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Site-occupancy of bats in relation to forested corridors

Cris D. Hein [1], Steven B. Castleberry *, Karl V. Miller

D.B. Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602, USA

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ABSTRACT

Although use of corridors by some wildlife species has been extensively examined, use by bats is poorly understood. From 1 June to 31 August (2004–2005), we used Anabat II detectors to examine bat activity and species occupancy relative to forested corridors on an intensively managed forest landscape in southern South Carolina, USA. We compared bat activity among corridor interiors, corridor edges, and stands adjacent to corridors. We also compared models relating occupancy of bat species to site-level characteristics using an information theoretic approach. We identified 16,235 call sequences of 8 species and detected bat presence at 89% ($n = 320$) of sites sampled. Our results indicate higher occupancy rates for bats along corridor edges compared to interior corridor or adjacent stands. Although we found few differences among species with respect to site-level characteristics, occupancy of all bat species was positively associated with corridor overstory height and negatively associated with adjacent stand age. The presence of roads adjacent to corridors positively influenced occupancy of *Eptesicus fuscus*, *Lasiurus seminolus*, and *Perimyotis subflavus*. Our results suggest management practices designed to create and enhance corridors may represent an ecologically sound method for maintaining important bat habitat features (i.e., edge) across managed forest landscapes.

1. Introduction

The southeastern United States is undergoing unprecedented landscape changes caused by rapid growth in human population and urban expansion (Wear and Greis, 2002). Although the area covered by industrial forests in the southeastern United States is expected to remain relatively constant for the next 20 years (National Commission on Science for Sustainable Forestry, 2005), habitat alteration may continue if existing forest lands are converted to more intensively managed plantation systems that produce timber products more efficiently and economically (Wear and Greis, 2002). Increased intensity of forest management often results in shorter harvest rotations, loss of late-successional forests, and declining species diversity in local vegetation communities (Allen et al., 1996).

Creating forested corridors is a suggested approach for maintaining forest heterogeneity across fragmented landscapes. Juxtaposition of late-successional corridors within a mosaic of younger forests may help conserve native flora and fauna, provide wildlife habitat, protect water quality, enhance aesthetics, and facilitate wildlife movement (Hobbs, 1992). For bats, linear landscape features may provide greater insect abundance and availability, navigational references, protection from wind and predators, and roost sites (Limpens and Kapteyn, 1991; Verboom and Huitema, 1997; Estrada and Coates-Estrada, 2001; Hein, 2008; Hein et al., 2008).

Previous studies have identified positive associations between bats and linear landscape features (i.e., tree lines, hedgerows, streamside management zones, forested corridors). Two decades of field studies in The Netherlands indicate most bat species fly along linear landscape elements instead of crossing open areas (Limpens and Kapteyn, 1991; Verboom and Huitema, 1997; Verboom and Spoelstra, 1999; Verboom et al., 1999). In Britain, Walsh and Harris (1996) similarly report bats using linear features across a range of land classes and ownerships. Hedgerows and vegetated stream corridors provide connectivity for commuting and foraging bats to isolated forest patches in Mexico (Estrada and Coates-Estrada, 2001). In the southeastern United States, Hein (2008) document selection of corridors as roost-sites for both cavity- and foliage-roosting bats. However, the influence of forested corridors on bat activity in this region is still unknown.

Information on bat responses to various forest management practices in the southeastern United States is limited (Menzel et al., 2002; Elmore et al., 2005; Miles, 2006). Miller et al. (2003) recommended conducting research across an array of forest

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* Corresponding author. Tel.: +1 706 542 3929; fax: +1 706 542 8356.
E-mail address: scastle@warnell.uga.edu (S.B. Castleberry).

[1] Present address: ABR, Inc., P.O. Box 249, Forest Grove, OR 97116, USA.

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landscapes to examine impacts of different harvest strategies on bat populations. Our goal was to investigate the relationship between bats and forested corridors in an intensively managed landscape. Because corridors are relatively narrow features, bat activity is likely impacted by adjacent stands. Furthermore, bat activity may be influenced by nearby roads and distance to water. Therefore, we examined the influence of site-level characteristics to determine which corridors provide suitable habitat for bats. Based on ecomorphology of bat species (Aldridge and Rautenbach, 1987), we predicted less maneuverable bats that use low-frequency echolocation would have higher occupancy in open habitats (i.e., open-canopy adjacent stands). We predicted higher occupancy for high-frequency, highly maneuverable bats in forested corridors. Finally, we predicted greater occupancy of all bat species along edges.

