Habitat Associations of Bats in South-central West Virginia

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Abstract: We conducted acoustic surveys at National Park Service and state park properties in south-central West Virginia to create bat habitat association models across a large, topographically complex and relatively intact Appalachian Hardwood landscape representative of the Allegheny Plateau portion of the central Appalachians. We developed generalized and species-specific groups of *a priori* habitat association models to predict bat presence using various microhabitat and landscape features linked to body-size, wing morphology, food habits and echolocation call characteristics for seven species. Habitat associations for the species generally followed expectations based on previous research in the region. Although variable among species, riparian areas were important components of foraging habitat, with open, less structurally cluttered zones most important for little brown myotis (*Myotis lucifugus*), eastern pipistrelles (*Pipistrellus subflavus*), and big brown bats (*Eptesicus fuscus*), and to a lesser extent eastern red bats (*Lasiurus borealis*). Riparian areas with closed-canopy forests were important for Indiana myotis (*M. sodalis*) and northern myotis (*M. septentrionalis*). Current regulations and guidelines that ensure protection and maintenance of riparian health and integrity concomitantly will provide protection of important bat foraging habitat in the region.

Key words: acoustical sampling, bat, foraging, central Appalachians, habitat model, West Virginia

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Traditionally, studies on bat habitat associations of forest bats were conducted at small spatial scales and were restricted in inference to the forest stand level (Miller et al. 2003, Miles et al. 2006). While small-scale studies provide insight into bat habitat relationships, bats likely select habitat based on multiple-scale criteria. More recently studies have begun to examine larger-scale features influencing bat habitat selection (Ford et al. 2005, Miles et al. 2006). For example, several studies in North America have identified edge as an important habitat feature for bats (Crampton and Barclay 1998, Hogberg et al. 2002, Menzel et al. 2002), concluding that edge provides habitat with low structural complexity and high insect abundance. These studies on bat habitat relationships across larger scales and landscapes have been facilitated by the use of acoustic detection systems (Johnson et al. 2002, Ford et al. 2005).

Two studies have used acoustic detectors to examine the importance of habitat features to bats in the Allegheny Mountain region of east-central West Virginia. Owen et al. (2004) quantified bat habitat associations among replicated silvicultural treatments, whereas Ford et al. (2005) measured associations across a gradient of forest conditions, elevations, and site indices. Both studies documented that microhabitat factors, including canopy cover, forest gap metrics, and stream proximity, were most important in explaining bat species presence. Presence of little brown myotis (*Myotis lucifugus*), eastern red bats (*Lasiurus borealis*), and big brown bats (*Eptesicus fuscus*) was linked to larger forest canopy gaps and openings, whereas presence of Indiana myotis (*M. sodalis*) and northern myotis (*M. septentrionalis*) were linked to increased canopy cover (Owen et al. 2004, Ford et al. 2005). These studies demonstrated that bat habitat relationships reasonably matched expectations based on food habits, body size, wing morphology, and echolocation call characteristics of individual bat species. Nonetheless, these studies were limited by sample size and overall lack of inference across a larger central Appalachian landscape. Our objective was to examine bat-habitat associations derived from acoustic data collected across a large, topographically complex and relatively intact, forested landscape to compliment exist-

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ing information for the region. We modeled individual bat species presence relative to microhabitat and landscape level variables and evaluated models in an information theoretic framework.

Study Area

We conducted our study at the Bluestone National Scenic River, Gauley River National Recreation Area, New River Gorge National River, Carnifex Ferry Battlefield State Park, Pipestem State Park, and Grandview State Park covering portions of Fayette, Mercer, Nicholas, Raleigh and Summers counties in south-central West Virginia. Study areas were located in the Unglaciated Allegheny Plateau, which is a subsection of the Appalachian Plateau physiographic province of the central Appalachian Mountains. The region is characterized by steep slopes with numerous vertical cliff-faces and colluvial breakdown, narrow valleys, and plateau-like ridge tops of highly resistant sandstone (Fenneman 1938). Elevations of our study sites ranged from approximately 250 to 1,000 m. Annual precipitation averaged 130 cm. A substantial legacy of anthropogenic impacts existed in the study area, with railroad grades, roads, abandoned buildings and mineshafts present throughout from past logging and coal mining.

