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Source: Journal of Wildlife Management, 70(5):1238-1248.

Published By: The Wildlife Society

DOI: http://dx.doi.org/10.2193/0022-541X(2006)70[1238:EOFSAF]2.0.CO;2

URL: http://www.bioone.org/doi/full/10.2193/0022-541X%282006%2970%5B1238%3AEOFSAF%5D2.0.CO%3B2

Research Article

Effect of Forest Structure and Fragmentation on Site Occupancy of Bat Species in Missouri Ozark Forests

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Abstract

*Changes in structure and arrangement of forests may influence the distribution of bat communities by affecting roosting and foraging habitat. Using Anabat bat detectors, we determined presence of bat species at 316 sample plots in southeastern Missouri, USA, through qualitative identification of echolocation calls collected. We used maximum-likelihood estimation techniques incorporating detection probabilities into estimation of site occupancy by species of bats. We compared a priori models at 2 geographic scales using information theoretic methods. At the local-site scale, eastern pipistrelle (*Pipistrellus subflavus*) and red bat (*Lasiurus borealis*) occupancy was most influenced by structural characteristics of forested areas, whereas Indiana bats (*Myotis sodalis*) were influenced most by density of large-diameter snags that could provide roosting habitat. At the landscape scale, occupancy of Indiana bats was directly related to amount of nonforested land cover. Northern long-eared bat (*M. septentrionalis*) occupancy was inversely related to edge. These data describe implications of forest fragmentation and provide information that can be used when integrating forest-management practices into bat conservation.* (JOURNAL OF WILDLIFE MANAGEMENT 70(5):1238–1248; 2006)

Key words

acoustic detection, forest fragmentation, Lasiurus borealis, *Missouri Ozarks,* Myotis septentrionalis, Myotis sodalis, *occupancy,* Pipistrellus subflavus.

The continued decline of several bat species associated with forests underscores the need for increased understanding of habitat relationships for North American bats (Fenton 1997, O'Shea et al. 2003, Menzel et al. 2005*a*). Miller et al. (2003) noted the paucity of research on forest-dwelling bats, with particular gaps in studies conducted in the midwestern United States. As with many other species, habitat suitability for bats may be influenced by various factors at multiple spatial scales (Balcom and Yahner 1996, Grindal and Brigham 1999, Hagan and Meehan 2002). These factors and scales may be particularly important for bats because of differences between roosting and foraging requirements (Mager and Nelson 2001, Menzel et al. 2005*a*). At smaller stand scales, basal area and size distribution of trees and snags (Crampton and Barclay 1998, Waldien et al. 2000, Aguirre et al. 2003), solar exposure (Callahan et al. 1997, Lacki and Schwierjohann 2001), and stand openness (Thomas 1988, Ford et al. 2005) have been found to influence bat presence. Supporting this, Aldridge and Rautenbauch (1987) and Norberg and Rayner (1987) described morphological differences in echolocation call structure and wing form that may influence species response to forest structure characteristics. In addition, the presence of water has been cited as being of great importance as a habitat resource for bat species, particularly for gray (*Myotis grisescens*) and Indiana bats (*M. sodalis*; Menzel et al. 2001, Johnson 2002, Ford et al. 2005, Menzel et al. 2005*b*).

Fewer studies have investigated habitat characteristics of bats at larger landscape scales. Krusic et al. (1996) discussed the importance of a matrix of different land cover types to fulfill all of the habitat requirements of bats. Gorresen and Willig (2004) found that bat diversity in a tropical forest was greatest in a landscape of diverse cover types. Example landscape characteristics that influence bat species distribution include extent of fragmentation, patch size, and presence of edge habitat (Grindal and Brigham 1999, Law et al. 1999, Estrada and Coates-Estrada 2002).

Current shifts in land use and land ownership patterns influence forest structure and composition characteristics at both the local site and landscape scale (Sampson and DeCoster 2000). Shifts in ownership patterns of the Midwest may indicate increased fragmentation due to development and greater number of forest-management units (Gobster et al. 2000), and parcelization affects age structure and arrangement of forest landscapes (Ko 2005). In Southeastern Missouri 82% of the forested area is held by nonindustrial private landowners (Moser et al. 2003). With increased pressure on forest ecosystems for a variety of resources, a critical component of forest-management planning should include an understanding of how changes across a forested landscape affect bat distribution. Accordingly, our goal was to determine the influence of forest composition, structure, and arrangement at multiple scales on the occupancy of bat species across 2 forested watersheds in the Ozark Highlands of Missouri, USA.

Study Area

We conducted our study within the upper portions of the St. Francis and Black River watersheds of southeastern Missouri (Fig. 1) during summers of 2002, 2003, and 2004. These 2 adjacent watersheds encompassed 708,000 ha (1.75 million acres) of the central hardwood forest region (Braun 1950) within the Ozark Highlands section, which