2. Methods

2.1. *Study area*

We conducted our study on MeadWestvaco Corporation's South Region in southern South Carolina, USA. The area is located in the Lower Coastal Plain physiographic province and is characterized by flat topography (slopes <2%) and elevations ranging from 20 to 30 m above mean sea level. Summers are warm and humid; monthly temperatures and precipitation average 27 °C and 186 mm, respectively (NOAA-National Climatic Data Center, http://www.ncdc.noaa.gov).

The 41,365 ha study area was intensively managed for wood and fiber products and consisted of even-aged stands of loblolly pine (*Pinus taeda*) in various successional stages. Plantation stands typically were clearcut at 20–25 years of age. Silvicultural practices included chemical and mechanical site preparation and planting of cleared stands, 1–2 commercial thinnings, and vegetation management via prescribed fire. Approximately 25% of the area was young stands and regeneration areas (≤5 years), 15% was closed-canopy plantations (6–11 years), and 33% was mid-rotation stands (12–22 years). Mature forest stands (≥23 years) included pine (6%), mixed pine-hardwood (10%), and hardwood (8%). The remaining the 3% of the area was water or anthropogenic structures. At the time of our study, MeadWestvaco employed a forest management system known as Ecosystem-Based Forestry that was designed to increase diversity of forest structure and composition across the landscape (Constantine et al., 2005). This approach maintained a system of approximately 100–200 m wide corridors comprised of mature forests within a mosaic of younger plantation stands. Three types of corridors were retained in harvested areas: visual corridors located along public roads, water quality corridors designed to protect wet areas and reduce soil erosion, and habitat diversity corridors intended to enhance biodiversity and wildlife habitat. Forested corridors composed of mature pine, mixed pine-hardwood, or hardwood habitat constituted 11% of the total study area.

2.2. *Acoustic detection and analysis*

From 1 June to 31 August (2004–2005), we recorded bat echolocation sequences using Anabat II detectors (Titley Eectronics, Ballina, New South Wales, Australia) coupled to Zero-Crossing Analysis Interface Modules with CF memory card storage (Anabat CF Storage ZCAIM). We calibrated detectors to minimize variation in reception zones prior to field sampling (Larson and Hayes, 2000). Detector systems were housed in waterproof plastic containers atop tripods 1.5 m above the ground with the microphone oriented at a 45° angle (Weller and Zabel, 2002). We programmed detectors to begin recording 15 min prior to sunset and end 15 min after sunrise. We avoided sampling on nights with moderate to heavy rain.

We randomly selected one habitat diversity and one water quality corridor with similarly aged adjacent stands for simultaneous sampling for two consecutive nights. We chose a subset of 32 pairs of corridors systems and sampled each pair once during the study. We placed one detector system in the corridor interior, one along each corridor edge, and one in each adjacent stand for a total of 10 sample sites per night (5 detectors/corridor system × 2 corridor systems). To maximize independence of observations and reduce edge effects, we positioned detectors in the center of each corridor and at least 40 m from adjacent stand edges (Grindal and Brigham, 1999). We oriented detectors in the corridor interior and on edges along corridor axes. Detectors in adjacent stands were oriented away from the corridor. To maximize number of calls and standardize area sampled by detectors, we oriented detectors away from structural clutter (Grindal and Brigham, 1999; Weller and Zabel, 2002).

We analyzed echolocation sequences using Analook v4.9j software (Titley Electronics, Ballina, New South Wales, Australia). We used a customized filter to retain sequences of ≥5 calls and remove all recordings not consistent with properties of search-phase echolocation call sequences (Britzke and Murray, 2000). We used Analook to calculate 10 parameter values for each call in a sequence (Britzke, 2003). We quantitatively identified each call sequence using a discriminant function analysis (DFA) model based on an extensive call library of bats in the eastern United States (Britzke, 2003). We calculated the percent of call sequences that were correctly identified (accuracy rate) and the percent of sequences that were misidentified by species (Britzke, 2003). Species identification can be difficult when multiple species use similar search-phase calls. However, as the number of sequences identified for a species increase at a site, so does the accuracy rate of identification, particularly if few calls of a similar species are recorded at that site (Britzke et al., 2002). Therefore, we considered a species present at a site if accuracy rates were ≥80% and ≥2 call sequences from that species were recorded. Species with accuracy rates <80% were considered present if ≥4 call sequences were recorded. Hoary bats (*Lasiurus cinereus*), Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) and northern yellow bats (*Lasiurus intermedius*) were excluded from the DFA model prior to analysis. Hoary bats migrate through the region and are considered rare in summer (Menzel et al., 2003). Northern yellow bats are rarely encountered and Rafinesque's big-eared bats are difficult to detect acoustically with zero-crossing systems.

