

# Habitat Use by Forest Bats in South Carolina in Relation to Local, Stand, and Landscape Characteristics

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## Abstract

*Knowledge and understanding of bat habitat associations and the responses of bats to forest management are critical for effective bat conservation and management. Few studies have been conducted on bat habitat use in the southeast, despite the high number of endangered and sensitive species in the region. Our objective was to identify important local, stand, and landscape factors influencing bat habitat use in northwestern South Carolina, USA. We hypothesized that use would be greatest 1) at points with relatively sparse vegetation, 2) in early successional and mature stands, and 3) at points close to streams. We also predicted that species would exhibit different patterns of habitat use based on morphology. We placed Anabat II bat detectors at points located in 3 forest types and 3 age classes to record bats from May–August 2004 and 2005. We used an information theoretic approach to determine the variables that best predicted use by bats. Vegetation density at the sample point was the best predictor of overall bat presence in 2004. In 2005 vegetation density and distance to the closest road were the best predictors of overall bat use; the model containing age class also had good support. Bats were more likely to be recorded at points with sparse vegetation, farther from roads, and in early successional stands. Vegetation density was also the best predictor of habitat use by big brown bats (*Eptesicus fuscus*) and red bats (*Lasiurus borealis*); both species were far more likely to be recorded at points with sparse vegetation at the sample point. Eastern pipistrelles (*Pipistrellus subflavus*) were also more likely to be recorded at points with sparse vegetation and in early successional stands. The best predictors of northern long-eared bat (*Myotis septentrionalis*) habitat use were vegetation density and age class. Northern long-eared bats were more likely to be recorded at points with sparse vegetation and in mature stands. Our results suggest that early successional habitats and small openings and gaps within forest stands provide suitable commuting and foraging bat habitat in northwestern South Carolina. However, mature forests are also important for some species. Forest management practices that provide a variety of age classes across the landscape and that create gaps and openings within mid- and late-successional stands will likely provide suitable habitat for bats in the mountains of South Carolina. (JOURNAL OF WILDLIFE MANAGEMENT 70(5):1210–1218; 2006)*

## Key words

*acoustic sampling, bats, clutter, forest structure, gaps, habitat use, South Carolina.*

Interest in use of forests by bats and the effects of forest management on their populations has increased greatly in the past 2 decades. This interest has been sparked by greater awareness of bats' ecological role in maintaining forest health (Marcot 1996) as well as concern about the conservation status of many species of forest bats (Pierson 1998). Technological advances in radiotelemetry and acoustical sampling over the past 20 years have also allowed researchers to test more specific hypotheses about the ecological relationships of bats and the effects of forest management.

Most studies conducted to understand the forest habitat relationships of bats have been done at the stand level. For example, many studies have examined the relative activity of bats in various forest types and ages (Thomas 1988, Krusic et al. 1996, Crampton and Barclay 1998, Grindal and Brigham 1999, Jung et al. 1999, Kalcounis et al. 1999, Ford et al. 2005) or in relation to forest management practices such as clearcutting (Ellis et al. 2002, Menzel et al. 2005), selective harvest (Menzel et al. 2002a, Owen et al. 2004), or thinning (Humes et al. 1999, Patriquin and Barclay 2003).

While a few studies have found that forest type is an important factor determining habitat use (Kalcounis et al. 1999, Patriquin and Barclay 2003), most studies have found that forest structure is the most important factor determining habitat use. In general, bats use more open stand types, such as recently clearcut stands and/or mature forests, rather than stands with greater structural clutter, such as those in early and mid-development (Thomas 1988, Erickson and West 1996, Krusic et al. 1996, Crampton and Barclay 1998, Jung et al. 1999, Ellis et al. 2002, Patriquin and Barclay 2003). Decreasing structural clutter by thinning increases bat use of midsuccessional conifer stands in Oregon (Humes et al. 1999), but does not affect bat activity in 50-year-old red pine stands in Michigan (Tibbels and Kurta 2003) or in mixed-wood boreal forests of Alberta, Canada (Patriquin and Barclay 2003). Within stand variation has also been found to be an important determinant of bat activity. Bat activity is often greater in gaps and small openings within the stand than in intact portions of the stand (Law and Chidel 2002, Menzel et al. 2002a, Tibbels and Kurta 2003).

Habitat use by bats often varies among species depending on their body size, wing morphology, foraging mode, and echolocation call structure (Aldridge and Rautenbach 1987,

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Crome and Richards 1988, Fenton 1990). In general, larger species with higher wing aspect ratios and wing loading are expected to forage in open habitats, while smaller species with lower aspect ratios and wing loading are expected to use more cluttered environments. Thus, use of various habitats and responses to forest management often vary with species. For example, in mixed-wood forests of Alberta, Canada, silver-haired bats (*Lasionycteris noctivagans*) prefer clearcuts, whereas smaller, more agile northern long-eared bats (*Myotis septentrionalis*) prefer interior forests (Patriquin and Barclay 2003). In mixed forests of West Virginia, big brown bats (*Eptesicus fuscus*) and red bats (*Lasurus borealis*) are more likely to occur in stands with larger canopy gaps and lower canopy cover, while northern long-eared bats and Indiana bats (*M. sodalis*) are more common in stands with greater canopy cover (Ford et al. 2005). However, in mixed woods of central Ontario, the large-bodied hoary bat (*Lasionycteris cinereus*) does not use habitats in the predicted manner, using old pine stands significantly more than recently logged stands (Jung et al. 1999).

