a DBH <2.5 cm and >0.5 m tall in a 5-m radius around the point. We contacted site managers to determine the number of fires in the past 10 years.

We used ArcMap to condense the land classifications from the National Land Cover Database (Fry et al. 2006) to forest, open, and urban land cover. This classification included forest and woodland communities as forest land cover, but savanna may have been included in forest or open land cover,

depending on how may trees were present on a pixel. We measured the percent of the landscape in forest, open, and urban land cover within a 2-km and 16-km buffer (Amelon 2007) around each survey point. We used FRAGSTATS 3.3 (McGarigal and Marks 1995) to calculate percent area in forest, open, and urban land cover. We calculated distance to nearest road (m) using statewide layers of transportation data for Missouri (Missouri Spatial Data Information Service 2011) and Arkansas (State of Arkansas 2009). We used a statewide layer of hydrography for Missouri from the National Hydrography Dataset Plus (U.S. Geologic Survey 2005) to calculate distance to nearest water (m).

We compiled weather data from the National Climatic Data Center (2011) for the stations closest to each site: Rolla, Kaiser Lake Ozark, Farmington, Cape Girardeau, West Plains, Springfield, Whiteman Air Force Base, Spirit of St. Louis Airport, and Poplar Bluff. We calculated maximum dry bulb temperature (°C), maximum relative humidity (%), and mean barometric pressure (in. Hg) from hourly values for the 2 sampling periods.

Data Analysis

Although echolocation detectors allow researchers to efficiently survey sites for the presence of bat species, the probability of detecting bats with acoustic detectors varies and is generally <1. We therefore used site-occupancy models to determine relationships between habitat variables and site occupancy (Ψ) while accounting for probability of detection (p; MacKenzie et al. 2006, Yates and Muzika 2006, Gorresen et al. 2008, Hein et al. 2009, Roberts et al. 2011). Specifically, we fit single-season occupancy models (Royle and Nichols 2003, MacKenzie et al. 2006) for each species with the program PRESENCE 5.3. We evaluated *a priori* hypotheses by building models to represent hypotheses and using Akaike's Information Criteria (AIC) to select the model that best explained the empirical data. All covariates were standardized to a mean of zero and standard deviation of 1 before running the models in PRESENCE to facilitate model convergence, but we back-transformed values to their original units when discussing model predictions. We first determined the best model for estimating p and then

included the covariates from the best model for p while evaluating covariates for Ψ. We considered visit, temperature, relative humidity, barometric pressure, Julian date, distance to nearest water source, and percent stand stocking as covariates for p individually and in additive combinations.

We evaluated the relationship of Ψ with 13 continuous covariates (Table 2). We hypothesized that any additive combination of these 13 covariates could be related to Ψ with the following exceptions: we included or excluded the 4 stem-density variables from models as a group (referred to hereafter as 'stems') because the variables collectively described the tree size-class distribution at a point; we did not use landscape variables from both radii in combination to avoid cross-scale correlations; and we only included covariates in additive combinations when their single-variate models were better than the null model.

These steps reduced the number of candidate models fit from potentially hundreds to 10–20/species (Appendix A). The global model for each species consisted of all the covariates included with the set candidate models. We examined tolerance values for covariates in the global model and all values were >0.4, so we concluded multicollinearity was not a problem (Allison 1999). We evaluated the overdispersion parameter and the goodness-of-fit test for evidence of lack of fit for the global model and then proceeded with model selection (Burnham and Anderson 2002).

We identified a confidence set of models with ΔAIC <4 and model-averaged models in the confidence set to obtain the average coefficients, unconditional standard errors, and 95% confidence interval for covariates (Burnham and Anderson 2002). We demonstrated effects of covariates by plotting model-averaged predictions of Ψ across the range of covariates represented by 7 points evenly spaced from 1st to 99th percentile, while holding other covariates at their mean. We interpreted all effects with model-averaged confidence intervals for coefficients that did not overlap zero and some other effects in the confidence set with effect sizes that warranted discussion, but explicitly noted in these cases that confidence intervals overlapped zero. Effect sizes should be considered for biological relevance, and confidence intervals for model-averaged parameters should not necessarily be treated like hypothesis tests (Burnham and Anderson 2002).

Table 2. Minimum, maximum, mean, and SE of continuous covariates that were used in an occupancy study of 5 bat species in the Missouri Ozark Highlands, USA, 2010–2012.