2.3. *Habitat metrics*

At each survey site, we recorded habitat type (corridor, edge, or adjacent stand), corridor type (habitat diversity or water quality), age of adjacent stands, and presence/absence of an adjacent road. We used ArcView 3.2 (ESRI, 2000) to measure distance (km) from each site to the nearest available water source (pond, river, drainage ditch). For each corridor, we used the point-centered-quarter method to determine basal area (BA), and mean height of overstory (≥10 cm) and midstory (3–10 cm) trees (Cottam and Curtis, 1956).

2.4. *Model selection*

We developed logistic regression models to estimate proportion of sites occupied (ψ) by each bat species using 9 explanatory variables (Table 1) with detection/non-detection as the binary response. Prior to model analysis we conducted correlation tests to ensure no pairs of variables were highly correlated (Spearman's r

Table 1
Variables included in the global model relating bat species occupancy with corridor survey sites in southern South Carolina, June–August, 2004–2005.

Variable	Definition
Habitat type (habitat)	Categorical variable (1 = corridor interior, 0 = otherwise)
Edge (edge)	Categorical variable (1 = corridor edge, 0 = otherwise)
Corridor type (ctype)	Categorical variable (1 = habitat diversity, 0 = water quality)
Stand age (sage)	Age (years) of adjacent stand
Basal area (ba)	Density (m^2/ha) of trees in corridor stand
Overstory height (oht)	Average height (m) of overstory trees in corridor stand
Midstory height (mht)	Average height (m) of midstory trees in corridor stand
Road (rd)	Categorical variable (1 = road present, 0 = road absent)
Distance to water (dw)	Distance (km) to nearest water source (pond, drainage ditch, river)

>0.7). We fit a global logistic regression model for each species using all 9 explanatory variables. In addition to our global model, we selected 19 of a possible 511 candidate models based on our hypotheses relating bat species occupancy at survey sites. We used the same set of candidate models for all bat species. We examined temporal autocorrelation (year effects) on our data by conducting an analysis of variance of residuals from the global model for each species, using year as our independent variable. Our results indicated no temporal autocorrelation. Therefore, we conducted our analysis using traditional logistic regression techniques (Sokal and Rohlf, 1995).

We estimated detection probability for each bat species using program PRESENCE (MacKenzie et al., 2002). We included year, Julian date, and temperature as covariates in detection probability models to account for their potential affects on detectability. We used Akaike's Information Criterion for small sample sizes ($\mathrm{AIC_c}$) to compare 8 detection probability (p) models for each species. Our model set included all possible additive combinations of covariates. For each species, we compared the $\mathrm{AIC_c}$ values for our 8 models and incorporated the most parsimonious model of detection into all occupancy models.

We assessed goodness-of-fit of our global model for each species using methods described by MacKenzie and Bailey (2004). Because our assessment indicated poor fit by the global model, we used the overdispersion factor ($\hat{c}$) to calculate QAICc. We calculated Akaike weights (ω_i) for each model to evaluate and select the most parsimonious model (Burnham and Anderson, 2002). We established a confidence set by including models with Akaike weights within 10% of the highest value (Royall, 1997). We used model averaging to incorporate model selection uncertainty directly into parameter estimates and standard errors using Akaike weights. We based all inferences of parameter effects on this composite model. We calculated odds ratios (OR) from averaged parameter estimates. We evaluated ecological importance of each variable in the composite model by computing 90% confidence intervals for OR and interpreting the magnitude of the values within these intervals (Gerard et al., 1998).

3. Results

We identified 16,235 call sequences from 32 pairs of corridors systems over 2 years. We detected bat presence at 89% (285/320) of sample sites. Six species were present at ≥15% of sample sites and used for further analysis. We recorded 3233 big brown bat (*Eptesicus fuscus*) sequences at 161 sites, 3638 red bat (*Lasiurus borealis*) sequences at 117 sites, 2972 Seminole bat (*L. seminolus*) sequences at 98 sites, 702 little brown bat (*M. lucifugus*) sequences at 76 sites, 1610 evening bat (*Nycticeius humeralis*) sequences at 140 sites, and 1736 eastern pipistrelle (*Perimyotis subflavus*) sequences at 122 sites. We also identified call sequences from silver-haired bats (*Lasionycteris noctivagans*, 359 sequences at 20 sites), southeastern myotis (*Myotis austroriparius*, 968 sequences at 44 sites) and Mexican free-tailed bats (*Tadarida brasiliensis*, 1017 sequences at 40 sites), but calls of those species occurred at <15% of total sites sampled and were not included in analyses. We recorded more sequences along edges ($n = 13{,}884$; 54 call sequences/detector night) compared to adjacent stands ($n = 1754$; 12 call sequences/detector night) and corridor interiors ($n = 1581$; 7 call sequences/detector night).