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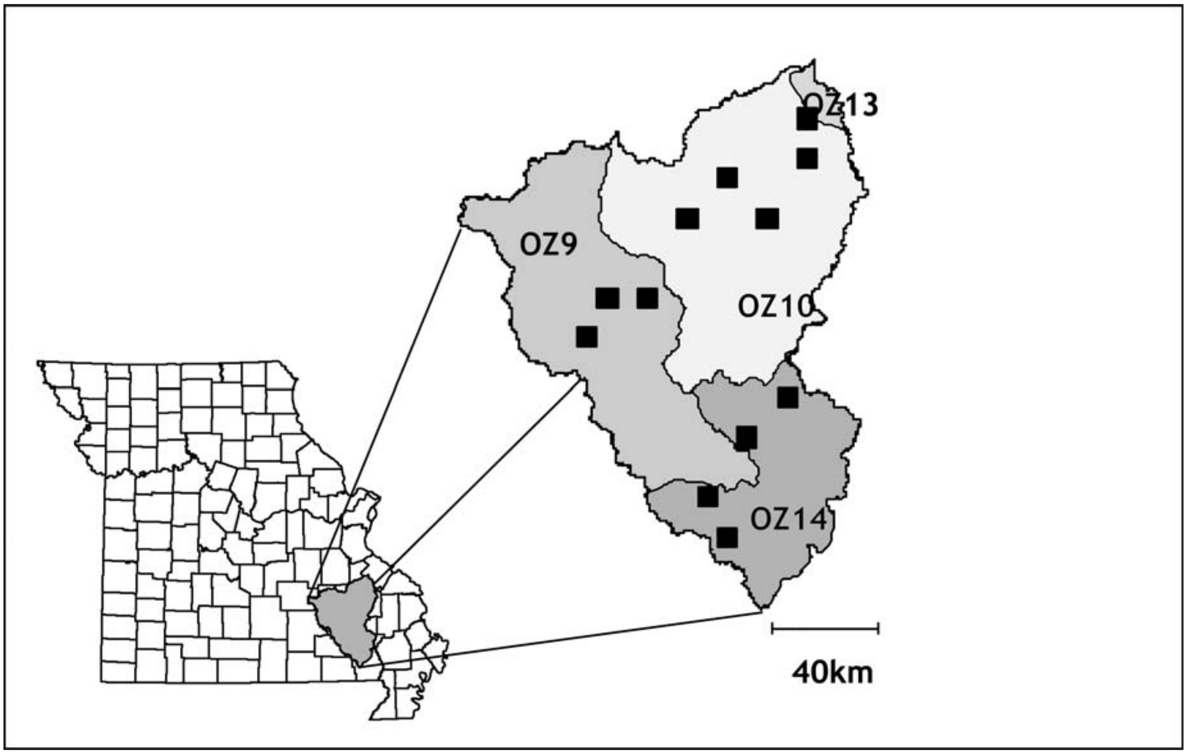

Figure 1. Study area (inset) in southeastern Missouri, USA, encompassing the watersheds of the St. Francis and Black Rivers. Ecological subsections of the study area are identified by shading and designated as OZ9, Current River Hills; OZ 10, St. Francis Knobs and Basins; OZ 13, Inner Ozark Border; and OZ 14, Black River Ozark Border. Squares represent locations of individual 23.3-km^2 study cells used for bat and habitat sampling in 2002–2004.

contained 4 different ecological subsections as described by Nigh and Schroeder (2002): 1) Current River Hills (OZ 9), 2) St. Francis Knobs and Basins (OZ 10), 3) Inner Ozark Border (OZ 13), and 4) Black River Ozark Border (OZ 14). This area was highly topographically dissected and geologically heterogeneous with a considerable number of karst features. Land cover classification derived from 30-m × 30-m-resolution Landsat imagery (1992) as determined by Missouri Resource Assessment Partnership (MoRAP) revealed a dominance of forested cover (90%), mostly in upland deciduous oak (*Quercus* spp.) forests with a lesser proportion in shortleaf pine (*Pinus echinata*)–mixed-hardwood forests.

Methods

Acoustic Detection

We collected bat echolocation calls using Anabat II bat detectors coupled with Zero-Crossing Analysis Interface Modules with CF memory card storage (CF ZCAIM; Titley Electronics, Ballina, New South Wales, Australia), passively sampling each location. To protect detectors from inclement weather, we housed the equipment in plastic containers with the microphone aligned with an opening leading to a 45° polyvinyl chloride (PVC) elbow directed upwards. We placed 2 detector units at each location for one evening during the 2002 and 2003 field season and 2 consecutive evenings during the 2004 field season. During the 2002 field season, we conducted acoustic sampling from July to the first week of September. During the 2003 and 2004 field seasons, we conducted acoustic sampling from mid-May to the first week of September. We suspended detectors 1 m above the ground and oriented detectors at a sample point to maximize the probability of recording bat calls and minimize overlap of detection zones between detectors (Larson and Hayes 2000, Weller and Zabel 2002, Duchamp et al. 2006). We calibrated detectors to minimize variation in zone of reception among detectors as described by Livengood (2003), as this variation can result in unequal sampling areas among detector sites and lead to biased occupancy rates associated with certain detectors (Hayes 2000, Larson and Hayes 2000). We recalibrated detectors from one field season to the next to minimize detector biases.

We downloaded the bat echolocation calls that were collected, and we analyzed them using Analook software (http://users.lmi.net/corben/anabat.htm). We identified species based on qualitative and quantitative parameters from known call libraries (C. Corben and M. O'Farrell, O'Farrell Biological Consulting, unpublished data) and published accounts (Fenton and Bell 1981, O'Farrell et al. 1999, Livengood 2003, Menzel et al. 2003). We made species determination by using call characteristics such as slope, and minimum frequency as calculated by Analook, as well as general shape and consistency of minimum frequency throughout the call sequence. To minimize error rates, we used a strict filter (Britzke 2003) to eliminate call sequences

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Table 1. Model name, habitat covariates, and range of data values of each covariate included in a priori models used to explain bat occupancy at the local site scale during 2002–2004 in the St. Francis and Black River watersheds, Missouri, USA.