Covariate	Min.	Max.	Mean	SE
Conifer basal area	0.0	105.9	11.4	24.8
Fires in 10 yr	0.0	8.0	1.8	1.7
Sapling stems/ha	0.0	1,647.8	156.7	285.2
Poletimber stems/ha	0.0	575.7	51.2	56.7
Sawtimber stems/ha	0.0	283.2	21.7	26.2
Small stems/ha	0.0	66,817.9	6,316.2	16,645.6
Tree stocking %	0.0	225.3	84.7	40.3
Distance to water in m	1.8	548.1	238.2	143.3
Distance to road in m	2.1	1,992.9	467.7	460.5
% forest in 2-km radius	59.7	97.9	87.7	8.5
% urban in 2-km radius	0.6	21.3	4.0	3.5
% forest in 16-km radius	24.2	92.2	70.2	15.9
% urban in 16-km radius	2.3	11.5	5.2	2.4

RESULTS

We surveyed 369 points at 26 study areas; however, detectors failed at 27 points resulting in 342 points with data (Table 1). Tree stocking averaged 85% (Table 2) and 149, 165, and 28 points had levels of stocking associated with forest, woodland, and savanna communities, respectively. Percent forest in a 16-km radius ranged from 24% to 92% (Table 2). We recorded 565,624 call files with bat detectors across all years and sites and we detected all 5 focal species at ≥82 points.

Big Brown Bat
We detected big brown bats at 65% of points. The best model for estimating p included stand stocking, relative humidity, and Julian date (Table 3) and average $p = 0.580$. There was no evidence of lack of fit for the global model ($\hat{c} = 1.079$, $P = 0.304$). There were 2 models for estimating Ψ in the confidence set and the best model included 16klandcover, stems, and conifer basal area (Table 3). Site occupancy increased from 0.35 to 0.63 from 24% to 92% forest cover within 16 km and Ψ increased from 0.43 to 0.65 from 2% to 12% urban cover within 16 km (Fig. 1). The confidence intervals for the effect of stems and conifer basal area included 0 and coefficients were small (Table 4).

Eastern Red Bat
We detected eastern red bats at 91% of points. The best model for estimating p included stand stocking, distance to water, and Julian date (Table 3) and average $p = 0.870$. There was no evidence of lack of fit for the global model ($\hat{c} = 1.188$, $P = 0.295$). There were 2 models for estimating Ψ in the confidence set; the best model included 16klandcover, stems, and distance to road (Table 3). Site occupancy decreased 0.99

to 0.94 from 0 to 250 poletimber stems/ha (Fig. 2), Ψ decreased 0.98 to 0.92 from 2 m to 1,993 m from a road, and Ψ increased 0.91 to 0.99 from 24% to 92% forest (Fig. 1). All other covariates had confidence intervals that overlapped zero and effects were small (Table 4).

Northern Long-eared Bat
We detected northern long-eared bats at 61% of points. The best model for estimating p included distance to water, relative humidity, and barometric pressure (Table 3) and average $p = 0.680$. There was no evidence of lack of fit for the global model ($\hat{c} = 1.334$, $P = 0.256$). The best model for estimating Ψ in the confidence set included stems and 16klandcover (Table 3). Site occupancy decreased 0.78 to 0.09 from 0 to 66,818 small stems/ha, Ψ decreased 0.76 to 0.27 from 0 to 1,574 saplings/ha (Fig. 2), Ψ increased 0.41–0.83 from 24–92% forest cover, and Ψ decreased 0.84–0.37 from 2–12% urban cover (Fig. 1). Site occupancy increased slightly with poletimber stems/ha and decreased slightly with sawtimber stems/ha (Fig. 2), but coefficients for these effects overlapped zero (Table 4).

Evening Bat
We detected evening bats at 24% of points. The best model for estimating p included stand stocking, barometric pressure, and Julian date (Table 3) and average $p = 0.460$. There was no evidence of lack of fit for the global model ($\hat{c} = 1.095$, $P = 0.325$). Only 2 models for estimating Ψ were in the confidence set, and the best model included 16klandcover, stems, and fire (Table 3). Site occupancy decreased 0.79 to 0.16 from 24% to 92% forest cover, Ψ decreased 0.57 to 0.06 from 2% to 12% urban cover (Fig. 1), and Ψ increased from 0.22 to 0.77 from 0 to 8 fires in the past 10 years (Fig. 3). Small stems/ha and saplings/ha had positive

Table 3. The most supported site-occupancy models (ΔAIC <4) for 5 bat species in the Missouri Ozark Highlands, USA, 2010–2012. We present number of model parameters (K), log likelihood (LogLik), Akaike's Information Criterion (AIC), delta AIC (ΔAIC), and AIC weight (w_i) for each model. Models are composed of covariates affecting the probability a species occurred at a site (Ψ) and the probability of detecting a species, given it is present at a site (p).