Combined, our study sites contained approximately 40,000 ha of second- or third-growth forests dominated by the mixed mesophytic and oak (*Quercus* spp.)-hickory (*Carya* spp.) forest types on sideslopes and ridges. The larger riparian zones contained forest communities consisting of American sycamore (*Platanus occidentalis*), river birch (*Betula nigra*), green ash (*Fraxinus pennsylvanica*), and ironwood (*Carpinus caroliniana*). Eastern hemlock (*Tsuga canadensis*), sweet birch (*Betula lenta*), and rosebay rhododendron (*Rhododendron maximum*) dominated smaller streamside corridors and drainages.

Methods

We conducted acoustic surveys at 680 locations across the study area from July to September 2003 and May to August 2004 using Anabat II detectors (Titley Electronics, Ballina, Australia). In 2003, 270 stations were located at the forest edge along hiking trails and roads. The first station was located at a randomly selected distance along a road or trail, and subsequent stations were established systematically every 5-minutes' walking duration along the road or trail. In 2004, an additional 410 stations were surveyed in forest interiors away from trails and roads. We located stations by randomly choosing a point along a road or trail as the beginning point of a line transect. The direction of the transect was a randomly selected compass bearing constrained so that the transect was not parallel to the road or trail. Acoustic survey stations (5–6/transect) were systematically located at 100 m intervals along the transect with the first station at 100 m from the road or trail. All survey stations were surveyed once. Stations were geo-referenced using a Global Positioning System (Trimble III, Sunnyvale, California or Garmin GPS V, Olathe, Kansas) for later use in spatial analyses.

At each station, we conducted passive sampling by placing detectors on the ground with the detection cone point directly perpendicular to the ground for 20 min. We conducted surveys during the first 2–3 h after sunset (Ford et al. 2005). We did not sample on nights with strong wind (>10 km/hr) or temperatures below 10 C. We recorded bat echolocation call sequences on compact flash cards within the Zero Crossings Analysis Interface Module (Titley Electronics, Ballina, Australia), and downloaded them to a laptop computer.

We identified echolocation call sequences with Analook v4.9 software (Titley Electronics, Ballina, Australia). We processed all call sequences through customized filters to remove fragmented calls, echoes, extraneous noise and all other call sequences not consistent with the properties of search-phase echolocation calls (Britzke and Murray 2000, Ford et al. 2005). After filtering, we only retained sequences with ≥5 call pulses to increase identification accuracy.

We assigned calls to species using a discriminate function analysis (DFA) model and a comprehensive call library for the eastern United States (Britzke 2003). We determined accuracy of identification rates for each species by performing cross-validation of the DFA on known calls for bat species known to have distributions that overlapped our study sites. Cross-validation involved developing the DFA model from two-thirds of the Britzke (2003) call library for our chosen suite of species and validating the model for those species using the remaining calls. Accuracy rates were based on single call sequences and, therefore, represented minimum rates. However, identification accuracy rates for a species increases as the number of call sequences at a site increases, but decreases when calls of other species with similar call characteristics are recorded during the same sampling period (Britzke et al. 2002). Therefore, we only considered a species present at a site if ≥2 call sequences from that species were recorded during the 20-min sampling period. Although Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) and Virginia big-eared bat (*C. townsendii*) were present on our study sites (Johnson et al. 2003, Johnson et al. 2005), they were excluded from analyses because their low intensity calls are difficult to record and identify using acoustical detectors (Owen et al. 2004).