Model name	Covariates	Covariate value range	k^a
Topography model 1	Aspect	0–360°	2
Topography model 2	Aspect, % slope	0–360° 0–60%	3
Topography model 3	Aspect, Relative slope position	0–360° 1–10[b]	3
Roosting model 1	BA of live trees >30 cm dbh	0–23 m^2/ha	2
Roosting model 2	BA of snags >30 cm dbh	0–3 m^2/ha	2
Roosting model 3	BA of live trees >30 cm dbh, BA of snags >30 cm dbh, Overstory height	0–23 m^2/ha 0–3 m^2/ha 6–30 m	4
Roosting model 4	BA of all snags	0–7 m^2/ha	2
Roosting model 5	BA of shortleaf pine >30 cm dbh	0–14 m^2/ha	2
Clutter model 1	BA of all live trees, Canopy closure	8–45 m^2/ha 1–10[c]	3
Clutter model 2	BA of all live trees, Understory density from 1–2 m, Understory density from 2–3 m	8–45 m^2/ha 0–28[d] 0–30[d]	3
Clutter model 3	Understory density from 1–2 m, Understory density from 2–3 m, Overstory height	0–28[d] 0–30[d] 6–30 m	3
Water Model 1	Distance to nearest water	0.008–5.7 km	2

[a] k represents the number of variables incorporated in the model with the addition of 1 for the intercept.

[b] Relative slope measured as a categorical variable where 1 represents bottom of the slope and 10 the top of the slope.

[c] Canopy closure measured as categorical variable where 1 = ≤5% canopy closure, 2 = 5–25% canopy closure, 3 = 25–50% canopy closure, 4 = 50–75% canopy closure, and 5 = 75–100% canopy closure.

[d] Understory density consists of 2 measurements each representing the number of 10-cm squares obscured more than 50% from a total of 30 squares.

Table 2. Model name, landscape covariates, and range of data values of each covariate included in a priori models used to explain bat occupancy at the landscape scale during 2002–2004 in the St. Francis and Black River watersheds, Missouri, USA. Landscape metrics were derived using Fragstats and all values other than proportional land cover are unitless.

Model name	Covariates	Covariate value range	k^a
Landtype model 1	Ecological subsection		4
Land index model 1	Patch richness density	827–1861	2
Land index model 2	Area-weighted shape index	1.18–1.47	2
Land index model 3	Contagion	70–89	2
Land index model 4	Area-weighted shape index, Contagion	1.18–1.47 70–89	3
Land cover model 1	Upland deciduous forest cover, Area-weighted mean patch area	31–90% 3.4–7.8	3
Land cover model 2	Non-forested cover, Area-weighted mean patch area	6–64% 3.4–7.8	3
Land cover model 3	Urban cover, Area-weighted mean patch area	0–1% 3.4–7.8	3

[a] k represents the number of variables incorporated in the model with addition of 1 for the intercept.

with <5 call pulses as well as call sequences of poor quality, and we identified each call sequence twice. If the 2 identifications of the call sequence differed, we accessed it a third time.

Bats are known to switch frequently among roost trees within a defined area (Lewis 1995, Vonhof and Barclay 1996, Brigham et al. 1997*b*, Hutchinson and Lacki 2000, Menzel et al. 2000, Mager and Nelson 2001). Therefore, to meet the requirement of a closed population, we divided a single evening into 4 equal time periods (2000–2230, 2230–0100, 0100–0330, and 0330–0600 hours) with each time period treated as a sampling visit. If a call was recorded during that time period, we considered that species present and occupying the site. We defined occupancy as having a species present during the time sampled. If no identifiable call was recorded during a time period, we considered that species as not detected. We analyzed the resulting detection history with methods discussed in MacKenzie et al. (2002) using the software package PRESENCE to estimate proportion of sites occupied (http://www.mbr-pwrc.usgs.gov/software.html#surviv).

Study Area and Sample Point Selection

Using Global Information System, we superimposed the 2 watersheds with a grid of cells each 23.3 km^2 (9 mile^2) in size. We randomly selected 12 cells distributed across the 2 watersheds as study cells in which to focus our acoustic sampling effort. Our study was a portion of a larger project accessing the sustainability of central hardwood forests incorporating social, economic, and biological dimensions of natural resource management (Swihart and Slade 2004). We selected these 2 watersheds as representative in both landownership patterns and land cover found in the Ozark Highlands of Missouri. Therefore, we delineated size of the study cell to encompass the needs of multiple research projects. To determine placement of sample points within each study cell, we used a random point generator in ArcView 3.2 under the constraint of being within either upland deciduous forest or shortleaf pine–mixed-hardwood forest. We categorized forest patches in either of these cover types into 1 of 3 size classes: small (0.5–25 ha), medium (25–100 ha), and large (>100 ha), for a total of 6 sample-unit categories. We apportioned sample effort according to relative area in each size class–forest cover type combination.

Model Selection

We developed a priori models to examine the relationship between bat species occupancy and site (Table 1) and landscape (Table 2) characteristics based on the literature and field observations. We used information theoretic methods to determine which of the models within the selected set provided the best fit with the fewest parameters (i.e., most parsimonious model [Anderson et al. 2000]). Due to the relatively low number of sample points in relation to the number of covariates used in the models, we used Akaike's Information Criteria adjusted for small sample size (AIC_c) in the model selection process. We considered the model with the smallest AIC_c value to best fit the data in relation to others in the given model set. We tested data for each species at each spatial scale to determine if the sampling variance exceeded theoretical sampling variance using methods described by MacKenzie and Bailey (2004). We developed these models for both local site and landscape scale from our field observations and from results in related literature (Decher and Choate 1995, Vonhof and Barclay 1996, Carter et al. 1999, Foster and Kurta 1999, Mager and Nelson 2001).