Models[a] by species	K	LogLik	AIC	ΔAIC	w_i
Big brown bat					
Ψ[a] (16klandcover, stems, cona), p[b] (stocking, rh, date)	12	841.17	865.17	0	0.538
Ψ (16klandcover, conba), p (stocking, rh, date)	8	850.41	866.41	1.24	0.289
Eastern red bat					
Ψ (stems,16klandcover, road), p (stocking, water, date)	12	527.65	551.65	0	0.469
Ψ (stems,16klandcover, road, water), p (stocking, water, date)	13	525.84	551.84	0.19	0.426
Northern long-eared bat					
Ψ (16klandcover, stems), p (water, rh, bp)	11	806.95	828.95	0	0.449
Ψ (16klandcover, stems, fire), p (water, rh, bp)	12	806.29	830.29	1.34	0.230
Ψ (16klandcover, stems, conba), p (water, rh, bp)	12	806.93	830.93	1.98	0.167
Ψ (16klandcover, stems, conba, fire), p (water, rh, bp)	13	806.23	832.23	3.28	0.087
Ψ (global), p (water, rh, bp)	15	802.94	832.94	3.99	0.061
Evening bat					
Ψ (16klandcover, stems, fire), p (stocking, bp, date)	12	504.51	528.51	0	0.613
Ψ (16klandcover, fire), p (stocking, bp, date)	8	513.89	529.89	1.38	0.308
Tri-colored bat					
Ψ (16klandcover), p (stocking, temp, bp)	7	824.93	838.93	0	0.482
Ψ (16klandcover, fire), p (stocking, temp, bp)	8	823.73	839.73	0.8	0.323

[a] Occupancy covariates were as follows: conba = basal area of conifers; fire = the no. of fires in the past 10 year; stems = sapling stems/ha, poletimber stems/ha, sawtimber stems/ha, and small stems/ha; 16klandcover = % forest in 16 k and % urban in 16 k radius; water = distance to water in meters; road = distance to road in meters.

[b] Detection covariates were as follows: stocking = % tree stocking; rh = max. relative humidity, date = Julian date, water = distance to water in meters, temp = max. temperature, bp = mean barometric pressure.
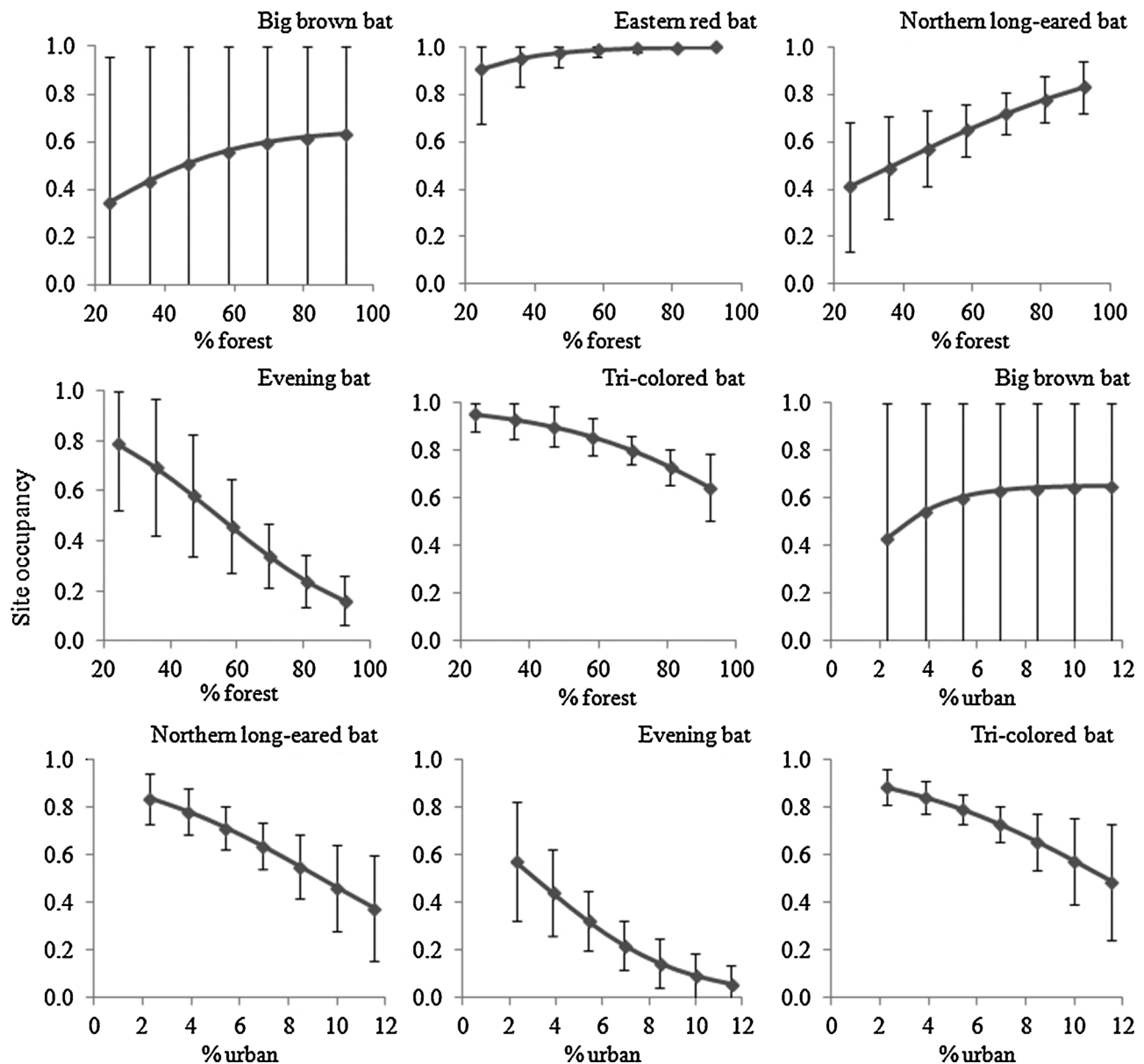
Figure 1. Probability of occupancy (Ψ) across the range of percent forest land cover in a 16-km radius for the big brown bat, eastern red bat, northern long-eared bat, evening bat, and tri-colored bat; and probability of occupancy across the range of percent urban land cover in a 16-km radius for the big brown bat, northern long-eared bat, evening bat, and tri-colored bat in the Missouri Ozark Highlands, USA, 2010–2012.