Accuracy rates for species identification ranged from 100% to 33%, with 4 species ≥80% and 5 species <80% based on a single call sequence (Table 2). Accuracy rates increased to 98.5% for *E. fuscus*, 99.8% for *M. lucifugus*, and 96.0% for *N. humeralis* using 2 call sequences, and 88.7% for *L. borealis* and 80.2% for *L. seminolus* using 4 call sequences. The DFA model commonly confused *M. austroriparius* calls with *M. lucifugus*. *Tadarida brasiliensis* calls were most commonly confused with *E. fuscus*. In contrast to many studies (Menzel et al., 2002; Ford et al., 2006), *L. borealis* and *L. seminolus* were not commonly mistaken for one another in our study and were not combined into one species group.

We found no evidence of temporal autocorrelation between years and no correlation among covariates for species occurrence

Table 2
Percent classification rates for *Eptesicus fuscus* (EPFU), *Lasiurus borealis* (LABO), *Lasionycteris noctivagans* (LANO), *Lasiurus seminolus* (LASE), *Myotis austroriparius* (MYAU), *M. lucifugus* (MYLU), *Nycticeius humeralis* (NYHU), *Perimyotis subflavus* (PESU), and *Tadarida brasiliensis* (TABR) recorded at survey sites in southern South Carolina, June–August 2004–2005. Values in columns represent the percentage of calls identified as the corresponding species in each row based on a single call sequence. Classification rates in the bottom row represent rates based on multiple call sequences for species in each column.

	EPFU	LABO	LANO	LASE	MYAU	MYLU	NYHU	PESU	TABR
EPFU	87.8	–	11.1	–	–	–	–	–	50.0
LABO	–	42.0	–	–	12.5	–	12.0	–	–
LANO	10.4	–	66.7	–	–	–	–	–	–
LASE	–	8.0	–	33.3	–	–	8.0	–	–
MYAU	–	–	–	33.3	50.0	4.3	–	–	–
MYLU	–	2.0	–	–	25.0	95.7	–	–	–
NYHU	–	36.0	–	–	–	–	80.0	–	–
PESU	–	12.0	–	33.3	12.5	–	–	100.0	–
TABR	1.7	–	22.2	–	–	–	–	–	50.0
	98.5[a]	88.7[b]	98.7[b]	80.2[b]	93.75[b]	99.8[a]	96.0[a]	100.0[a]	93.8[b]

[a] Percent classification rate based on 2 call sequences.

[b] Percent classification rate based on 4 call sequences.

Table 3
Model, number of parameters in the model (K), Quasi-Akaike's Information Criterion adjusted for small samples ($QAIC_c$), difference of $QAIC_c$ between a model and the model with the lowest $QAIC_c$ ($\Delta QAIC_c$), and model weights (ω_i) for the confidence sets of models used to predict occupancy (ψ) given detection probability (p) of 6 bat species at corridor survey sites in southern South Carolina, June–August, 2004–2005. Model variables defined in Table 1. Detection probability covariates include Julian date (julian) and temperature (temp).

Model	K	QAICc	ΔQAIC	ω_i
EPFU				
Ψ (habitat edge sage oht) $p(.)$	6	240.14	0.00	0.3132
Ψ (edge sage oht) $p(.)$	5	240.56	0.42	0.2537
Ψ (habitat edge sage oht rd) $p(.)$	7	240.57	0.43	0.2529
Ψ (habitat edge ctype oht) $p(.)$	6	242.48	2.34	0.0972
LABO				
Ψ (habitat edge sage oht) p(julian)	7	135.99	0.00	0.5281
Ψ (habitat edge sage oht rd) p(julian)	8	137.95	1.96	0.1987
Ψ (edge sage oht) p(julian)	6	138.70	2.71	0.1366
LASE				
Ψ (edge sage oht) p(julian)	6	96.13	0.00	0.3895
Ψ (habitat edge sage oht) p(julian)	7	96.95	0.82	0.2595
Ψ (habitat edge sage oht rd) p(julian)	8	98.15	2.02	0.1419
Ψ (habitat edge ctype sage) p(julian)	7	98.41	2.28	0.1251
MYLU				
Ψ (habitat edge sage oht) p(julian)	7	113.59	0.00	0.2894
Ψ (habitat edge ctype sage) p(julian)	7	114.86	1.27	0.1531
Ψ (habitat edge sage oht rd) p(julian)	8	115.29	1.70	0.1236
Ψ (habitat edge ctype oht) p(julian)	7	115.45	1.86	0.1142
Ψ (habitat edge ctype sage dw) p(julian)	8	115.79	2.20	0.0961
Ψ (edge sage oht) p(julian)	6	116.63	3.04	0.0633
NYHU				
Ψ (edge sage oht) p(temp)	6	164.61	0.00	0.3744
Ψ (habitat edge sage oht) p(temp)	7	165.77	1.16	0.2094
Ψ (habitat edge sage oht rd) p(temp)	8	167.16	2.55	0.1046
Ψ (habitat edge ctype sage) p(temp)	7	167.38	2.77	0.0937
PISU				
Ψ (edge sage oht) p(julian)	6	165.11	0.00	0.2696
Ψ (habitat edge sage oht) p(julian)	7	165.21	0.10	0.2560
Ψ (habitat edge sage oht rd) p(julian)	8	165.89	0.78	0.1829
Ψ (habitat edge ctype sage) p(julian)	7	167.95	2.84	0.0654