To incorporate detection probability properly into estimation of occupancy, we compared models influencing ability to detect a bat species using AIC_c (Hayes 2000, Sherwin et al. 2000, Weller and Zabel 2002, Patriquin et al. 2003, Broders et al. 2004). Covariates for detectability included year, time of season a site was sampled as divided into 7 2-week time periods (25 May–31 Aug), Julian date, understory density, minimum temperature (range 6–25°C), maximum temperature (range 17–38°C), and total precipitation during the day sampling took place (range 0–3.8 cm). We obtained weather data from 4 weather stations within the bounds of the 2 watersheds from National Climate Data Center on the National Oceanic and Atmospheric Administration website. We used existing literature to develop a list of covariates that could be used to explain detectability of bat echolocation calls. We did not, however, conclude that existing knowledge on the topic was sufficiently comprehensive to allow for the creation of a priori models. Using the program PRESENCE, we compared the AIC_c values of each of the detection covariates alone, and we then combined the 2 covariates with the highest values to see if the combination yielded a model that better fit the data than the highest single covariate alone. Once we determined the most parsimonious combination of covariates for each species, we included this detection probability model as part of all occupancy model comparisons for both the local site and landscape scales of that species.

We used AIC_c weights (w_i) for model selection among a priori habitat occupancy models at both spatial scales. We used the global model containing all habitat covariates for a given scale to test whether a significant difference existed between the covariates of the detectability model alone and occupancy model with the lowest w_i, using likelihood ratio test ($P < 0.1$; Anderson et al. 2000). Due to high levels of model uncertainty, we used model averaging as described by Anderson et al. (2000) to increase precision and minimize bias of parameter estimates. For model averaging we included the model with the highest w_i, adding additional models of the next-highest w_i until their sum was ≥ 0.95. We considered covariates included in models within 2 AIC_c units of the best model important in describing probability of occupancy of a bat species at that spatial scale.

Forest Structure and Composition

We determined basal area (BA) of each sample site using a 10-factor prism and 5 variable-radius plots arrayed around the sample site (Avery and Burkhart 2002). At point center, we took a single variable-radius plot measurement and at 60 m in each cardinal direction from the center. We used these measures to estimate size and species composition of tree species at forest plots. We estimated overstory and understory density at each sample point by taking measurements 5 m from center in each cardinal direction. By observing the number of 10 × 10-cm squares obscured on a 3-m × 0.3-m-tall density cover board from plot center in each cardinal direction, we estimated the density of the understory (Nudds 1977) from 1–2 m and from 2–3 m. We measured overstory canopy closure using a 12.5-cm section of 5-cm-diameter PVC pipe and estimating amount of canopy closure as viewed through the tube and assigned measurement values into one of 5 categorical classifications. We measured distance to water in km from a particular sample plot center to the nearest water source designated in land cover image.

Landscape Metrics

To assess landscape-level habitat metrics, and to avoid the abrupt delineation associated with the cell, we digitally circumscribed each 23.3-km^2 study cell with a 1.6-km (1-mile) buffer. The buffer incorporated additional area surrounding each study cell to ensure that landscape characteristics influencing sample locations near the edge of the 23.3-km^2 cell would be included in the calculation of metrics at this scale. We calculated landscape metrics from the resulting 64.8-km^2 (25-$mile^2$) area of each study cell, using FRAGSTATS 3.3 (MacGarigal et al. 2002). We used area-weighted mean shape index as a measure of the patch shape complexity, with increasing values indicating greater complexity and amount of edge present in the landscape. We used contagion as index of land cover interspersion, where a low value indicated high levels of interspersion and, thus, indicated higher levels of fragmentation. Patch richness density reflected the diversity of patch types within a study cell. Area-weighted mean patch size represented a measure of the average patch size within a study cell. We calculated the proportion of the landscape found in upland deciduous forest, nonforested and urban cover types within the GIS of each of the study cells. The nonforested coverage class incorporated agricultural lands, glades, and grasslands, whereas urban and upland-deciduous forest cover types remained as defined by MoRAP classification.

Results

We detected bat presence at 48% of 316 sites. From bat calls, we identified 9 species; 5 of these were present at $\geq$10% of the sample points, and we used them for further

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Table 3. Covariates incorporated into models for detection probability of each bat species as determined by lowest value of Aikaike's Information Criterion adjusted for small sample size. The indicated covariates were used as the null model during model selection process for occupancy rates during 2002–2004 in the St. Francis and Black River watersheds, Missouri, USA.

Species	Covariates	k[a]
Eastern pipistrelle	Minimum temperature, within-season time period	8
Red bat	Precipitation	2
Northern long-eared bat	Year, precipitation	4
Indiana bat	Year	3
Gray bat	Year	3

[a] k represents the number of variables incorporated in the model with addition of 1 for the intercept.

analysis: 1) eastern pipistrelle (*Pipistrellus subflavus*; 25% of sites), 2) red bat (*Lasiurus borealis*; 20% of sites), 3) northern long-eared bat (*Myotis septentrionalis*; 19% of sites), 4) gray bat (10% of sites), and 5) Indiana bat (11% of sites).

Detection Probability

The most parsimonious model for detectability varied among species (Table 3). Year during which sampling occurred was the most-frequently included covariate in the detectability model with the lowest AIC_c weight. Year alone was the model with the most support for both the gray bat ($AIC_c = 399.2$) and the Indiana bat ($AIC_c = 469.6$). For both of these species, detectability was lowest during the 2002 field season and highest during the 2003 field season. Year and precipitation (range = 0–3.75 cm) were the covariates in the detectability model with the most support for northern long-eared bat ($AIC_c = 684.3$). Detectability for the northern long-eared bat was lowest during 2002 and highest in 2003, while an inverse relationship existed between detectability and precipitation during sampling. Precipitation alone was the detectability model with lowest AIC_c value for red bat ($AIC_c = 795.8$) with an inverse relationship between detectability and precipitation. The detectability model with the most support for eastern pipistrelle included minimum temperature (range = 6–25°C) and 2-week period of field season during which sampling occurred ($AIC_c = 894.3$). Minimum temperature was inversely related to detectability. Detectability varied across field season with the sixth 2-week time period having the highest and the seventh 2-week period having the lowest detectability.