Bats move over large distances on a nightly basis (Henry et al. 2002, Elmore et al. 2005). Consequently, landscape features and the spatial distribution of forest types and age classes may also be important determinants of bat habitat use. Two recent studies examined the effects of the composition and structure of the landscape on bat habitat use, one in a forested environment (Erickson and West 2003) and one in an urban environment (Gehrt and Chelvig 2003). Several studies have also examined the importance of riparian areas (Grindal et al. 1999, Seidman and Zabel 2001, Ellis et al. 2002, Law and Chidel 2002, Menzel et al. 2005) and elevation (Grindal et al. 1999) as landscape features affecting bat habitat use.

Research on forest habitat relationships of bats has been conducted primarily using acoustic sampling techniques and in the Pacific Northwest (e.g., Thomas 1988, Humes et al. 1999, Erickson and West 2003), Canada (e.g., Crampton and Barclay 1998, Grindal and Brigham 1999, Jung et al. 1999), and the northeastern United States (e.g., Krusic et al. 1996, Zimmerman and Glanz 2000, Ford et al. 2005). Only a few bat studies using acoustic techniques have been conducted in the southeastern United States (Ellis et al. 2002, Menzel et al. 2002a, 2005, Ford et al. 2006). In the Southeast, the Indiana bat, the gray bat (*M. grisescens*), and the Virginia big-eared bat (*Corynorhinus townsendii virginianus*) are listed as federally endangered, and several other species are considered sensitive species, including Rafinesque's big-eared bat (*C. rafinesquii*), the southeastern myotis (*M. austroriparius*), and the small-footed bat (*M. leibii*). Timber production in the southeast is expected to increase considerably during the next several decades, and considerable forested habitat is expected to be lost to development (Wear and Greis 2002). Thus, understanding the habitat requirements of forest bats in the southeast and their responses to forest management is critical to bat conservation and management.

Our objective was to determine the most important factors

associated with bat habitat use on the Sumter National Forest in northwestern South Carolina, USA, at various spatial scales. Because response to forest structure and type often varies among species due to roosting requirements and foraging modes, we examined overall bat habitat use and species-specific habitat use in relation to habitat characteristics at the sampling point and stand scales, as well as the position of the stand on the landscape. Based on previous work in other forests in North America, we predicted that use would be greatest 1) at points with relatively sparse vegetation, 2) in early successional and mature stands, and 3) at points close to streams. We also predicted that the most common bats would use habitats differently. Specifically, we predicted that the larger big brown bat would use early successional stands more than sapling/pole and mature stands and be more common at points with sparse vegetation; the smaller northern long-eared bat and eastern pipistrelle (*Pipistrellus subflavus*) would use points with denser vegetation and be more common in sapling/pole and mature forest stands; and red bats would use most habitat types.