effects on Ψ and sawtimber stems/ha and poletimber stems/ha had negative effects on Ψ (Fig. 2), but confidence intervals for these effects overlapped zero (Table 4).

Tri-colored Bat

We detected tri-colored bats at 73% of points. The best model for estimating p included stand stocking, temperature, and barometric pressure (Table 3) and average $p = 0.750$. There was no evidence of lack of fit for the global model ($\hat{c} = 0.555$, $P = 0.495$). There were 2 models for estimating Ψ in the confidence set and the best model included 16klandcover (Table 3). Site occupancy decreased 0.95 to 0.64 from 24% to 92% forest cover in 16 km and Ψ decreased 0.88 to 0.49 from 2% to 12% urban cover in 16 km (Fig. 1). The number of fires in the past 10 years had a small positive effect on Ψ but its confidence interval overlapped zero (Table 4).

DISCUSSION

Most species had moderate to high site occupancy across the gradient of savanna, woodland, and forest. Tree densities varied greatly across this gradient, but there were only limited cases where bat species' site occupancy was related to densities of tree stems in different DBH classes. We hypothesized that big brown bats, eastern red bats, evening bats, and tri-colored bats would have greater site occupancy at sites with low tree density that were managed for savanna and woodland conditions than in denser non-managed forests. Our results for evening bats were consistent with our hypothesis. Evening bats occurred primarily in stands with lower densities of poletimber-size and sawtimber-size trees, which suggests savannas and woodlands are more suitable for this species than denser forests. Also, evening bats occurred

Table 4. Model-averaged coefficients, unconditional standard errors (SE), and the upper and lower bounds for the 95% confidence intervals for a confidence set of occupancy models with ΔAIC <4 for 5 bat species in the Missouri Ozark Highlands, USA, 2010–2012.

Variables by species	Coeff.	SE	Lower CI	Upper CI
Big brown bat				
% forest in 16-km radius	0.853	0.355	0.158	1.548
% urban in 16-km radius	1.529	0.615	0.325	2.734
Sapling stems/ha	−0.047	0.273	−0.583	0.488
Poletimber stems/ha	−0.118	0.310	−0.725	0.490
Sawtimber stems/ha	0.275	0.415	−0.539	1.090
Small stems/ha	1.194	1.196	−1.150	3.538
Conifer basal area	1.832	1.388	−0.889	4.552
Eastern red bat				
% forest in 16-km radius	0.958	0.408	0.158	1.758
% urban in 16-km radius	0.402	0.371	−0.326	1.130
Sapling stems/ha	0.122	0.415	−0.691	0.935
Poletimber stems/ha	−0.641	0.325	−1.277	−0.005
Sawtimber stems/ha	−0.096	0.341	−0.764	0.572
Small stems/ha	7.430	3.970	−0.351	15.211
Distance to road in m	−0.804	0.261	−1.316	−0.292
Distance to water in m	0.183	0.263	−0.332	0.698
Northern long-eared bat				
% forest in 16-km radius	0.455	0.201	0.060	0.849
% urban in 16-km radius	−0.560	0.201	−0.954	−0.166
Conifer basal area	−0.014	0.075	−0.160	0.133
Sapling stems/ha	−0.388	0.170	−0.721	−0.054
Poletimber stems/ha	0.127	0.185	−0.236	0.490
Sawtimber stems/ha	−0.120	0.163	−0.439	0.200
Small stems/ha	−0.886	0.342	−1.557	−0.215
Fires in 10 year	0.064	0.123	−0.177	0.305
Distance to water in m	−0.019	0.040	−0.098	0.060
Distance to road in m	0.014	0.031	−0.047	0.074
Evening bat				
% forest in 16-km radius	−0.702	0.240	−1.173	−0.231
% urban in 16-km radius	−0.809	0.300	−1.398	−0.221
Sapling stems/ha	0.013	0.167	−0.314	0.339
Poletimber stems/ha	−0.136	0.245	−0.617	0.345
Sawtimber stems/ha	−0.263	0.336	−0.921	0.395
Small stems/ha	0.529	0.512	−0.474	1.532
Fires in 10 yearr	0.552	0.173	0.214	0.890
Tri-colored bat				
% forest in 16-km radius	−0.568	0.249	−1.055	−0.080
% urban in 16-km radius	−0.545	0.207	−0.951	−0.139