Local-Site Scale

None of the a priori models were significantly better than the null model at explaining the occupancy of gray bat or northern long-eared bat across the 2 watersheds ($P > 0.1$). Among the remaining 3 species, the global model including all of the site covariates in addition to the most parsimonious sampling covariate model was significantly greater than the null model consisting of sampling covariates ($P < 0.1$).

At the local-site scale, the model with the highest AIC_c weight for eastern pipistrelle consisted of variables describing structural complexity of the forest (Table 4). Live BA was inversely related to occurrence (odds ratio = 0.95, SE = 0.05), whereas overstory canopy density was directly related to occurrence (odds ratio = 1.08, SE = 0.14) of eastern pipistrelle. The second-most-important model included live BA and understory density. Understory density from 1–2 m was directly related (odds ratio = 1.01, SE = 0.02), whereas understory density from 2–3 m was inversely related to probability of site occupancy (odds ratio = 0.99, SE = 0.01). The averaged model output for eastern pipistrelle estimated the proportion of sites occupied as 0.31 (SE = 0.032), an increase of 0.06 over observed occupancy.

Red bat occurrence at a site was best explained by the same covariate model as eastern pipistrelle (Table 4), with an inverse relationship with live BA (odds ratio = 0.97, SE = 0.03) and a direct relationship with overstory canopy density

Table 4. All a priori local-site habitat characteristic models for 3 species of forest-dwelling bats in the Ozark Highlands of Missouri, USA. Covariate components[a] of each model listed with the number of parameters (k), Aikaike's Information Criterion adjusted for small sample size (AIC_C), distance from the most parsimonious model (ΔAIC_C) and AIC_C weight (w_i). Lower AIC_C and ΔAIC_C and greater w_i represent models with more substantial support.

	Eastern pipistrelle				Red bat				Indiana bat			
Model	k	AIC_c	ΔAIC_c	w_i	k	AIC_c	ΔAIC_c	w_i	k	AIC_c	ΔAIC_c	w_i
Null	9	912.9	5.08	0.03	3	795.8	4.43	0.04	4	469.6	5.71	0.03
Topography model 1	10	911.8	3.95	0.06	4	796.2	4.80	0.03	5	471.7	7.77	0.01
Topography model 2	11	913.9	6.10	0.02	5	792.2	0.81	0.24	6	473.4	9.53	0.005
Topography model 3	11	913.8	6.02	0.02	5	798.2	6.86	0.01	6	471.6	7.68	0.01
Roosting model 1	10	914.7	6.93	0.01	4	796.0	4.64	0.04	5	470.0	6.05	0.03
Roosting model 2	10	910.5	2.68	0.11	4	795.0	3.65	0.06	5	463.9	0	0.54
Roosting model 3	12	914.4	6.58	0.02	6	797.0	5.60	0.02	7	466.1	2.14	0.18
Roosting model 4	10	913.1	5.35	0.03	4	797.9	6.45	0.01	5	468.7	4.80	0.05
Roosting model 5	10	910.1	2.28	0.13	4	797.0	5.63	0.02	5	471.8	7.76	0.01
Clutter model 1	11	907.8	0	0.41	5	791.4	0	0.35	6	469.4	5.50	0.03
Clutter model 2	12	909.7	1.88	0.16	6	796.6	5.26	0.03	7	468.9	4.99	0.04
Clutter model 3	12	917.6	9.75	0.003	6	797.2	5.81	0.02	7	469.7	5.79	0.03
Water Model	10	914.53	6.73	0.01	4	797.8	6.42	0.01	5	470.0	6.1	0.03
Global	21	920.3	12.45	0.001	15	793.6	2.20	0.12	16	475.6	11.66	0.002

[a] Specific covariates for each model are described in Table 1.

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Table 5. All a priori landscape habitat characteristic models for 3 species of forest-dwelling bats in the Ozark Highlands of Missouri, USA. Covariate components[a] of each model listed with the number of parameters (k), Aikaike's Information Criterion adjusted for small sample size (AIC_c), distance from the most parsimonious model (ΔAIC_c) and AIC_c weight (w_i). Lower AIC_c and ΔAIC_c and greater w_i represent models with more substantial support.

	Red bat				Northern long-eared bat				Indiana bat			
Model	k	AIC_c	ΔAIC_c	w_i	k	AIC_c	ΔAIC_c	w_i	k	AIC_c	ΔAIC_c	w_i
Null	3	795.8	4.71	0.03	5	684.3	7.09	0.02	4	469.6	8.90	0.01
Land index model 1	4	793.7	2.64	0.10	6	683.4	6.23	0.03	5	470.6	9.84	0.01
Land index model 2	4	796.4	5.35	0.03	6	677.2	0	0.57	5	468.1	7.38	0.02
Land index model 3	4	797.7	6.57	0.01	6	682.8	5.62	0.03	5	468.4	7.65	0.02
Land index model 4	5	798.5	7.37	0.01	7	679.0	1.82	0.23	6	469.1	8.42	0.01
Land type model 1	6	791.9	0.83	0.24	8	682.1	4.89	0.05	7	468.4	7.64	0.02
Land cover model 1	5	792.4	1.31	0.19	7	687.6	10.38	0.003	6	469.1	8.37	0.01
Land cover model 2	5	798.5	7.42	0.01	7	683.3	6.13	0.03	6	460.7	0	0.82
Land cover model 3	5	797.2	6.08	0.02	7	686.8	9.65	0.004	6	470.2	9.46	0.01
Global	13	791.1	0	0.36	16	682.6	5.46	0.07	14	465.7	4.98	0.07

[a] Specific covariates for each model are described in Table 2.