We recorded potential bat habitat parameters in the field and derived parameters using a Geographic Information System (GIS; ArcGIS and ArcView 3.2, ERSI Inc., Redlands, California; Table 1) for each sampling location. We calculated topographic variables including slope, aspect, and elevation using a 30-m digital elevation model (DEM; West Virginia GIS Technical Center 2000). We

Table 1. Variables collected at acoustic survey sites included in *a priori* habitat association models for seven bat species in Bluestone National Scenic River, Gauley River National Recreation Area, New River Gorge National River, and surrounding areas of West Virginia, 2003–2004.

Variable	Description
Slope (S)	Slope measured from 30-m DEM; categorized as gentle (0–15°), moderate (16°–25°), or steep (>26°).
Aspect (A)	Transformed aspect value from mesic to xeric (0–2) measured from 30-m DEM
Elevation (E)	Elevation (m) measured from 30-m DEM
Distance to stream (DS)	Distance to nearest stream (1st–4th order; m)
Distance to major stream (DMS)	Distance to the nearest major river (m): Bluestone, Gauley, Little Bluestone, Meadow, or New rivers
Proximity to water (PW)	Distance to water sources other than 1st–4th order stream or major stream (m)
Distance to nearest water (DW)	Distance to the nearest water source (m)
Distance to mine (DM)	Distance to nearest mine (m)
Distance to cliff line (DC)	Distance from site to nearest cliff lines (m); cliff lines were identified as an abrupt change in slope
Linear measurement of road (LR)	Cumulative length of roads (m) within 150 m buffer encircling survey site
Percent forest (PF)	Percent forest from land use and land cover within 150 m buffer encircling survey site
Stand class (SC)	Stand class category: 1) regeneration (0–5 cm dbh), 2) seedling-sapling (5.1–23.0 cm dbh), 3) small sawtimber (23.1–46.0 cm dbh), 4) large sawtimber (>46 cm dbh)
Midstory (MS)	A visual estimate of mid-story woody percent coverage categories: 0%–25%, 25%–50%, 50%–75%, 75%–100%
Habitat type (H)	Category that represents habitat type at each site as either open canopy (0%–50%) or closed (51%–100%) canopy
Width of corridor (WC)	An estimate of corridor width or forest canopy gap diam. (m) at each site
Temperature (T)	Temperature (C) at end of 20-min sampling period
Water at the site (WS)	Presence or absence of water within 40 m of site

transformed aspect into a linear gradient (0, 1, or 2) related to moisture, with 2 representing the most xeric landscape position (south-facing) and 0 representing the most mesic (north-facing; Odom and McNab 2000, Ford et al. 2002b). One was assigned to a flat aspect. We placed slope into three categories: (1) gentle (0°–15°), (2) moderate (15°–25°), and (3) steep (>26°). We calculated distance to nearest stream (ranked 1st through 4th order) and nearest large watercourse (Bluestone, Gauley, Little Bluestone, Meadow, or New rivers) using a digitized stream layer (30-m resolution) by measuring straight-line distance from each station. We determined proximity to water sources other than streams (i.e., ponds and lakes) by digitizing water from digital orthophotos (West Virginia Department of Environmental Protection 2007), and measuring the straight-line distance from each station to the water source. In ArcView, we calculated distances to mines by measuring the distance from each station to the nearest mine portal, and we calculated distance to the nearest cliffline from the digital orthophotos. We measured the cumulative linear measurement (m) of roads and estimated percent forest cover within a 150-m buffer around each station using the Land Use and Land Cover layer from 1992 Landsat imagery at 30-m resolution (U.S. Geological Survey Earth Observation Systems Data Center 2007). At each station, we visually estimated stand-class as (1) regeneration (0.0–5.0 cm diameter at breast height [dbh]), (2) seedling-sapling (5.1–23.0 cm dbh), (3) small sawtimber (23.1–46.0 cm dbh), or (4) large sawtimber (>46 cm dbh) and midstory density as 0%–25%, 25%–50%, 50%–75%, or 75%–100%. We classified canopy cover at each station as either open (0%–50%) or closed (51%–100%). We estimated corridor width (road, trail, abandoned railroad grade, or watercourse channel) or forest canopy gap (m) as appropriate. We measured temperature at each station at the end of each 20-min sampling period using a digital thermometer (Acurite Inc., Jamestown, New York).