in stands with higher small-stem densities and increased frequency of fire, which indicates that these bats respond to management. Management, either from fire or mechanical thinning, results in more open canopies, which can lead to higher understory densities if fires are at irregular intervals that allow periodic re-sprouting of shrubs and trees. Armitage and Ober (2012) also found higher overall bat activity below the forest canopy in pine forests in Florida with frequent prescribed fire than in forests without fire. Loeb and Waldrop (2008) also found higher bat activity in pine forest treated with both thinning and prescribed fire than in control stands.

We found little or no support for relationships between occupancy of big brown bats, eastern red bats, and tri-colored bats with stem densities or fire, so these species did not appear to be positively or negatively affected by savanna woodland restoration in the region. Red bats, evening bats, tri-colored bats (eastern pipistrelles), and big brown bats were detected more often in open habitats than in closed forest in the coastal plain of South Carolina, USA (Ford et al. 2006) and big brown bats, eastern red bats, northern long-eared bats, and tri-colored bats were detected more in forests

with less dense vegetation in western South Carolina (Loeb and O'Keefe 2006). Occupancy of eastern red bats and tri-colored bats were also negatively related to basal area in another Missouri study (Yates and Muzika 2006). In our study, occupancy model coefficients were negative for density of poletimber or sawtimber for big brown and eastern red bats, but effect sizes were small and confidence intervals overlapped zero. We may have found weaker relationships with tree density or basal area for these species than in some previous studies (Ford et al. 2006, Loeb and O'Keefe 2006, Yates and Muzika 2006) because those studies included non-forested habitats, which could have driven relationships with tree density. Another reason for weaker relationships in our study between eastern red bats and tree density was that they were ubiquitous in our landscape.

We found some support for our hypothesis that northern long-eared bats were the most adapted species to cluttered environments, such as non-managed forest. Site occupancy was positively related to density of poletimber-sized trees, and high densities of pole-timber sized trees are indicative of mid-successional, non-managed forest (Oliver and Larson 1990). Northern long-eared bat was the most adapted of the

species we studied to cluttered (i.e., dense vegetation) habitats based on its wing morphology and exclusive use of frequency-modulated calls (Neuweiler 1989, Norberg 1994, Amelon 2007).

We found support for large-scale landscape relationships (16-km radius around points), and perhaps surprisingly these relationships were more prevalent across species than for point-level vegetation structure. Bats can use large areas and different resources for foraging and roosting, so it is not surprising to us that land-cover composition was important at this scale. Big brown bats travel up to 11 km to reach foraging sites (Arbuthnott and Brigham 2007); and other insectivorous bats, such as the spotted bat (*Euderma maculatum*) and Virginia big-eared bat (*Corynorhinus townsendii virginianus*), travel up to 36.3 km and 8.4 km, respectively (Adam et al. 1994, Chambers et al. 2011). Yates and Muzika (2006) found support for effects of landscape factors on site occupancy of eastern red bats and northern long-eared bats, but not tri-colored bats. Loeb and O'Keefe (2006) did not find any support for relationships between bat habitat use and landscape features in South Carolina; however, they suggested looking at other landscape features that might have support. Our study and others show that it is important to look at both a large landscape and habitat scales when assessing habitat relationships of bats.

Urban areas may have lower bat occurrence than forest because they can have less vegetation, insect abundance, and diversity than rural and forested areas (Faeth and Kane 1978). Northern long-eared, evening, and tri-colored bat occurrence was decreased with percent urban land cover, but big brown bat occurrence increased. The big brown bat is the most common bat to be found in urban areas and is usually the species inhabiting buildings, so while this species also uses forested areas, it has habituated to using urban areas (Agosta 2002). Although our landscapes were mostly forested, urban areas can provide islands of habitat in agricultural areas (Gehrt and Chelsvig 2003).