(odds ratio = 1.32, SE = 0.32). The model with next-highest AIC_c weight included aspect (odds ratio = 0.91, SE = 0.16) and percent slope (odds ratio = 0.99, SE = 0.02). Probability of red bats occurring at a site decreased as the aspect deviated from south and decreased with steeper slopes. Estimated proportion of sites occupied from averaged model was 0.24 (SE = 0.028), an increase of 0.04 over observed occupancy.

The greatest weighted model for Indiana bat occurrence at the local-site scale involved BA of snags >30-cm diameter at breast height (dbh; Table 4). There was a direct relationship between the number of large-diameter snags (odds ratio = 2.06, SE = 0.51) and occurrence of Indiana bats. No other model was within 2 AIC_c units of this model. Using model averaging, the proportion of sites occupied was estimated to be 0.18 (SE = 0.032), an increase of 0.07 over observed occupancy.

Landscape Scale

None of the a priori models were significantly better than the null model at explaining the occupancy of gray bats and eastern pipistrelle across the 2 watersheds ($P > 0.1$). There was a significant difference between the global model and the null model for the red bat, northern long-eared bat, and Indiana bat ($P < 0.1$).

At the landscape scale the model with the greatest support for red bat was the global model containing all landscape covariates (Table 5). The model with the second-highest AIC_c weight incorporated ecological subsection. The red bat was most likely to be found in St. Francis Knobs and Basins ecological subsection (odds ratio = 6.8, SE = 2.52) and least likely to be found in the Black River Ozark Border subsection (odds ratio = 0.93, SE = 0.79). A model consisting of proportion of the landscape in upland-deciduous forest cover type (odds ratio = 2.85, SE = 4.20) and average patch size (odds ratio = 1.50, SE = 0.58) was also within 2 AIC_c units. Estimated proportion of sites occupied from model averaging was 0.24 (SE = 0.029), an increase of 0.04 over the observed occupancy.

Northern long-eared bat occupancy was best explained by area-weighted shape index (odds ratio = 0.91, SE = 0.07) where probability of northern long-eared bat occupancy decreased as average patch shape increased in complexity (Table 5). The second-most supported model included area-weighted shape index and contagion (odds ratio = 0.97, SE = 0.08). Although decreasing with shape complexity, northern long-eared bat occupancy increased with greater interspersion of patch types. Estimated proportion of sites occupied using model averaging was 0.31 (SE = 0.043), an increase of 0.12 over the observed occupancy rate.

The best model for the Indiana bat included area-weighted mean patch size and the proportion of landscape in nonforested cover types (Table 5). There was a direct relationship between both area-weighted mean patch size (odds ratio = 1.64, SE = 0.27) and proportion of landscape in nonforested cover type (odds ratio = 217.75, SE = 2.50) and the probability of Indiana bat occupancy at a sample point. There was no other model within 2 AIC_c units of this model. The average proportion of sites occupied by Indiana bat as estimated through model averaging was 0.16 (SE = 0.002), an increase of 0.05 over the observed occupancy rate.

Discussion

Species occupancy rates were influenced by characteristics at both the local site and landscape scales in the St. Francis and Black River watersheds during this study. Significant trends were found for red bats and Indiana bats at both the local site and landscape scales. Only models including variables measured at the local-site scale influenced the occupancy rates of eastern pipistrelle, while landscape metrics more appropriately explained the occupancy of northern long-eared bats. None of the variables measured at either scale adequately explained the occupancy of gray bats.

Detection Probability

While not directly influencing occupancy, the ability to detect species may drastically influence perceived occupancy as data from this study indicate. It is important, therefore, to highlight the environmental factors influencing the acoustic detection of species in forested areas. The probability of detecting a given species is generally <1 (MacKenzie et al. 2002, Gu and Swihart 2004), and this is particularly true of bats (Hayes 2000, Sherwin et al. 2000, Patriquin et al. 2003, Duchamp et al. 2006). We used methods described by MacKenzie et al. (2002) to incorporate estimates of detection probability into occupancy estimates. Gu and Swihart (2004) suggested that some variables are interpreted as affecting occupancy when they may actually be influencing detection, leading to inappropriate conclusions. With this in mind, we included year as a detectability covariate rather than a covariate estimating occupancy.

Detection probabilities for the gray bat, the Indiana bat, and the northern long-eared bat were lowest in 2002. While annual shifts in population size may alter site occupancy among species with high reproductive potential, bats are long-lived and have low reproductive rates with noncyclic population patterns (Kunz and Racey 1998, Kunz and Fenton 2003). Small changes in population density may affect detectability of a species in a landscape, while not influencing occupancy (Royle and Nichols 2003). Shifts in general weather conditions among years may also influence levels of bat activity. Erickson and West (2002) found that bat detections in the Pacific Northwest were highest in areas with low precipitation and high temperatures. Shifts in overall weather patterns among years may have had a similar impact on the activity levels of bats during our study. Additionally, experience in placement of detectors gained during the 2002 field season may have led to increased detectability during 2003 and 2004. Weller and Zabel (2002) highlighted the impact of positioning of detectors on detectability of bats during acoustic surveys. Our use of 2 detectors at each sample location on each evening may compensate in part for inadequate placement for presence data; however, having 2 detectors did not eliminate the problems with detection from inappropriate placement.