## Study Area

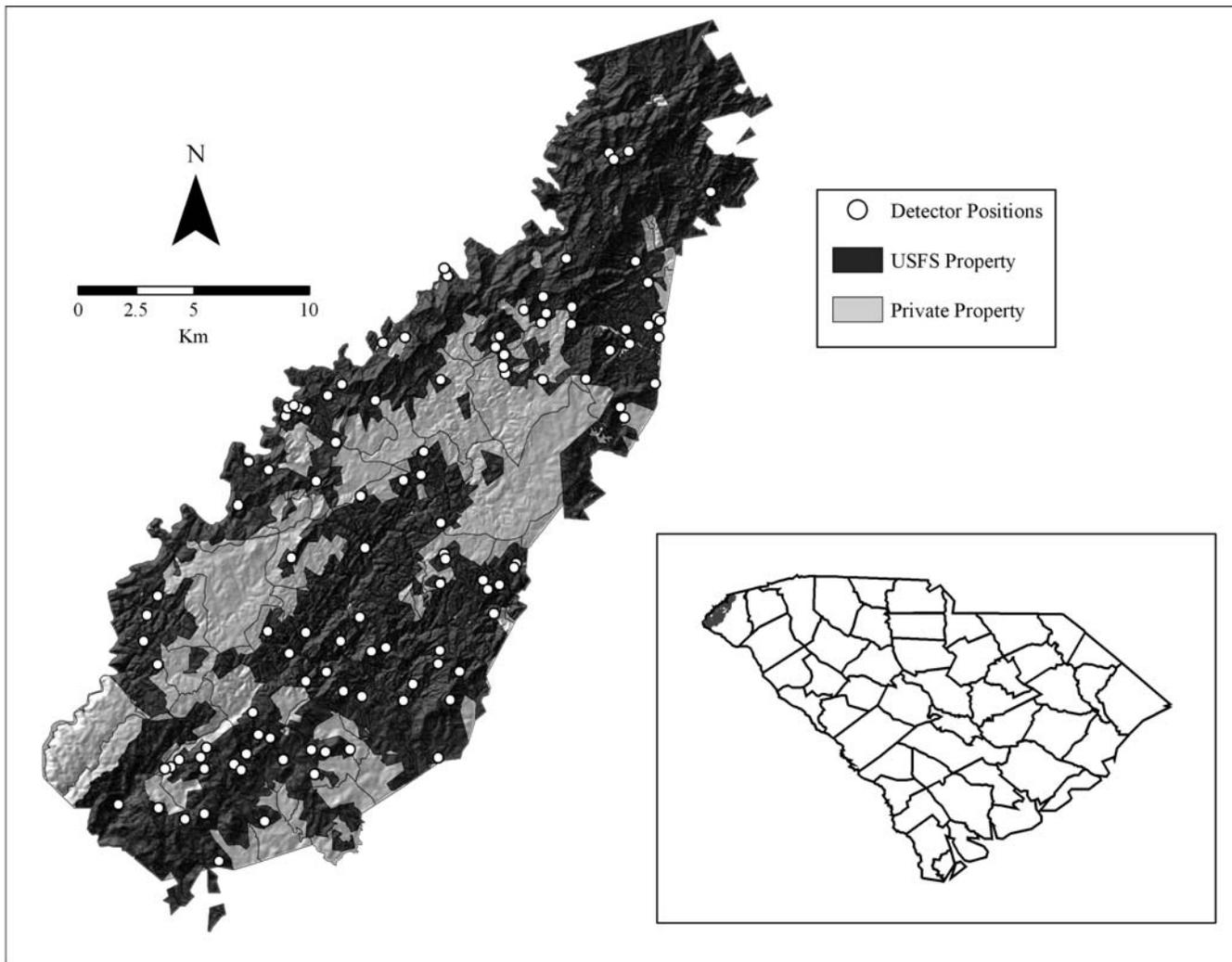
We conducted our study on the Andrew Pickens District (APD) of the Sumter National Forest in Oconee County in northwestern South Carolina. The APD was situated in the Upper Piedmont and Mountain Physiographic Regions. The topography ranged from gentle slopes and hills in the Piedmont to steep slopes in the Mountains (Fig. 1); elevations ranged from 218 to 995 m. The climate was temperate with mean minimum temperatures ranging from  $-1^{\circ}\text{C}$  in January to  $18.4^{\circ}\text{C}$  in July, and mean maximum temperatures ranged from  $11.6^{\circ}\text{C}$  in January to  $31.4^{\circ}\text{C}$  in July. Average annual precipitation was 154 cm.

The APD was 34,220 ha, much of which was interspersed with private land (Fig. 1). Forest types on the district included several pine types (*Pinus* spp.; 37%), mixed pine and hardwood (36%), upland hardwood (22%), and cove hardwood (5%). Approximately 5% of the stands were early successional ( $\leq 15$  yr), 34% sapling/pole (16–39 yr), 22% midsuccessional (40–79 yr), and 38% late successional ( $\geq 80$  yr). Numerous streams of various orders were found throughout the APD. The Chattooga River, a wild and scenic river, was on the western boundary of the APD and the Chauga River bisected the APD and drained most of the area.

## Methods

### Habitat Use

Our acoustic sampling sites were pre-existing points established for long-term bird monitoring in 6 forest types and 4 age classes. We selected stand types to represent the full range of forest types and structures on the APD. We used the Forest Service Continuous Inventory of Stand Condition database to make the initial stand selection, but we verified age and forest types when stands were installed. When necessary, we deleted stands and substituted others to



**Figure 1.** Location of acoustic sampling points for bats on the Andrew Pickens District of the Sumter National Forest in northwestern South Carolina, USA, May–Aug, 2004–2005.

ensure that we placed points in the correct forest type and age class. Stands containing the sampling points ranged in size from 2 to 105 ha. Our sampling points were at least 50 m from the edge of the stand. We marked each point with a rebar stake and georeferenced with a Global Positioning System (GPS). Points occurred in cove hardwood, upland hardwood, mixed pine–hardwood, white pine (*Pinus strobus*), Virginia pine (*Pinus virginiana*), and yellow pine forest types. Age classes were as we described above; however, we chose to combine the mid- and late-successional habitats due to small sample sizes and few differences in bat detections between age classes. We also combined the 6 forest types into 3 types: hardwood, pine, and mixed pine–hardwood.