Based on findings of previous acoustic bat surveys from the nearby Allegheny Mountain region (Owen et al. 2004, Ford et al. 2005) and data from other acoustic or radio-telemetry research in the eastern United States (Kiser and Elliot 1996, Menzel et al. 2002, Menzel et al. 2005*a*, Menzel et al. 2005*b*, Menzel et al. 2005*c*, Johnson et al. 2003, Johnson et al. 2005, Owen et al. 2003), we developed six generalized habitat models for seven bat species (Table 2). The MACRO TO LANDSCAPE model contained landscape-level variables, while the FOREST STRUCTURE model represented measurements of forest structure collected at survey stations. The SIMPLE STRUCTURE model contained variables representing simple habitat measurements at each station (i.e., presence of water and open or closed forest canopy). We created two variations of the SIMPLE STRUCTURE model: SIMPLE STRUCTURE plus physical variables including slope, aspect, and elevation (SIMPLE

Table 2. Variable composition of *a priori* bat-habitat association models in Bluestone National Scenic River, Gauley River National Recreation Area, New River Gorge National River, and surrounding areas of West Virginia, 2003–2004.

Model	Variables
Macro To Landscape	DM[a], DC, DS, DMS, PW, LR, PF
Forest Structure	SC, MS, DW, WC
Simple Structure	H, WS
Simple Structure + Physical	H, WS, S, A, E
Simple Structure + Temp	H, WS, T
Global	DM, DC, DS, DMS, PW, LR, PF, SC, MS, DW, WC, H, WS, S, A, E, T
Combo (species-specific)	
Little brown myotis	DS, DMS, WC, E
Northern myotis	SC, MS
Indiana myotis	SC, MS, DS, PW, A
Eastern small-footed myotis	DM, DC DW
Eastern pipistrelle	DS, DMS, SC
Big brown bat	E, WC, DW
Eastern red bat	WC, DW

a. Variable acronyms are as follows: DM = distance to mine, DC = distance to cliff line, DS = distance to stream, PW = proximity to water, LR = linear measurement of road, PF = percent forest, SC = stand class, MS = midstory, DW = distance to nearest water, WC = width of corridor, H = habitat type, WS = water at the site, S = slope, A = aspect, E = elevation, T = temperature.

STRUCTURE + PHYSICAL) and SIMPLE STRUCTURE plus temperature (SIMPLE STRUCTURE + TEMP). The GLOBAL model contained all habitat variables for each monitoring site. Lastly, we constructed species-specific combination models (COMBO; Table 2) using habitat variables related to wing morphology, echolocation call characteristics, food habits, and roosting structure preference in the Allegheny Mountains and Plateau as reported by Carter et al. (2003), Owen et al. (2004) and Ford et al. (2005).

We pooled acoustic data across years and study sites to provide a more robust analysis of habitat parameters that were most important to each species across the landscape. Prior to developing models, we removed highly correlated predictor variables from the analyses (i.e., Spearman rank correlation, $r_s > 0.7$), retaining the most biologically meaningful variable. The response variable for model development was species presence. We developed models using logistic regression on a binary response variable of bat presence (1) or absence (0) by species and used second order Akaike's Information Criterion (AIC_c) to identify the most parsimonious model and predict variable importance (Burnham and Anderson 2002). Models with the lowest AIC_c and all models <4 Δ_i ($\Delta_i = AIC_c - \min AIC_c$) were considered the top- and best-approximating models, respectively. We also calculated the Akaike weight (w_i) for each model, which represented the probability it was the best model in the set of candidate models (Burnham and Anderson 2002). To assess relative model fit and strength for the best approximating model for each bat species presence, we calculated Hosmer and Lemeshow's Goodness-of-Fit and Nagelkerke's rescaled R^2, respectively (SAS 1995). With a probability cutoff value of 0.50, we also used a jackknife procedure to estimate correct variable classification rates. We used Wald's χ^2 values of parameter estimates to identify importance and relationship of variables with bat species presence.