Precipitation influenced the probability of detection for both the northern long-eared bat and the red bat. Precipitation can influence both activity levels of bat species and the attenuation of echolocation calls (Hayes 2000, Erickson and West 2002). Increased humidity following rainfall may negatively affect echolocation call detection distance, resulting in a decrease in the probability that a bat would fly through the zone of reception (Griffin 1971, Livengood 2003).

Eastern pipistrelle detection was most influenced by minimum air temperature and 2-week time period during the field season. Changes in detectability across field season could represent shifts in foraging activity caused by changing energy requirements during birth and rearing of pups (Racey and Swift 1985, Barclay 1989). Increases in foraging activity and more frequent returns to roosting location increase the probability of detection for lactating bats (Clark et al. 2002). The lowest probability of detection occurred during the fourth 2-week time period (7–20 Jul) and coincided with the onset of juvenile volancy (Whitaker 1998). Immediately after 20 July, an increase in detection probability occurred for 4 weeks until a decrease in the final 2-week time period. Increases in activity likely correspond with increasing temperature, a trend noted by Erickson and West (2002).

There were no significant models at either scale describing gray bat occupancy, even though calls were identified at 10% of the study sites. While variables included in models at both scales are appropriate for describing habitat for forest-dwelling bats, the gray bat is a cave-obligate species, using caves as both winter and summer roost sites (Decher and Choate 1995). A dependence on cave habitat may supersede other forest habitat characteristics in determining its distribution across the landscape. Although including cave locations could provide improved modeling information these data were not available. Open water or large rivers represent dominant foraging areas for gray bats (LaVal et al. 1977, Johnson 2002); hence, the time this species spends in the forest would be minimized, thereby explaining the lack of correlation between species presence and measured habitat characteristics we observed.

Local-Site Scale

The most parsimonious occupancy models at this scale for eastern pipistrelle and red bat included total BA as a covariate. Increases in live BA corresponded with decreases in the occupancy rate of these 2 bat species. The red bat is a foliage-roosting species, preferring clumps of leaves at the end of branches of deciduous trees as day roosts (Shump and Shump 1982, Hutchinson and Lacki 2000, Schwartz and Schwartz 2001). Eastern pipistrelles are known to roost in anthropogenic structures (Fujita and Kunz 1984, Whitaker 1998, Schwartz and Schwartz 2001); however, Veilleux et al. (2003) found eastern pipistrelles roosting in foliage of deciduous trees in Indiana, and others have reported eastern pipistrelles roosting in cavities (Carter et al. 1999, Kurta et al. 1999). Carter and Menzel (2006) further discuss the importance of foliage roost sites for eastern pipistrelle bats. Upland deciduous tree species (e.g., oak and hickory [*Carya* spp.]) dominated the 2 watersheds in our study, providing abundant roost sites across the landscape for foliage-roosting species (Lewis 1995).

Elmore et al. (2004) found that stand-level characteristics were more important than individual tree characteristics in explaining roost location for the red bat. Contrary to our findings, Hutchinson and Lacki (2000) found significantly lower BA surrounding red bat roost sites. The covariate of live BA includes all size classes and therefore could represent an increase in structural complexity within the stand a potential impediment for navigation (Crome and Richards 1988, Erikson and West 1996, Brigham et al. 1997*a*).

Although red bats are known to forage along forest edges, above canopies, and in forest openings, Mager and Nelson (2001) found that selected roosts were larger in diameter than randomly selected trees and suggested that the thicker canopies of such trees provided greater concealment from predators or protection from wind (Menzel et al. 2003, Elmore et al. 2004). Similarly, Menzel et al. (2000) found red bats roosting in areas with relatively dense overstory canopies.

The model with the second-highest AIC$_c$ weight for eastern pipistrelle included live BA and measures of understory density. Probability of occupancy for eastern pipistrelle was directly related to density at 1–2 m and inversely related to density at 2–3 m. Increased density of vegetation from 2–3 m represented a greater amount of shrubs and midstory vegetation in the forest, creating additional obstacles during commutes from roosting sites to foraging areas. Meanwhile, increases in vegetation density from 1–2 m represented greater density of lower shrubs, which may indicate a less dense midstory and greater light levels reaching the forest floor. This pattern represents additional evidence that changes in structural complexity beneath the forest canopy impact the occupancy of a site by eastern pipistrelle.

Aspect and slope were components of the model with the second-highest AIC_c weight for the red bat and the probability of occupancy decreased with deviance from south. This trend may be linked to thermoregulation needs during diurnal roosting periods since less solar exposure might compromise the increased energy requirements of lactating females and developing young (Crampton and Barclay 1998). Hutchinson and Lacki (2000) noted that red bats prefer upland habitats rather than bottomland habitats and attributed this habitat preference to increased solar radiation. Probability of red bat occupancy decreased as percent slope increased.

The most parsimonious model for the Indiana bat indicated a direct relation between the probability of occupancy and BA of large-diameter snags. Previous studies have indicated the use of large-diameter trees and snags by Indiana bats as roosting sites for maternity colonies (Callahan et al. 1997, Foster and Kurta 1999, Britzke et al. 2003, Carter and Feldhamer 2005). Larger snags can contain larger cavities and areas of loose bark, providing greater-capacity roosts for sheltering numerous bats. This increase in numbers of individuals in a roost provides greater thermoregulatory benefits for pup-rearing females in maternity colonies through concentrating of body heat. Other benefits may include possible information transfer among individuals within the same roost about quality foraging areas (Wilkinson 1992).