models. Values of $\hat{c}$ for individual species global models were ≤ 4 suggesting no structural lack-of-fit (Burnham and Anderson, 2002).

The most parsimonious model for detectability incorporated Julian date and was included in occupancy models for 4 species (*L. borealis*, *L. seminolus*, *M. lucifugus*, and *P. subflavus*). For these species, detectability increased from May to August. Temperature received the most support for detecting *N. humeralis*, with detection negatively related to temperature. The detectability of *E. fuscus* was not influenced by any covariate or combination of covariates.

Three models predicting occurrence of *E. fuscus* were considered strongly competing with ΔQAICc values within 0.43 units (Table 3). These models were >2.6 times more likely than the next best approximating model. The confidence set included the top 4 models with a sum of $\omega_i = 0.92$ indicating a 92% chance that one of these models was the best approximating model among on our candidate models. There was insufficient evidence to consider any additional candidate models as plausible explanations for predicting *E. fuscus* occurrence. Edge and overstory height were included in all 4 models, and habitat type and stand age were included in 3 of the 4 models from the confidence set. The composite model contained 5 parameters (habitat type, edge, stand age, overstory height, and road) whose model-averaged 90% confidence intervals did not include zero, indicating they provided useful information in predicting *E. fuscus* occurrence (Table 4). Habitat type, edge, overstory height and road were positively related, and stand age was negatively related to occurrence. Odds of *E. fuscus* occurrence were 27 times greater along edges and 5.8 times greater if a road was present.

The best approximating model for *L. borealis* incorporated habitat type, edge, stand age, and overstory height with a 53% probability of being the best approximating model (Table 3). This model was 2.7 times more likely than the next best model. The confidence set included the top 4 models with a sum of $\omega_i = 0.86$. Edge, stand age, and overstory height were included in all 3 models, and habitat type was included in 2 of the 3 models from the confidence set. The composite model contained 4 parameters whose 90% confidence intervals did not include zero (habitat type, edge, stand age, and overstory height), all of which were positively related to occurrence except stand age (Table 4). Odds of *L. borealis* occurring were 103 and 10 times greater along edge and interior corridor stands, respectively.

The best approximating model for *L. seminolus* incorporated edge, stand age, and overstory height with a 39% probability of being the best approximating model (Table 3). This model was 1.5 and 2.7 times more likely than the next two models, respectively. The confidence set included the top 4 models with a sum of $\omega_i = 0.92$. Edge and stand age were included in all 4 models, and habitat type and overstory height were included in 3 of the 4 models from the confidence set. The composite model contained 5 parameters whose 90% confidence intervals did not include zero (Table 4). Edge, overstory height, and road were positively related to occurrence, and habitat type and stand age were negatively related. Odds of *L. seminolus* occurring were 28 and 5 times greater along edges and in adjacent stands, respectively. Odds of *L. seminolus* occurring were 5.3 times greater if a road was present.

The best approximating model for *M. lucifugus* incorporated habitat type, edge, stand age, and overstory height with a 29% probability (Table 3). The confidence set included the top 6 models with a sum of $\omega_i = 0.84$. Edge was the only parameter included in all 6 models. Habitat type and stand age were included in 5 models, overstory height was included in 4 models, and corridor type was included in 3 models in the confidence set. The composite model contained 6 parameters whose 90% confidence intervals did not include zero (Table 4). Habitat type, edge, corridor type, and overstory height were positively related with occurrence, and stand age and distance to water were negatively related. Odds of *M. lucifugus* occurring were 58 times greater along edges, 17 times greater in interior corridor stands and 4 times greater in habitat diversity corridor systems.