Results

We recorded 3,365 search-phase echolocation passes that met our quality criteria at 680 acoustical survey sites during 2003 and 2004. For modeling purposes, our final analyses included only 540 sites because we excluded 140 sites where species identification accuracy results were unacceptably low or because a full set of habitat parameters were unavailable. We detected northern myotis ($n = 117$), eastern pipistrelles (*Pipistrellus subflavus*; $n = 69$), Indiana myotis ($n = 66$), big brown bats ($n = 64$), eastern small-footed myotis (*M. leibii*; $n = 52$), little brown myotis ($n = 49$), eastern red bats ($n = 39$), silver-haired bats (*Lasionycteris noctivagans*; $n = 11$), and hoary bats (*Lasiurus cinereus*; $n = 2$). Identification accuracy for each species detected ranged from 82.1% to 100% and averaged 88% for a single call sequence across species.

We had sufficient sample size to create predictive logistic regression models for little brown myotis, northern myotis, Indiana myotis, eastern small-footed myotis, eastern pipistrelle, eastern red bat, and big brown bat. The SIMPLE STRUCTURE was the top-approximating model for the eastern small-footed myotis (rescaled $R^2 = 0.06$, goodness-of-fit $P = 0.36$, correct classification = 92%), although the SIMPLE STRUCTURE + TEMP and SIMPLE STRUCTURE + PHYSICAL models also received support (Tables 3 and 4). Presence of water was important in predicting presence of eastern small-footed myotis (Table 4). The SIMPLE STRUCTURE + TEMP was the top-approximating model for little brown myotis (rescaled $R^2 = 0.10$, goodness-of-fit $P = 0.07$, correct classification = 94%), eastern pipistrelle (rescaled $R^2 = 0.12$, goodness-of-fit $P = 0.33$, correct classification = 90%), and eastern red bat (rescaled $R^2 = 0.15$, goodness-of-fit $P = 0.68$, correct classification = 95%, Tables 3 and 4). For the eastern pipistrelle and eastern red bat, SIMPLE STRUCTURE model also received support (Table 3). Open canopy habitat and higher temperature during the survey were important in predicting presence of little brown myotis and eastern red bat, whereas open canopy habitat and presence of water were most important for eastern pipistrelle (Table 4).

For northern myotis, MACRO to LANDSCAPE was the top-approximating model ($R^2 = 0.042$, $P = 0.83$, correct classification =

Table 3. The best-approximating logistic regression models (within 4 AICc) for seven bat species. Models were used to predict the probability of occurrence in the New River Gorge National River, Gauley River National Recreation Area, Bluestone National Scenic River, and surrounding areas of West Virginia, 2003–2004.

Model	K[a]	AIC[c]	Δ*i*[b]	W*i*[c]
Little brown myotis				
Simple Structure + Temp	4	230.91	0.00	0.79
Northern myotis				
Macro To Landscape	8	486.10	0.00	0.38
Simple Structure + Temp	4	486.42	0.32	0.32
Simple Structure	3	487.88	1.78	0.15
Combo	3	489.01	2.91	0.09
Indiana myotis				
Global	18	321.49	0.00	0.70
Macro To Landscape	8	323.73	2.24	0.23
Eastern small-footed myotis				
Simple Structure	3	297.29	0.00	0.50
Simple Structure + Temp	4	299.31	2.03	0.18
Simple Structure + Physical	6	299.42	2.14	0.17
Eastern pipistrelle				
Simple Structure + Temp	4	317.87	0.00	0.68
Simple Structure	3	319.54	1.68	0.29
Big brown bat				
Global	18	314.23	0.00	0.99
Eastern red bat				
Simple Structure + Temp	4	190.487	0.00	0.75
Simple Structure	3	192.962	2.45	0.22

a. Number of parameters in the model.
b. Difference of the model from the best model ($\Delta i = AICc - \min AICc$).
c. The estimated probability of being the best model (Akaike weight).