Big brown, eastern red, and northern long-eared bat occurrence increased with percent forest cover in a 16-km landscape, while evening and tri-colored bat occurrence decreased with forest cover. Other studies have shown that the northern long-eared bat roosts and forages in intact forests and that in fragmented landscapes it is constrained to using only forested areas (Sasse and Pekins 1996, Carter and Feldhamer 2005, Broders et al. 2006, Yates and Muzika 2006, Henderson and Broders 2008), so it is not surprising that their occurrence increased with the amount of forest in the landscape. Big brown and eastern red bat make use of open and urban areas and are adapted to foraging in less cluttered habitats, so we think it is important to note these species are still responding to the amount of forest in the landscape. For red bats, this is likely because they roost in tree canopies in the breeding season and leaf litter on the forest floor during winter (Mager and Nelson 2001, Mormann and Robbins 2007). Evening bats had greater occurrence in stands with lower tree density, so perhaps at a landscape scale they prefer less tree cover as well. Savanna and woodlands (i.e., forest with low tree density) are ecotonal communities and are, therefore, likely to occur in landscapes with some amount of open land. The occurrence of tri-colored bats declined with forest and urban cover, suggesting that some complement of open land in the landscape was desirable.
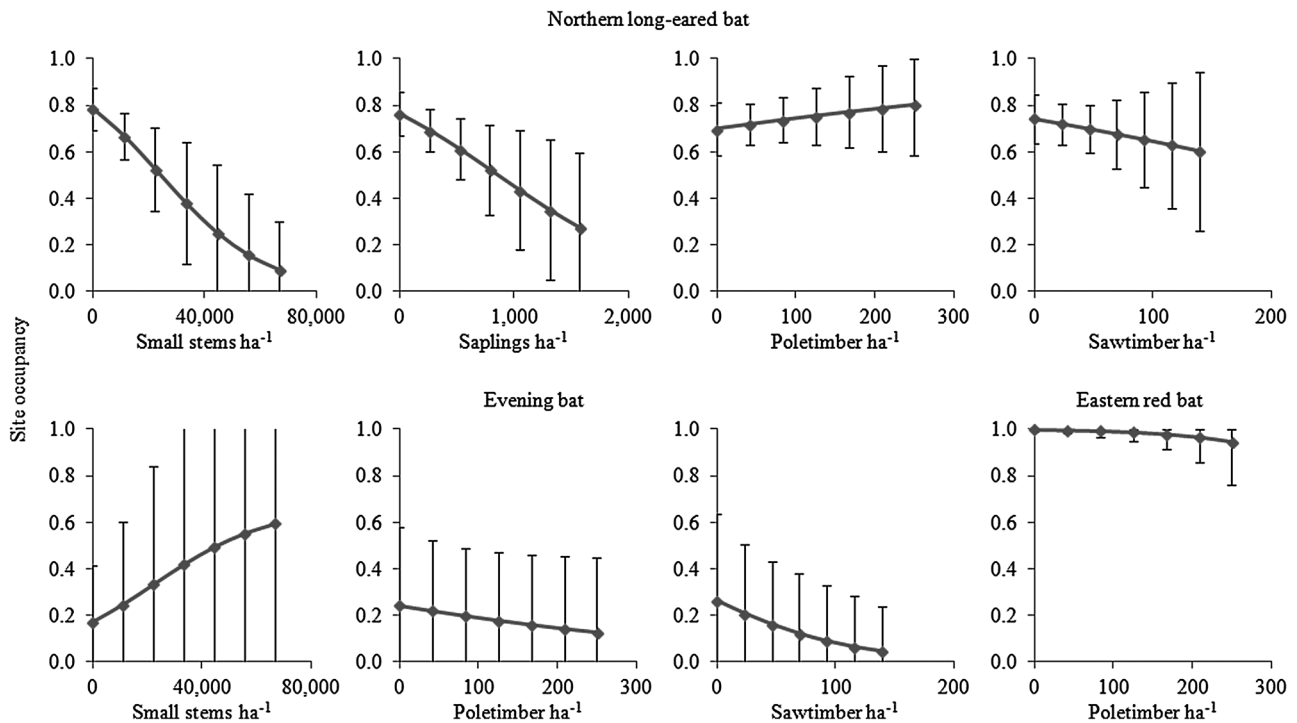

Figure 2. Probability of occupancy (Ψ) across the range of small stems/ha, saplings/ha, poletimber/ha, and sawtimber/ha for the northern long-eared bat; probability of occupancy across the range of small stems/ha, poletimber/ha, and sawtimber/ha for the evening bat; and probability of occupancy across the range of poletimber/ha for the eastern red bat in the Missouri Ozark Highlands, USA, 2010–2012.
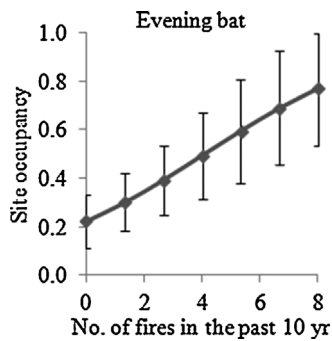
Figure 3. Probability of occupancy (Ψ) across the range of number of fires in the past 10 years for the evening bat in the Missouri Ozark Highlands, USA, 2010–2012.