We passively sampled each point with an Anabat II bat detector (Titley Electronics, Ballina, New South Wales, Australia) connected to a programmable zero-crossings analysis interface module (Anabat CF Storage ZCAIM). (Note: The use of trade or firm names in this publication is for reader information and does not imply endorsement by the United States Department of Agriculture of any product

or service). In 2004, we sampled 80 of the 89 points for only 1 night; in 2005 we sampled points for 1–3 nights. We programmed detectors to start recording at approximately 15 minutes prior to sunset and end at approximately 15 minutes after sunrise. We placed the detectors and ZCAIMs in waterproof containers with a 45° tube (O’Farrell 1998). We attached the containers to tripods set at approximately 1.3 m, and oriented them in the direction with the least clutter (Weller and Zabel 2002). We sampled from 24 May to 24 August 2004 and from 23 May to 10 August 2005. We did not sample during periods of extended rain. Due to logistics, we were not able to stratify our nightly samples by forest type and age. However, we attempted to sample a variety of forest types and age classes on a nightly basis and to move to different areas of the APD each night. The number of points sampled each night varied due to logistics.

We uploaded data after we sampled each point, and we used Analook (Version 4.9j, 2004) to analyze the calls. We used 2 filters to assess bat habitat use: an identification filter and a use/activity filter. Both of these filters were designed

for bats in the eastern United States. The identification filter selected call sequences or passes with at least 5 calls that, in general, were search-phase calls (Britzke and Murray 2000). We examined each file that passed through the identification filter and eliminated those passes that did not contain search-phase calls. We used a combination of quantitative and qualitative methods to identify each pass to species. First, we used a discriminant function model based on a call library of over 23,000 calls to identify each call and pass to species (Britzke 2003). Next we qualitatively examined each pass (O'Farrell et al. 1999) to confirm or correct the quantitative identification. To assess overall bat habitat use, we used a more liberal filter (see Britzke 2003). This filter required that each pass had  $\geq 1$  call and allowed lower quality calls to pass the filter. We did not identify these passes to species. If we sampled a point for  $>1$  night per summer, we averaged the number of passes over the 2 or 3 nights.

We also captured bats with mist nets throughout the APD during the summers of 2002–2004 to document the resident species in the area. We placed mist nets (2.6 or 5.2 m in height and 2.6, 6, or 9 m wide) across roads, streams, and trails. We checked nets every 15 minutes and removed all bats from the nets. We identified all bats to species, placed an aluminum-lipped numbered band on their forearm (Lambournes Ltd., Birmingham, United Kingdom), and recorded standard measurements such as forearm length, age, sex, and reproductive condition.

### Habitat Analysis

We obtained age class and forest type of each stand using the Forest Service Continuous Inventory of Stand Conditions database. In 2005, we characterized the amount of clutter above and immediately surrounding each sampling point as sparse, medium, or dense. We overlaid the GPS locations of the sampling points on Geographic Information System (GIS) data layers of the APD, and we analyzed spatial data with ArcMap 9.0 (ESRI, Redlands, California). Data layers included elevation (30-m digital elevation models), streams, waterbodies, and roads. We subdivided the stream layer into 3 classes by order: small (orders 0–2), medium (orders 3 and 4), and large (orders 5–7). For each point, we extracted elevation, percent slope, and distance to each stream class and drivable road.

### Statistical Analysis

We used the Likelihood Ratio  $\chi^2$  (PROC FREQ; SAS 1999) to test whether the number of points where bats were detected varied between years and whether vegetation density was related to age class. We used a Mann–Whitney  $U$  test to determine whether overall activity varied between years. We used an information theoretic approach (Burnham and Anderson 2002) to develop and select the best models of overall bat and individual species presence. We developed 12 a priori models focused on sampling point, stand, sampling point plus stand, and landscape characteristics. Our predictor variables were vegetation density for the sampling point; forest type and age class for the stand level;

elevation, slope, and distance to closest stream regardless of stream order; distance to small, medium, and large streams; and distance to the nearest road for the landscape scale. We used logistic regression to predict presence of bats in relation to each of these sets of variables (PROC LOGISTIC; SAS 1999).

Two models, the global model and one that included the interaction between habitat type and age class, were consistently unreliable due to quasicomplete separation of data points. Thus, we deleted these models from the model set. For the remaining 10 models we calculated Akaike's Information Criterion corrected for small sample sizes ( $AIC_c$ ), the difference between the model with lowest  $AIC_c$  and the  $AIC_c$  for the  $i$ th model ( $\Delta_i$ ), and Akaike weights ( $w_i$ ). We considered models with  $\Delta_i \leq 2$  to have substantial support, whereas we considered models with  $\Delta_i$  between 3 and 7 to have moderate support (Burnham and Anderson 2002). We also used  $w_i$  to evaluate models. We presented odds ratios and their 95% confidence intervals (CI) for variables in models with the greatest support. Because bat use of points sampled in both years was highly variable, we constructed separate models of overall bat use for 2004 and 2005. Parameter estimates for many models of individual species habitat use were invalid due to quasicomplete separation of data when we examined them by year. However, ranks of models were similar between years. We were able to obtain valid parameter estimates for most models by combining individual species data for the 2 years.