Table 4. The top-approximating logistic regression models (lowest AIC$_c$) explaining presences of seven bat species in the Bluestone National Scenic River, Gauley River National Recreation Area, New River Gorge National River, and surrounding areas of West Virginia, 2003–2004.

Parameter	Estimate	SE	$P > \text{Wald } \chi^2$	Odds ratio	95% CL
Little brown myotis (Simple Structure + Temp)					
Intercept	−8.6328	2.7048	0.0014	–	–
H	−1.29	0.4013	0.0013	0.275	0.125–0.604
WS	0.2466	0.4096	0.5471	1.28	0.573–2.856
T	0.0975	0.0401	0.015	1.102	1.019–1.192
Northern myotis (Macro to Landscape)					
Intercept	−0.6614	0.825	0.4228	–	–
DM	−0.00002	0.000013	0.1915	1.000	1.000–1.000
DC	−0.00039	0.000466	0.4086	1.000	0.999–1.001
DS	0.000601	0.000267	0.0245	1.001	1.000–1.001
DMS	0.000017	0.000076	0.8234	1.000	1.000–1.000
PW	0.000205	0.000241	0.3955	1.000	1.000–1.001
LR	0.000279	0.000692	0.6871	1.000	0.999–1.002
PF	−0.0141	0.00751	0.0605	0.986	0.972–1.001
Indiana myotis (Global)					
Intercept	−5.5282	3.058	0.0706	–	–
H	0.0922	0.4092	0.8216	1.097	0.492–2.445
WS	1.1309	0.4787	0.0181	3.099	1.213–7.918
T	0.0628	0.0373	0.0922	1.065	0.990–1.146
DM	1.92E–06	0.000021	0.9259	1.000	1.000–1.000
DMS	−0.00005	0.000208	0.8007	1.000	1.000–1.000
DC	0.000232	0.000685	0.7351	1.000	0.999–1.002
DS	0.0014	0.000411	0.0007	1.001	1.001–1.002
PW	0.000466	0.000376	0.2153	1.000	1.000–1.001
LR	−0.0003	0.00102	0.7703	1.000	0.998–1.002
PF	−0.00508	0.0104	0.6269	0.995	0.975–1.016
SC	0.2695	0.2682	0.3149	1.309	0.774–2.215
MS	−0.2604	0.191	0.1728	0.771	0.530–1.121
DW	0.000149	0.00104	0.8863	1.000	0.998–1.002
WC	0.00755	0.00575	0.1891	1.008	0.996–1.019
S	−0.2451	0.1959	0.2108	0.783	0.533–1.149
A	−0.2036	0.2481	0.412	0.816	0.502–1.327
E	−0.00367	0.00261	0.1602	0.996	0.991–1.001
Eastern small-footed myotis (Simple Structure)					
Intercept	−2.7261	0.3209	<0.0001	–	–
H	−0.1181	0.343	0.7306	0.889	0.454–1.741
WS	1.1905	0.3448	0.0006	3.289	1.673–6.464
Eastern pipistrelle (Simple Structure + Temp)					
Intercept	−5.8129	2.1075	0.0058	–	–
H	−1.1817	0.3231	0.0003	0.307	0.163–0.578
WS	0.8053	0.3204	0.012	2.237	1.194–4.193
T	0.0598	0.0316	0.0582	1.062	0.998–1.129
Big brown bat (Global)					
Intercept	−8.9692	3.2102	0.0052	–	–
H	−0.7703	0.399	0.0535	0.463	0.212–1.012
WS	0.7446	0.4829	0.1231	2.106	0.817–5.426
T	0.097	0.0408	0.0174	1.102	1.017–1.194
DM	−4.00E-06	0.00002	0.8395	1.000	1.000–1.000
DMS	0.000015	0.000159	0.9246	1.000	1.000–1.000
DC	0.00128	0.000565	0.0236	1.001	1.000–1.002
DS	0.00132	0.000442	0.0029	1.001	1.000–1.002
PW	0.00102	0.000368	0.0056	1.001	1.000–1.002
LR	−0.00134	0.00114	0.2424	0.999	0.996–1.001
PF	−0.00713	0.0101	0.4812	0.993	0.973–1.013
SC	−0.0357	0.2793	0.8984	0.965	0.558–1.668
MS	−0.6856	0.2267	0.0025	0.504	0.323–0.786
DW	−0.00256	0.00104	0.0142	0.997	0.995–0.999
WC	−0.00748	0.00801	0.3504	0.993	0.977–1.008
S	−0.4099	0.2055	0.0461	0.664	0.444–0.993
A	0.104	0.2447	0.6709	1.110	0.687–1.793
E	0.00301	0.00241	0.2108	1.003	0.998–1.008
Eastern red bat (Simple Structure + Temp)					
Intercept	−8.527	3.072	0.0055	–	–
H	−1.7924	0.4918	0.0003	0.167	0.064–0.437
WS	0.4894	0.434	0.2595	1.631	0.697–3.819
T	0.0934	0.0455	0.0401	1.098	1.004–1.200