Ethier and Fahrig (2011) similarly found that the relative abundance of tri-colored bats decreased as the amount of forest cover increased in the landscape in eastern Ontario, Canada.

MANAGEMENT IMPLICATIONS

To be most successful, bat conservation will likely need to consider individual species of bats because habitat and landscape relationships varied among bat species. Land managers should be cognizant of large-scale land cover composition and structure, even if it is beyond their control, because it provides important constraints or context for what they manage locally. It may not be sensible to manage local habitat structure for a species in a landscape that is not suitable for it. We suggest the use of prescribed fire and forest thinning to restore and maintain savanna and woodlands has minimal, if any, negative effects on these bat species and may benefit some species. Therefore, managers can promote certain vegetation communities for target species, or manage for a diversity of communities within the landscape to meet the needs of the species we studied.

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Appendix A.

Appendix A. The number of parameters (*K*), log likelihood (LogLik), Akaike's Information Criterion (AIC), delta AIC (ΔAIC), and AIC weight (w_i) for candidate models used to determine relationships between site occupancy for 5 bats and habitat and landscape factors in the Missouri Ozark Highlands, USA, 2010–2012. Models are composed of covariates affecting the probability a species occurred at a site (Ψ) and the probability of detecting a species, given it is present at a site (*P*).

Models[a] by species	K	LogLike	AIC	ΔAIC	w_i
Big brown bat					
Ψ[b] (stocking, rh, date)	12	841.17	865.17	0.00	0.538
Ψ (16klandcover, conba), *p* (stocking, rh, date)	8	850.41	866.41	1.24	0.289
Ψ (16klandcover, stems), *p* (stocking, rh, date)	11	848.04	870.04	4.87	0.047
Ψ (global), *p* (stocking, rh, date)	15	840.30	870.30	5.13	0.041
Ψ (16klandcover), *p* (stocking, rh, date)	7	857.13	871.13	5.96	0.027
Ψ (stems, conba), *p* (stocking, rh, date)	10	851.29	871.29	6.12	0.025
Ψ (conba), *p* (stocking, rh, date)	6	859.77	871.77	6.60	0.020
Ψ (stems), *p* (stocking, rh, date)	9	856.59	874.59	9.42	0.005
Ψ (.), *p* (stocking, rh, date)	5	865.73	875.73	10.56	0.003
Ψ (fire), *p* (stocking, rh, date)	6	865.44	877.44	12.27	0.001
Ψ (2klandcover), *p* (stocking, rh, date)	7	863.46	877.46	12.29	0.001
Ψ (water), *p* (stocking, rh, date)	6	865.56	877.56	12.39	0.001
Ψ (road), *p* (stocking, rh, date)	6	865.64	877.64	12.47	0.001
Eastern red bat					
Ψ (stems, 16klandcover, road), *p* (stocking, water, date)	12	527.65	551.65	0.00	0.469
Ψ (stems, 16klandcover, road, water), *p* (stocking, water, date)	13	525.84	551.84	0.19	0.426

(*Continued*)