The best approximating model for *N. humeralis* incorporated edge, stand age, and overstory height with a 37% probability (Table 3). This model was 1.8 and 3.6 times more likely than the next two approximating models, respectively. The confidence set included the top 4 models with a sum of $\omega_i = 0.78$. Edge and stand age were included in all 4 models, and habitat type and overstory height were included in 3 of the 4 models from the confidence set. The composite model contained 5 parameters whose 90% confidence intervals did not include zero (habitat type, edge, corridor type, stand age, and overstory height); all except stand age were positively related to occurrence (Table 4). Odds of *N. humeralis* occurring were 9 times greater along edges.

Three models predicting occurrence of *P. subflavus* were considered strongly competing (ΔQAICc ≤0.78 units apart; Table 3). These models were >2.8 times more likely than the next best approximating model. The confidence set included the top 4 models with a sum of $\omega_i = 0.77$. Edge and stand age were included in all 4 models, and habitat type and overstory height were included in 3 of 4 models from the confident set. The

Table 4
Model-averaged parameter estimates and standard errors (SE), lower and upper 90% confidence intervals (CI) on parameter estimates, odds ratios (OR), and lower and upper 90% confidence intervals (CI) on odds ratios for parameters included in the confidence set of models used to predict occupancy (ψ) of 6 bat species at corridor survey sites in southern South Carolina, June–August, 2004–2005. Variables defined in Table 1.

Parameter	Estimate (SE)	Lower 90% CI	Upper 90% CI	OR	Lower OR 90% CI	Upper OR 90% CI
EPFU						
ψ (intercept)	−5.82 (1.12)	−7.66	−3.98			
habitat	1.01 (0.40)	0.35	1.66	2.74	1.43	5.27
edge	3.28 (0.47)	2.51	4.06	26.71	12.32	57.88
ctype	−0.30 (0.33)	−0.84	0.25	0.74	0.43	1.28
sage	−0.15 (0.06)	−0.24	−0.05	0.86	0.79	0.95
oht	0.23 (0.08)	0.10	0.36	1.26	1.10	1.44
rd	1.76 (1.00)	0.12	3.40	5.80	1.26	29.91
p (intercept)	0.85 (0.04)	0.79	0.90			
LABO						
ψ (intercept)	−6.83 (1.60)	−9.46	−4.20			
habitat	2.32 (0.58)	1.37	3.28	10.19	3.93	26.45
edge	4.64 (0.81)	3.31	5.97	103.55	27.43	390.93
sage	−0.41 (0.10)	−0.57	−0.24	0.66	0.56	0.79
oht	0.28 (0.07)	0.16	0.39	1.32	1.18	1.48
rd	0.66 (0.88)	−0.78	2.11	1.94	0.45	8.22
p (intercept)	−6.44 (0.26)	−6.87	−6.01			
julian	0.035 (0.001)	0.033	0.037	1.036	1.034	1.039
LASE						
ψ (intercept)	−3.07 (1.72)	−5.89	−0.24			
habitat	−1.59 (0.67)	−2.68	−0.48	0.20	0.07	0.61
edge	3.34 (0.59)	2.36	4.31	28.13	10.63	74.41
ctype	0.57 (0.41)	−0.10	1.25	1.77	0.90	3.48
sage	−0.50 (0.09)	−0.66	−0.35	0.60	0.52	0.70
oht	0.19 (0.06)	0.09	0.29	1.21	1.09	1.34
rd	1.67 (0.82	0.31	3.02	5.30	1.37	20.49
p (intercept)	−12.54 (0.32)	−13.06	−12.02			
julian	0.067 (0.001)	0.065	0.069	1.068	1.066	1.071
MYLU						
ψ (intercept)	−6.16 (2.99)	−11.06	−1.25			
habitat	2.82 (0.74)	1.61	4.04	16.81	4.99	56.55
edge	4.06 (0.91)	2.57	5.55	57.96	13.01	258.20
ctype	1.43 (0.57)	0.48	2.37	4.16	1.62	10.65
sage	−0.37 (0.13)	−0.57	−0.16	0.69	0.56	0.85
oht	0.28 (0.08)	0.15	0.411	1.32	1.16	1.51
rd	1.09 (0.89)	−0.37	2.56	2.99	0.69	12.93
dw	−0.71 (0.36)	−1.3	−0.12	0.49	0.27	0.89
p (intercept)	−5.61 (0.32)	−6.14	−5.08			
julian	0.026 (0.002)	0.024	0.029	1.027	1.024	1.03
NYHU						
ψ (intercept)	−2.84 (1.20)	−4.81	−0.88			
habitat	0.77 (0.40)	0.10	1.43	2.15	1.11	4.18
edge	2.19 (0.38)	1.57	2.82	8.98	4.79	16.82
ctype	0.54 (0.30)	0.05	1.03	1.71	1.05	2.80
sage	−0.28 (0.06)	−0.37	−0.18	0.76	0.69	0.84
oht	0.14 (0.05)	0.07	0.22	1.15	1.07	1.25
rd	1.14 (0.77)	−0.13	2.40	3.12	0.88	11.06
p (intercept)	4.19 (2.50)	0.08	8.30			
temp	−0.15 (0.11)	−0.33	0.02	0.86	0.72	1.02
PISU						
ψ (intercept)	−3.64 (1.61)	−6.28	−1.01			
habitat	1.32 (0.54)	0.44	2.20	3.75	1.55	9.06
edge	4.19 (0.72)	3.01	5.37	66.14	20.31	215.4
ctype	0.003 (0.42)	−0.68	0.69	1.00	0.51	1.99
sage	−0.35 (0.09)	−0.50	−0.21	0.70	0.54	0.92
oht	0.18 (0.06)	0.07	0.28	1.19	1.08	1.32
rd	2.15 (1.06)	0.41	3.90	8.61	1.51	49.21
p (intercept)	−8.74 (0.27)	−9.18	−8.31			
julian	0.046 (0.004)	0.039	0.053	1.047	1.054	1.040