84%), although SIMPLE STRUCTURE + TEMP, SIMPLE STRUCTURE, and COMBO models also received support (Tables 3 and 4). For northern myotis, distance to smaller order streams was identified as an important model component (Table 4). The GLOBAL model was the top approximating model for big brown bats (rescaled $R^2 = 0.26$, goodness-of-fit $P = 0.57$, correct classification = 90 %) and Indiana myotis (rescaled $R^2 = 0.20$, goodness-of-fit $P = 0.73$, correct classification = 91%, Tables 3 and 4). For Indiana myotis, the MACRO to LANDSCAPE model also received support (Table 3). Important model components associated with big brown bat presence were warm temperatures, low mid-story density, moderate slopes, distance to cliff-lines, and proximity to water (Table 4). For Indiana myotis, presence was predicted both by presence of water at the survey site and distance to smaller order streams (Table 4).

Discussion

With some exceptions, our results generally were consistent with previous research in the Appalachian region (Owen et al. 2004, Ford et al. 2005). Although model fit and classification rates for the top-approximating models generally were good, overall model strength was low ($R^2 \leq 0.26$) for all bat species. As a result, our ability to draw strong inferences on the importance of microhabitat and landscape features for our species was reduced. Nonetheless, the congruence of our results with previous studies suggests that the implications of our research to bat conservation in the Southeast are relevant.

Our model results suggest that simple habitat features, such as open or closed forest canopy and proximity to water, provided the most meaningful and resolute description of bat habitat associations at our study sites. As previously shown (Ford et al. 2005, Menzel et al. 2005*a*, Menzel et al. 2005*b*, Menzel et al. 2005*c*, Carter 2006), the largest proportion of bat activity in the region is associated with riparian and aquatic habitats. In our models, a spatial measure of water proximity was included in every best- and top-approximating model for all bat species. Assuming presence of water, little brown myotis and eastern pipistrelles were more likely to be present where forests were open, such as in large canopy gaps or along open corridors, whereas Indiana myotis was associated with closed forests. Within this landscape, most open, uncluttered habitats in proximity to water likely represent areas directly above larger-order streams and rivers which, due to their width, are void of vegetative cover. Forested sites near water are indicative lower order forested riparian zones which generally have closed canopy above making them functionally closed-canopy. Ford et al. (2005) reported similar patterns for little brown myotis, eastern pipistrelles, and Indiana myotis. For big brown bats, the GLOBAL model performed best and probably indicates other habitat features that we did not measure are important. However, as also noted by Ford et al. (2005) and Ford et al. (2006), our model indicated big brown bat association with open habitats or forested habitats with a more sparse midstory structure and always in association with riparian habitats.