Models[a] by species	K	LogLike	AIC	ΔAIC	w_i
Ψ (global), p (stocking, water, date)	15	525.83	555.83	4.18	0.058
Ψ (stems, road), p (stocking, water, date)	10	537.45	557.45	5.80	0.026
Ψ (stems, 16klandcover, water), p (stocking, water, date)	12	536.17	560.17	8.52	0.007
Ψ (stems, 16klandcover), p (stocking, water, date)	11	538.75	560.75	9.10	0.005
Ψ (stems, water), p (stocking, water, date)	10	541.19	561.19	9.54	0.004
Ψ (16klandcover, road), p (stocking, water, date)	8	545.84	561.84	10.19	0.003
Ψ (stems), p (stocking, water, date)	9	545.46	563.46	11.81	0.001
Ψ (16klandcover, road, water), p (stocking, water, date)	9	545.83	563.83	12.18	0.001
Ψ (road), p (stocking, water, date)	6	554.47	566.47	14.82	<0.001
Ψ (road, water), p (stocking, water, date)	7	552.48	566.48	14.83	<0.001
Ψ (16klandcover), p (stocking, water, date)	7	554.16	568.16	16.51	<0.001
Ψ (16klandcover, water), p (stocking, water, date)	8	553.40	569.40	17.75	<0.001
Ψ (water), p (stocking, water, date)	6	558.06	570.06	18.41	0.000
Ψ (.), p (stocking, water, date)	5	560.48	570.48	18.83	0.000
Ψ (conba), p (stocking, water, date)	6	560.01	572.01	20.36	0.000
Ψ (fire), p (stocking, water, date)	6	560.31	572.31	20.66	0.000
Ψ (2klandcover), p (stocking, water, date)	7	559.21	573.21	21.56	0.000
Northern long-eared bat					
Ψ (16klandcover, stems), p (water, rh, bp)	11	806.95	828.95	0.00	0.449
Ψ (16klandcover, stems, fire), p (water, rh, bp)	12	806.29	830.29	1.34	0.230
Ψ (16klandcover, stems, conba), p (water, rh, bp)	12	806.93	830.93	1.98	0.167
Ψ (16klandcover, stems, conba, fire), p (water, rh, bp)	13	806.23	832.23	3.28	0.087
Ψ (global), p (water, rh, bp)	15	802.94	832.94	3.99	0.061
Ψ (16klandcover, fire), p (water, rh, bp)	8	823.28	839.28	10.33	0.003
Ψ (16klandcover), p (water, rh, bp)	7	825.34	839.34	10.39	0.003
Ψ (16klandcover, conba, fire), p (water, rh, bp)	9	823.16	841.16	12.21	0.001
Ψ (16klandcover, conba), p (water, rh, bp)	8	825.20	841.2	12.25	0.001
Ψ (2klandcover), p (water, rh, bp)	7	835.88	849.88	20.93	0.000
Ψ (stems), p (water, rh, bp)	9	840.91	858.91	29.96	0.000
Ψ (stems, conba), p (water, rh, bp)	10	839.51	859.51	30.56	0.000
Ψ (stems, fire), p (water, rh, bp)	10	839.94	859.94	30.99	0.000
Ψ (stems, conba, fire), p (water, rh, bp)	11	838.58	860.58	31.63	0.000
Ψ (conba, fire), p (water, rh, bp)	7	850.68	864.68	35.73	0.000
Ψ (conba), p (water, rh, bp)	6	853.72	865.72	36.77	0.000
Ψ (fire), p (water, rh, bp)	6	853.74	865.74	36.79	0.000
Ψ (.), p (water, rh, bp)	5	856.45	866.45	37.50	0.000
Ψ (water), p (water, rh, bp)	6	856.02	868.02	39.07	0.000
Ψ (road), p (water, rh, bp)	6	856.22	868.22	39.27	0.000
Evening bat					
Ψ (16klandcover, stems, fire), p (stocking, bp, date)	12	504.51	528.51	0.00	0.613
Ψ (16klandcover, fire), p (stocking, bp, date)	8	513.89	529.89	1.38	0.308
Ψ (global), p (stocking, bp, date)	15	503.30	533.30	4.79	0.056
Ψ (stems, fire), p (stocking, bp, date)	10	516.10	536.10	7.59	0.014
Ψ (16klandcover), p (stocking, bp, date)	7	524.30	538.30	9.79	0.005
Ψ (16klandcover, stems), p (stocking, bp, date)	11	517.13	539.13	10.62	0.003
Ψ (fire), p (stocking, bp, date)	6	527.78	539.78	11.27	0.002
Ψ (stems), p (stocking, bp, date)	9	532.57	550.57	22.06	0.000
Ψ (.), p (stocking, bp, date)	5	543.22	553.22	24.71	0.000
Ψ (road), p (stocking, bp, date)	6	542.53	554.53	26.02	0.000
Ψ (conba), p (stocking, bp, date)	6	543.13	555.13	26.62	0.000
Ψ (water), p (stocking, bp, date)	6	543.13	555.13	26.62	0.000
Ψ (2klandcover), p (stocking, bp, date)	7	542.00	556.00	27.49	0.000
Tri-colored bat					
Ψ (16klandcover), p (stocking, temp, bp)	7	824.93	838.93	0.00	0.482
Ψ (16klandcover, fire), p (stocking, temp, bp)	8	823.73	839.73	0.80	0.323
Ψ (fire), p (stocking, temp, bp)	6	831.70	843.70	4.77	0.044
Ψ (.), p (stocking, temp, bp)	5	834.40	844.40	5.47	0.031
Ψ (stems), p (stocking, temp, bp)	9	826.62	844.62	5.69	0.028
Ψ (road), p (stocking, temp, bp)	6	832.77	844.77	5.84	0.026
Ψ (2klandcover), p (stocking, temp, bp)	7	831.06	845.06	6.13	0.023
Ψ (global), p (stocking, temp, bp)	15	815.48	845.48	6.55	0.018
Ψ (water), p (stocking, temp, bp)	6	834.15	846.15	7.22	0.013
Ψ (conba), p (stocking, temp, bp)	6	834.27	846.27	7.34	0.012

[a] Occupancy covariates were as follows: conba = basal area of conifers; fire = the no. of fires in the past 10 year; stems = sapling stems/ha, poletimber stems/ha, sawtimber stems/ha, and small stems/ha; 16klandcover = % forest in 16-km and % urban in 16-km radius; 2klandcover = % forest in 2-km and % urban in 2-km radius; water = distance to water in meters; road = distance to road in meters.
[b] Detection covariates were: stocking = % tree stocking; rh = max. relative humidity, date = Julian date, water = distance to water in meters, temp = max. temperature, bp = mean barometric pressure.