We applied Moran's (1950) test of spatial autocorrelation to assess the spatial distribution of the points used by bats. For each year, we tested whether the points at which we recorded bats were clustered, dispersed, or random using the spatial autocorrelation tool in ArcMap. We ran these tests for overall bat use and for each species.

## Results

We mist-netted 12 sites during 17 nights and captured 95 bats of 9 species. The most common species were red bats (31), little brown bats (30), northern long-eared bats (18), big brown bats (7), eastern pipistrelles (3), and evening bats (*Nycticeius humeralis*; 3). We also captured 1 Rafinesque's big-eared bat, 1 hoary bat, and 1 small-footed bat. We captured the 30 little brown bats at a site at the very northern part of the APD near a maternity colony in a building.

We acoustically sampled 89 points in 2004, and we sampled 98 points in 2005; we sampled 78 points in both years. Using the use/activity filter, we recorded 1,430 bat passes in 2004 and 2,419 bat passes in 2005. Bats were recorded at more points in 2004 (58 points, 63.7%) than in 2005 (52 points, 52.0%;  $\chi^2 = 2.687$ ,  $df = 1$ ,  $P = 0.101$ ), and the median number of passes per point per night was significantly greater in 2004 than in 2005 (3.5 vs. 0.5,  $U = 9,628$ ,  $P = 0.0195$ ).

We identified 8 species of bats from acoustic recordings; some calls could only be identified as a *Myotis* species. We recorded eastern pipistrelles in 31 stands; big brown bats in

**Table 1.** Number of estimated parameters (K), small sample Akaike's Information Criteria (AIC<sub>c</sub>), difference between model AIC<sub>c</sub> and that of the best model (Δ<sub>i</sub>), and Akaike's weight (w<sub>i</sub>) for logistic regression models to predict overall bat presence based on point, stand, point and stand, and landscape characteristics on the Andrew Pickens District of the Sumter National Forest, South Carolina, USA, May–Aug, 2004 and 2005.

Model	K	2004			2005		
		AIC <sub>c</sub>	Δ <sub>i</sub>	w <sub>i</sub>	AIC <sub>c</sub>	Δ <sub>i</sub>	w <sub>i</sub>
VegDen <sup>a</sup>	3	100.75	0	0.90	135.23	0.07	0.34
Type <sup>b</sup>	3	121.47	21.04	0.00	140.03	4.87	0.03
Age	3	118.48	18.05	0.00	137.20	2.03	0.13
VegDen + type + age	7	104.92	4.49	0.10	139.67	4.50	0.04
Elevation	2	120.15	19.72	0.00	139.63	4.46	0.04
Slope	2	120.40	19.97	0.00	139.67	4.51	0.04
Closest stream	2	119.31	18.88	0.00	139.49	4.32	0.04
Sm + med + large <sup>c</sup>	4	121.34	20.90	0.00	142.99	7.83	0.01
Distance road	2	119.66	19.22	0.00	135.16	0	0.35
Elevation + slope + sm + med + large + distance road	7	127.04	26.60	0.00	144.93	9.77	0.00

<sup>a</sup> VegDen = relative density of the vegetation at the sample point.

<sup>b</sup> Type = pine, mixed, or hardwood.

<sup>c</sup> Sm = 0–2 order streams, med = 3 and 3 order streams, large = 5–7 order streams.

15 stands; red bats in 22 stands; northern long-eared bats in 11 stands; evening bats in 3 stands; and hoary bats, small-footed bats, and *Myotis* spp. in 2 stands each. We only examined the relationship between habitat variables and species presence for eastern pipistrelles, big brown bats, red bats, and northern long-eared bats due to small sample sizes for other species. Points at which bats were recorded were not spatially correlated. Points at which any bats were recorded were randomly distributed across the landscape (Moran's Index = 0,  $P < 0.1$ ). Points where the 4 target species (big brown bats, red bats, northern long-eared bats, and eastern pipistrelles) were recorded in 2004 and 2005 were also randomly distributed (Moran's Index =  $0 \pm 0.04$ ,  $P < 0.1$ ). Further, vegetation density at the sample points was not significantly related to age class ( $\chi^2 = 0.9744$ ,  $df = 4$ ,  $P = 0.9137$ ).