Eastern red bats and northern myotis conformed less with our expectations. Based on its medium body size, mid-range echolocation characteristics, and food habits, the eastern red bat can show wide habitat associations, foraging in both uncluttered and cluttered environments (Carter et al. 2004, Menzel et al. 2005*b*), and in upland (Ford et al. 2005) and riparian (Owen et al. 2004, Muzika et al. 2005*b*) habitats. Our models suggest that eastern red bat presence mirrored that of little brown myotis and eastern pipistrelles which were linked to defined watercourses (Davis and Mumford 1962). In the Allegheny Mountains, Owen et al. (2003) indicated that the northern myotis was an interior-forest obligate linked to within-stand conditions as did Loeb and O'Keefe (2006) in the southern Appalachians of South Carolina. However, our top-approximating model included landscape and forest stand-level variables. Our model contained a species-specific suite of variables for the northern myotis, likely explaining the departure from results of previous studies that examined more coarse-scale variables. Paradoxically, there was a negative, non-significant relationship between northern myotis presence and percent forest cover, and a significant positive relationship to measures of water proximity. The reason for this disparity is unknown, but may be related to differences between the relatively intact forested landscape in our study and the highly dynamic and distrurbed study area of Owen et al. (2003) that consisted largely of industrial forests.

Higher evening temperatures were positively associated with presence of little brown myotis, eastern red bats, and big brown bats. Although, Kiser and Elliot (1996) observed Indiana myotis shifting foraging habitat use from cooler, mesic forest sites to warmer, more xeric sites during the fall swarm in Kentucky, we did not see any evidence of similar variation in spatial habitat use during summer by eastern red bats, little brown myotis or big brown bats. Nonetheless, during summer at our study sites, bat activity increased with temperature thereby resulting in a higher probability of recording a species in areas of suitable habitat.

We integrated existing information of bat habitat associations from the region when developing *a priori* models, however, given the general lack of definitive data about bat habitat associations, our choice of habitat parameters may not have been optimal for elucidating fine-scale bat habitat relationships across a large, complex landscape. Recent modeling efforts in the Coastal Plain of South Carolina (Menzel et al. 2005*b*, Ford et al. 2006) and the Ozark Mountains in Missouri (Yates and Muzika 2006) show that incorporation of expert opinion in habitat parameter selection can still result in only a generalized view of foraging habitat over larger scales. Undoubtedly, our use of passive sampling rather than active acoustical sampling also contributed to our lower resolution and equivocal results (Johnson et al. 2002).

Management Implications

Although bat foraging activity occurs over much of the central Appalachian landscape, our results support previous research results in showing that riparian areas are a critical component of bat foraging habitat in the region (Ford et al. 2005, Menzel et al. 2005*a*, Menzel et al. 2005*b*, Menzel et al. 2005*c*). Thus, current regulations and guidelines that ensure protection and maintenance of riparian health and integrity will concomitantly provide protection of bat foraging habitat. Although our findings are consistent with other studies in showing closed-canopy forested riparian areas to be important foraging habitat for Indiana myotis, further research using radiotelemetry will be needed to identify more delineated foraging habitat as well as roosting areas for this endangered species (Ford et al. 2002*a*).

Our data combined with recent day-roost findings (tree, cave, and cliff faces) in the region (Ford et al. 2002*a*, Menzel et al. 2002, Johnson et al. 2003, Johnson et al. 2005), suggest the need to link bat habitat management to other land management activities, such as prescribed fire. Keyser and Ford (2006) documented Indiana myotis maternity and bachelor roosts in snags and live trees with exfoliating bark (primarily sugar maple [*Acer saccharum*] and shagbark hickory [*C. ovata*] in heavily thinned, spring-burned forest stands in the Allegheny Mountains near known hibernacula and 1st–4th order forested riparian zones. Accordingly, forest community restoration activities designed to restore or perpetuate oak-hickory dominated stands or the recreation of historic oak savannas through prescribed burning could be prioritized near riparian zones where Indiana myotis were observed acoustically in this study.

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