composite model contained 5 parameters whose 90% confidence intervals did not include zero (habitat type, edge, stand age, overstory height, and road), all of which were positively related to occurrence except stand age (Table 4). Odds of *P. subflavus* occurring were 66 times greater along edges and 8.6 times greater if a road was present.

4. Discussion

Our findings are consistent with previous studies documenting the use of linear landscape features (i.e., vegetation and stream corridors, tree lines, and hedgerows) by commuting and foraging bats. Linear landscape features may provide bats with navigational references, commuting lanes, suitable foraging areas, and protection from wind and predators (Limpens and Kapteyn, 1991; Verboom and Huitema, 1997). Kalko and Schnitzler (1993) found that European pipistrelles (*Pipistrellus pipistrellus*) did not need landscape elements for acoustic landmarks. However, Verboom et al. (1999) argued that bats may use linear features as landmarks without remaining in constant acoustical contact. Linear features often facilitate commutes from roost sites to foraging areas (Racey and Swift, 1985; Limpens and Kapteyn, 1991; Murray and Kurta, 2004). Small bats (i.e., *Myotis* spp.) travel farther distances along tree-lined paths, rather than flying directly to foraging areas by crossing open stands (Murray and Kurta, 2004). In addition, Racey and Swift (1985) found that foraging often occurred along flight routes. Because insects often accumulate on the lee side of linear features (Lewis, 1970), bat activity may correlate with increases in insect abundance (Furlonger et al., 1987; Limpens and Kapteyn, 1991). Activity by bats along the leeward side also suggests the importance of corridors as shelter from wind (Limpens and Kapteyn, 1991; Verboom and Spoelstra, 1999). Higher rates of bat activity also may be influenced by proximity to roost-sites (Barclay and Kurta, 2007; Carter and Menzel, 2007). Estrada and Coates-Estrada (2001) reported numerous roosting sites within large vegetation corridors bordering streams in Mexico. Hein (2008) found both cavity- and foliage-roosting bats selecting corridor stands as roost sites in the southeastern United States.

We found detection probability positively related to Julian date for 4 bat species (*L. borealis*, *L. seminolus*, *M. lucifugus*, and *P. subflavus*). Increased energetic demands imposed on pregnant and lactating female bats may account for increases in bat activity in early summer (Racey and Swift, 1985; Barclay, 1989). Activity may increase further in late summer as pups become volant (Seidman and Zabel, 2001). Yates and Muzika (2006) reported an increase in detection probability for *P. subflavus* for 4 weeks immediately following the onset of juvenile volancy. We found higher detection probability of *N. humeralis* at cooler temperatures which is inconsistent with most previous studies which generally have found a positive relationship between temperature and bat activity (Hayes, 1997; Yates and Muzika, 2006; Schirmacher et al., 2007). Although temperature alone provided the most support for detecting *N. humeralis*, 90% confidence intervals from the composite model for this covariate included zero, suggesting temperature was not a useful predictor in our occupancy models. We did not include measures of vegetation density to determine detection probabilities. Patriquin et al. (2003) found vegetation density did not affect detectability of bats that echolocate near 40 kHz. Furthermore, they found that detecting bat echolocations near 25 kHz was unaffected in thinned conifer and mixed forests. Because corridors in our study were comprised of mature pine or mixed pine-hardwood stands that were previously thinned, we believe the influence of vegetative clutter on detection was minimal.