The model containing only vegetation density at the

sample point was the best predictor of overall bat presence in 2004 (Table 1). This model was 9 times more likely to be the best model than the second best model that included vegetation density, forest type, and age class. Based on the odds ratios, bats were 6.67 (95% CI: 1.46, 30.42) times more likely to be recorded at points with sparse vegetation than at points with dense vegetation and 1.98 (95% CI: 0.652, 6.039) times more likely to be recorded at points with medium vegetation than at points with dense vegetation. In 2005, 2 models were essentially tied for the best model explaining presence of bats (Table 1). Each model contained one variable: distance to the closest road and vegetation density at the sample point. The model that contained age class also had good support. The probability of bats being recorded increased by 1.002 (95% CI: 1.000, 1.004) for each meter from the road, and the probability of bats being recorded at points with sparse vegetation was 4.59 times

**Table 2.** Number of estimated parameters (K), small sample Akaike's Information Criteria (AIC<sub>c</sub>), difference between model AIC and that of the best model (Δ<sub>i</sub>), and Akaike's weight (w<sub>i</sub>) for logistic regression models to predict presence of big brown bats (EPFU), red bats (LABO), northern long-eared bats (MYSE), and eastern pipistrelles (PISU) based on point, stand, point and stand, and landscape characteristics on the Andrew Pickens District of the Sumter National Forest, South Carolina, USA, May–Aug, 2004 and 2005.

Model	K	EPFU			LABO			MYSE			PISU		
		AIC <sub>c</sub>	Δ <sub>i</sub>	w <sub>i</sub>	AIC <sub>c</sub>	Δ <sub>i</sub>	w <sub>i</sub>	AIC <sub>c</sub>	Δ <sub>i</sub>	w <sub>i</sub>	AIC <sub>c</sub>	Δ <sub>i</sub>	w <sub>i</sub>
VegDen <sup>a</sup>	3	79.48	0.00	0.97	91.45	0.00	0.95	67.00	1.38	0.25	116.22	0.00	0.76
Type <sup>b</sup>	3	93.38	13.89	0.00	110.97	19.52	0.00	77.37	11.74	0.00	136.07	19.85	0.00
Age	3	92.31	12.83	0.00	114.52	23.07	0.00	67.02 <sup>d</sup>	1.39	0.24	129.95	13.73	0.00
VegDen + type + age	7	87.72	8.24	0.02	97.23	5.78	0.05	65.63 <sup>d</sup>	0.00	0.49	118.54	2.32	0.24
Elevation	2	91.25	11.77	0.00	112.92	21.47	0.00	74.87	9.25	0.00	131.31	15.09	0.00
Slope	2	90.25	10.77	0.00	112.50	21.05	0.00	75.41	9.78	0.00	133.89	17.68	0.00
Closest stream	2	90.66	11.18	0.00	113.69	22.24	0.00	74.84	9.22	0.00	134.16	17.94	0.00
Sm + med + large <sup>c</sup>	4	91.31	11.82	0.00	113.09	21.65	0.00	78.26	12.63	0.00	136.89	20.67	0.00
Distance Road	2	91.24	11.75	0.00	113.68	22.23	0.00	74.56	8.94	0.01	132.17	15.96	0.00
Elevation + slope + sm + med + large + distance road	7	96.67	17.19	0.00	114.51	23.06	0.00	83.96	18.33	0.00	139.59	23.37	0.00

<sup>a</sup> VegDen = relative density of the vegetation at the sample point.

<sup>b</sup> Type = pine, mixed, or hardwood.

<sup>c</sup> Sm = 0–2 order streams, med = 3 and 4 order streams, large = 5–7 order streams.

<sup>d</sup> Quasicomplete separation of data. Model parameters could not be estimated.

(95% CI: 1.39, 15.15) more likely than their being recorded at points with dense vegetation. They were also 2.05 (95% CI: 0.76, 6.51) times more likely to be recorded at points with medium vegetation than at points with dense vegetation. Further, bats were 2.15 (95% CI: 0.51, 9.15) times more likely to be recorded at points in early successional stands than in mature stands, but they were 0.62 (0.26, 1.47) times less likely to be recorded in midsuccessional stands than in mature stands.

The model with vegetation density alone was the best model explaining the presence of big brown bats and red bats (Table 2). These models were 48.5 and 19 times more likely to be the best model than the next best models for big brown bats and red bats, respectively. Big brown bats were 6.58 (95% CI: 0.709, 61.08) times more likely to be recorded at points with open vegetation than at points with dense vegetation, and they were 4.17 (95% CI: 0.484, 35.88) times more likely to be recorded at points with medium vegetation density than at points with dense vegetation. Red bats were 21.15 (95% CI: 2.45, 182.25) times more likely to be recorded at points with open vegetation than at points with dense vegetation, and they were 4.88 (0.57, 41.34) times more likely to be recorded at points with medium vegetation density than at points with dense vegetation.

Although the model with only vegetation density was also the best model explaining the presence of eastern pipistrelles, the model that included vegetation density, forest type, and age class also had strong support (Table 2). Eastern pipistrelles were 8.75 (95% CI: 1.55, 49.29) times more likely to be recorded at points with open vegetation than at points with dense vegetation, and they were 6.67 (95% CI: 1.32, 33.65) times more likely to be recorded at points with medium vegetation density than at points with dense vegetation. Eastern pipistrelles were also 3.00 (95% CI: 0.68, 13.28) times more likely to be recorded in early successional stands than in mature stands, but they were 0.46 (95% CI: 0.15, 1.35) times as likely to be recorded in mid-successional stands as in mature stands. Logistic regression diagnostics suggested that there was little effect of forest type.