Surprisingly, the local-site model consisting of distance to water was ranked low for all species. Water is a dominant foraging habitat for several bat species (Krusic et al. 1996, Menzel et al. 2001, 2003, 2005*b*, Johnson 2002). This model was not included in any of the averaged models at the local-site scale, possibly attributed to the coarse scale at which we measured water. Owing to the ephemeral nature of many stream systems in the Ozark Highlands region (Nigh and Schroeder 2002), the land cover classification of water we used included only permanent water sources in the landscape easily visible from satellite imagery, and represents an under-representation of aquatic or riparian habitat.

Landscape Level

The global model including all covariates included in landscape models had the greatest amount of support for red bat, indicating that no one model was able to adequately predict occupancy of this species. Similarly, Elmore et al. (2004) failed to find distinguishing landscape characteristics influencing red bat roost selection, attributing this to the ubiquitous nature of foliage roost sites. Ecological subsection had the next-largest support for prediction of red bat occupancy. Additional investigation is necessary to further determine differences among these 4 subsections of the Ozark highlands. A third relevant model included a direct relationship with proportion of upland deciduous forest and an inverse relationship with mean patch size. Increase in upland deciduous forest type in the landscape would represent an increase in roosting habitat (Hutchinson and Lacki 2000).

The most parsimonious model for the northern long-eared bat indicated an inverse relation between occupancy and shape index. Higher values of shape index indicate a greater amount of edge in the landscape and can result in less core area of forest. Northern long-eared bats are associated with forested areas, roosting in snags and trees (Sasse and Pekins 1996, Waldien et al. 2000, Menzel et al. 2002), and foraging beneath the forest canopy (LaVal et al. 1977, Schwartz and Schwartz 2001, Owen et al. 2003, Ford et al. 2005). Our findings agree with studies that suggest this species requires contiguous tracts of forest cover (Lacki and Schwierjohann 2001, Owen et al. 2003). The model with the next-highest AIC_c weight for describing northern long-eared bat occupancy again inferred an inverse relationship with shape index, but it additionally suggests an inverse relationship with levels of contagion in the landscape. As cover type interspersion became greater, the probability of occupancy increased; therefore, it appears that fragmentation has no obvious negative influence on northern long-eared bats at levels found in these 2 watersheds. It should be noted that in the landscapes studied, the interspersion represents parcelization of different forest types rather than fragmentation by nonforested cover type.

Indiana bat occupancy at the landscape scale was directly related with the proportion of landscape in nonforested land cover type. Many studies have shown that Indiana bats roost and forage in forested and forest riparian areas (LaVal et al. 1977, Callahan et al. 1997, Ford et al. 2005, Menzel et al. 2005*a*), suggesting that increased proportion of nonforested area in the landscape should decrease the habitat occupancy of an area. Menzel et al. (2005*a*) tracked foraging Indiana bats and found that they avoided open areas, preferring bottomland forests and linear landscapes; however, the landscape in that study consisted of only 33% forested land cover, compared to 90% in our study. Miller (1996) found no significant difference in Indiana bat presence between forest- and nonforest-dominated landscapes in northern Missouri; however, Sparks et al. (2005) found that while Indiana bats foraged in forested areas more than expected by availability, they did spend nearly 50% of the time foraging over agricultural land cover types. Our results suggest that in a southern Missouri landscape dominated by forest cover, nonforest areas may provide landscape heterogeneity ful-

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filling some habitat requirement not provided in a fully forested landscape.

Caveats

Although acoustic data may provide insight into trends in bat activity, caution should be taken when using results to develop management plans. Inability to distinguish among individuals and sexes within species as well as variability in detectability can lead to limited interpretation of species data collected acoustically. Difficulty in separating certain groups, such as *Myotis*, must be acknowledged and efforts made to avoid errors in classification of recorded calls. One method of minimizing errors drawn from misidentified call sequences is to combine similar species into groups or clades. We chose not to combine since it may result in the homogenization of habitat characteristics among and between bat species. While acoustic detection methods indicate the presence of bats, these methods provide little insight into how bats are using the site, a primary concern when developing management plans. Using recent methods incorporating detection probability addresses some of the limitations associated with acoustic sampling. Results from this study demonstrate the need to further investigate habitat relationships for bats in the Missouri Ozark region.

Management Implications

Several species of bats are endangered or of special concern, making it important to include bat habitat considerations when developing management plans. The St. Francis and Black River watersheds are dominated by contiguous forest cover, yet even within a landscape with little fragmentation, our data indicate that bat occupancy rates can be influenced by forest-management practices. We found trends indicating that occupancy rates of red bat and eastern pipistrelle were higher in stands with a more open understory, particularly from 2–3 m in height. Our study also suggests that management practices promoting retention of large-diameter snags (>30-cm dbh) may provide valuable roosting habitat for the federally endangered Indiana bat. In addition, our results showed that in a heavily forested landscape some heterogeneity in land cover may fulfill some additional habitat requirements for both Indiana and northern long-eared bats.

Acknowledgments

Our study would not have been possible without the cooperation and work of a large number of people including all of those who assisted in the collection of this data: J. Beck, J. Motsinger, R. Landewe, J. Hayes, A. Schultz, D. Korenak, S. Hernke, K. Skahan, K. Menzel, K. Tenaglia, R. Burchfield, J. Wisdom, L. Murray, and D. Twyman. We also thank K. Hosman, J. Duchamp, J. Moore, D. Ko, J. Richter, F. Wolter, E. McMurray, and S. Voelker for input and assistance. Special thanks to S. Amelon, K. Livengood, and C. Corben. Thanks to anonymous reviewers for their comments. Our project was supported by Initiative for Future Agriculture and Food Systems Grant no. 00-52103-9643 from the United States Department of Agriculture Cooperative State Research, Education, and Extension Service.

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