For most species in our study, we found higher occupancy rates associated with corridor stands (interior and edge) than adjacent stands. Based on echomorphology of bats (i.e., body size, wing morphology, and echolocation call structure), we expected smaller, highly maneuverable bats to use corridor stands and larger, less maneuverable bats to use adjacent stands (Aldridge and Rautenbach, 1987). Use of corridor interiors by little brown bats was consistent with our predictions. These small-bodied bats are considered clutter-adapted species, exhibiting low wing-loading and high-frequency calls (Kalcounis and Brigham, 1995; Kalcounis et al., 1999; Patriquin and Barclay, 2003; Owen et al., 2004). Contrary to predictions, big brown bat detections also were positively related to corridor interiors. Although the echomorphology of this species (i.e., high wing-loading, low frequency calls) suggests it is better adapted for open habitats, evidence suggests big brown bats are generalized, opportunistic foragers (Brigham, 1991; Owen et al., 2004).

Only the Seminole bat had negative relationship with corridor stands, suggesting greater use of adjacent stands for foraging by this species. Although Seminole bats commonly roost in mature corridor stands (Hein et al., 2008), they apparently forage in adjacent, more open stands. In contrast, detection of the eastern red bats (a morphologically similar species) had a strong positive relationship with corridor stands. Previous studies have shown red bat activity is associated with a wide range of habitat types including cluttered areas (Carter et al., 2004; Menzel et al., 2005; Schirmacher et al., 2007). Use of different habitat types for these two similar species may represent a form of resource partitioning (Carter et al., 2004).

Bat occupancy was higher along corridor edges compared to corridor interiors or adjacent stands. Edge appears to be an important landscape component for free-flying bats (Kalko and Schnitzler, 1993; Brigham et al., 1997). Walsh and Harris (1996) reported bats selecting woodland edge more than any other habitat type, including forest gaps. In Canada, activity was greater along edge habitat than in cutblocks or interior forest stands (Grindal and Brigham, 1999). Kalko and Schnitzler (1993) suggested edge represents orderly and predictable clutter to bats. Several studies have shown higher activity levels in areas of low clutter (Brigham et al., 1997; Humes et al., 1999; Sleep and Brigham, 2003). Furthermore, Lewis (1970) reported higher insect abundance and availability along forested edges compared to interior stands.

Several studies have reported higher bat activity along riparian areas compared to upland sites (Zimmerman and Glanz, 2000; Estrada and Coates-Estrada, 2001; Ellis et al., 2002; Menzel et al., 2002; Owen et al., 2004; Schirmacher et al., 2007). In our study, corridor type had little influence on use, except for *M. lucifugus* and *N. humeralis*. Occupancy of these species was positively related to habitat diversity corridors. Kunz (1982) suggested that habitat selection may be driven by the interaction between foraging and roosting requirements. Hein (2008) found >50% of corridor roosts used by *N. humeralis* in habitat diversity corridors. Although roost locations of *M. lucifugus* were unknown on our site, other studies suggested that proximity to hibernacula and day roosts influenced activity of this species (Barclay, 1984; Furlonger et al., 1987).

Overstory height of corridors, adjacent stand age, and road presence also were important parameters predicting occupancy of forest bats along corridors. Occupancy was positively associated with overstory height in corridors. Limpens and Kapteyn (1991) and Verboom and Huitema (1997) also found a positive relationship between height of linear landscape elements and bat passes. Walsh and Harris (1996) noted that bats avoided stone walls without vegetation cover and low-cut hedges. Higher occupancy rates in our study also were associated with younger (0–5 years), open stands adjacent to corridors. The combination of these two features likely increased effective overstory height and visibility of edge, making these corridors more suitable for free-flying bats. Furthermore, many larger bat species forage over or near recently cleared stands (Verboom and Huitema, 1997; Grindal and Brigham, 1999; Patriquin and Barclay, 2003; Owen et al., 2004). We found presence of roads adjacent to corridors positively influenced use for all species, particularly for *E. fuscus*, *L. seminolus*, and *P. subflavus*. Use of roads is common for commuting and foraging bats (Krusic et al., 1996; Grindal and Brigham, 1998; Zimmerman and Glanz, 2000).

5. Conclusion

We found higher rates of bat activity and occupancy along corridor edges than in corridor interiors or adjacent stands. Edge appears to be an important habitat component for bat commuting and foraging and should be maintained across the landscape. Enhancing features associated with edge (i.e., increasing effective overstory height) may encourage bat activity and occupancy rates by forest bats. Retaining forested corridors in managed landscapes may represent an ecologically sound method for providing habitat features (i.e., edge) used by bats. Maintaining forested corridors is a relatively new concept in intensively managed landscapes of the southeastern United States. Additional research is needed to demonstrate the effectiveness of corridors in providing suitable commuting and foraging habitat in different regions and landscape conditions.

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