The model that included vegetation density, age class, and forest type was the best model explaining northern long-eared bat presence (Table 2). There was also strong support for the models containing only vegetation density and only age class. However, because there was quasicomplete separation of the data for the models containing age class and vegetation density + forest type + age class, coefficients for age class could not be estimated. This was most likely because 10 of the 11 stands in which northern long-eared bats were recorded were mature stands. Northern long-eared bats were 6.58 (95% CI: 0.71, 61.08) times more likely to be recorded at points with sparse vegetation at the sample point than at points with dense vegetation and 2.22 (95% CI: 0.24, 20.98) times more likely to be recorded at points with medium density vegetation than at points with dense vegetation.

## Discussion

Our results indicate that habitat use by bats is affected by factors at multiple spatial scales. We found that vegetation density at the sampling point was the best predictor of overall bat habitat use and use by all of the species examined. As we predicted, habitat use by bats was negatively related to the density of vegetation surrounding the detector. Stand age class was a good predictor of overall bat habitat use in 2005 and of eastern pipistrelle and northern long-eared bat habitat use. In contrast, landscape factors appeared to have little effect on bat habitat use.

Increased use of points with sparse vegetation surrounding the detector may have resulted simply from greater detectability of echolocation calls at more open sites (Hayes 2000). Because we only sampled most points once per year, we were not able to estimate detection probabilities (e.g., MacKenzie et al. 2002) by habitat type or age class. However, Patriquin et al. (2003) found that, although there are some differences in detectability among forest types, vegetation density does not affect the detectability of bats that echolocate in the 40 kHz range (e.g., *Myotis* and eastern pipistrelles) and stand age does not affect the detectability of bats that echolocate in the 25 kHz range (e.g., big brown bats). Thus, vegetation density probably had little influence on the effectiveness of our sampling.

Since vegetation density at the detector was not related to age class, we concluded that points with sparse vegetation represented small gaps or openings in intact forest, as well as stands in early stages of regeneration. Higher use of small gaps and openings within stands relative to intact forest has been observed in several other studies (Law and Chidel 2002, Menzel et al. 2002a, Tibbels and Kurta 2003) and may be related to greater insect availability, proximity to roosts, or decreased structural complexity. However, while some studies have found that insect abundance is higher in small openings (Tibbels and Kurta 2003) or clearcuts (Lunde and Harestad 1986), others have found that insects are more abundant in cluttered versus uncluttered habitats (Kalcounis and Brigham 1995, Grindal and Brigham 1999). Further, although bat activity is positively related to insect availability in some sites (Kalcounis and Brigham 1995, Tibbels and Kurta 2003), there is no relationship between bat activity and insect availability in others (Lunde and Harestad 1986, Grindal and Brigham 1999). Proximity to roosts may have also influenced activity in areas with sparse vegetation. Forest bats often select roosts located in or near gaps, areas with lower tree density, or in edge habitats to obtain more solar radiation (Barclay and Kurta, in press, Carter and Menzel, in press).

Reduced structural clutter at sample points with sparse vegetation may be one of the most important factors contributing to higher bat use of points with sparse vegetation. Both field (Humes et al. 1999, Erickson and West 2003) and experimental (Brigham et al. 1997, Sleep and Brigham 2003) studies suggest that bats avoid areas of high clutter and prefer areas of reduced clutter. However, response to structural clutter often varies with species

depending on body size, wing morphology, and echolocation call structure (Aldridge and Rautenbach 1987, Crome and Richards 1988, Fenton 1990). Despite differences in morphology and echolocation call structure of the 4 common species in our study area, we found that all species were more likely to be recorded at points with sparse vegetation. We expected these results for big brown bats, which are considered clutter intolerant species due to their morphology and call structure (Brigham et al. 1997, Menzel et al. 2005). However, because red bats are adapted for semicluttered habitats (Fenton 1990, Menzel et al. 2005) and northern long-eared bats (Farney and Fleharty 1969, Broders et al. 2004) and eastern pipistrelles (Farney and Fleharty 1969, Menzel et al. 2005) are morphologically adapted to cluttered environments, we expected these 3 species to make greater use of points with medium and dense clutter than we observed.

Bats were more likely to be recorded in early-successional habitats and least likely to be recorded in midsuccessional habitats which is consistent with several other studies. Preferential use of recently cut stands (Erickson and West 1996, Ellis et al. 2002), mature or old-growth forests (Thomas 1988, Crampton and Barclay 1998, Patriquin and Barclay 2003), or both recently cut and mature stands (Krusic et al. 1996, Menzel et al. 2005) is probably related to more open structures in clearcut and old-growth forests. Further, high activity in mature or old-growth forests may be related to increased availability of roosting structures such as large snags and large trees with cavities and hollows (Thomas 1988, Krusic et al. 1996, Crampton and Barclay 1998).

We predicted that big brown bats would primarily use early-successional habitats. However, stand age class was not an important predictor of big brown habitat use. Although big brown bats make greater use of early-successional habitats in some areas (Ellis et al. 2002), they roost in large trees in mature stands with relatively open canopies (Betts 1996, Cryan et al. 2001). This may contribute to their seeming lack of preference for early age class stands. As predicted, red bats did not show an affinity to any age class. Although red bats are often recorded more in open than cluttered habitats (Ellis et al. 2002, Menzel et al. 2005), a recent telemetry study in Mississippi showed that they do not select among stands of various age classes (Elmore et al. 2005). Surprisingly, eastern pipistrelles were more likely to be recorded in early-successional stands than in mature stands and least likely to be recorded in midsuccessional stands. Although they are considered to be a clutter adapted species (Menzel et al. 2005), other studies have also found that they do not make great use of mid- and late-successional stands (Ellis et al. 2002, Menzel et al. 2005). In contrast to the other species, northern long-eared bats were found almost exclusively in mature stands. Mature stands may be particularly important for northern long-eared bats because they are morphologically adapted to clutter, and their roost sites are in interior forests (Menzel et al. 2002*b*).

We found no significant relationships between bat use and

forest type suggesting that forest structure is a more important factor determining bat foraging and commuting habitat use than forest composition. Only a few studies have found significant differences in foraging and commuting habitat use among forest types (Krusic et al. 1996, Kalcounis et al. 1999). In contrast, forest type is an important factor in the roosting behavior of many species including red bats and northern long-eared bats (Menzel et al. 1998, Hutchinson and Lacki 2000, Mager and Nelson 2001, Broders and Forbes 2004). Therefore, the distribution of forest types across the landscape may be an important factor influencing bat foraging and commuting habitat use, and should be investigated in the future.

Although we predicted that proximity to riparian areas would be an important factor in bat habitat use, we saw no evidence that habitat use was related to distance to streams. In contrast, habitat use by several bat species in the hotter and drier Coastal Plain of South Carolina was positively related to proximity to water (Ford et al. 2006). Riparian areas are generally considered to be important to bats as sources of drinking water and food (Cross 1988, Racey 1998). Both 2004 and 2005 were relatively wet years, and rainfall during May, June, July, and August equaled or exceeded the 100-year averages. Thus, the importance of riparian areas as sources of drinking water during our study may have been minimal.

Bat activity levels in our study, as well in other studies conducted in the southeast (Ellis et al. 2002, Menzel et al. 2005), were relatively low. Further, because we were only able to identify a small proportion of bat passes to species, we probably underestimated species presence at some points and overestimated species absence at other points. However, we recorded all of the bats that have been captured on the APD except for Rafinesque's big-eared bats, which are rarely recorded through passive monitoring due to their very low intensity calls (Fenton 1982, Murray et al. 1999). Using an identification filter that required  $\geq 5$  calls/pass may have limited our identification rate in comparison to studies using passes with 2–4 calls (e.g., Kalcounis et al. 1999, Ellis et al. 2002, Ford et al. 2005, Menzel et al. 2005). However, restricting identification to passes with  $\geq 5$  calls increases the accuracy of species identification. Our use of passive monitoring may have also decreased our ability to identify passes compared to an active sampling approach (Johnson et al. 2002, Milne et al. 2004). However, the active monitoring method is typically conducted for only a short time at each sampling point, thus ignoring spatio-temporal variation in activity and perhaps, confounding results.

Conclusions about bat-habitat relationships based solely on data derived from acoustic sampling should be made with caution. For example, acoustic sampling techniques can only provide data on relative habitat use, whereas habitat preference must be determined using radiotelemetry (Miller et al. 2003). Nonetheless, data from acoustic sampling studies can be used to generate hypotheses about habitat use and selection at various spatial scales that can be tested with other techniques (Sherwin et al. 2000, Gannon et al. 2003).

Our results suggest that future studies should consider within stand variation when studying bat habitat use and selection at the stand and landscape levels. While the landscape features that we examined did not appear to be important determinants of habitat use, other landscape features such as fragmentation, diversity of stands, and anthropogenic influences (urban areas, agriculture) may be important and should be tested in the future.

## Management Implications

The strong positive relationship between sparse clutter at the detector and bat presence, and the lack of a relationship between clutter and stand age suggests that openings and gaps within mature forests as well as the presence of large open areas (e.g., regeneration sites, wildlife openings) will provide good habitat for bats. Management practices that create openings and gaps within mid- and late-successional stands are likely to make them more suitable for bats and increase the amount of usable habitat. Because most tree roosting eastern bats prefer large trees in mature stands situated near openings, these management practices would

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provide both foraging and roosting habitat. The variability in species responses to stand age class suggests that management strategies that provide a range of age class stands across the landscape will provide habitat for the entire bat community. Further, although forest type did not appear to be an important factor determining foraging and commuting habitat use, it is an important factor for some species' roosting ecology and thus, must also be considered in developing overall management strategies for bat conservation.

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