Relating bat species presence to simple habitat measures in a central Appalachian forest

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Abstract

We actively sampled the bat community at 63 sites using detection and non-detection metrics on the Fernow Experimental Forest (FEF) in the central Appalachians of West Virginia using Anabat acoustical equipment May–June 2001–2003 to relate species presence to simple habitat measures such as proximity to riparian areas, forest canopy cover, forest canopy gap width, and forest canopy height. We acoustically detected eight species on the FEF, including the endangered *Myotis sodalis*. The presence of *Lasiurus cinereus*, *M. lucifugus*, *M. sodalis*, and *Pipistrellus subflavus* was associated more with riparian areas than upland areas. Both univariate comparisons and multiple logistic regression modeling showed that the probability that clutter-adapted foraging species such as *M. septentrionalis* and *M. sodalis* would be detected was greater as forest canopy cover increased or forest canopy gap size decreased, whereas the opposite was true for open-adapted foraging species such as *Eptesicus fuscus* and *L. cinereus*. The overall proportion of unidentifiable bat echolocation sequences to those identified to species was related to upland sites with increasing forest canopy cover indicating some sampling bias between cluttered and uncluttered habitats. However, given sufficient sample points, bat community surveys using acoustical detection show the ability to quickly develop generalized habitat associations for rugged areas such as the central Appalachians where traditional mist-net survey efforts often are logistically difficult and are lacking in scope. Moreover, these acoustical surveys also could lend themselves to species-specific predictive mapping of foraging habitat as well as allowing researchers to formulate testable hypotheses about detailed bat habitat relationships to be definitively tested with radio-telemetry techniques.

Keywords: Acoustical survey; Anabat; Central Appalachians; Bats; Forests; Riparian areas

1. Introduction

Conservation of bats in North American forested landscapes is currently a research topic of considerable interest. Arnett (2003) identified bat habitat relationship responses to land management as one of the most critical information gaps hindering our understanding of how to better manage forests for bats. With the advent of miniaturized radio-transmitters, work identifying day-roosting substrates (e.g., snags, cavity trees, emergent rock, and caves) has become routine and commonplace research for many bats in the Vespertilionidae, particularly for endangered species such as *Myotis sodalis* (Menzel et al., 2002). Nonetheless, basic knowledge about foraging habitats (an equally important component of bat biology) often is lacking in eastern North America beyond anecdotal observations or partial quantitative analyses for many bat species, particularly those

that are endangered. When feasible, radio-telemetry used in day-roost research can generate quantitative foraging habitat use data for bats (Miller et al., 2003). Unfortunately, these efforts typically are hampered by the short-longevity and moderately weak signal of small transmitters suitable for bats, the inability to track numerous bats or multiple species within the logistical and funding constraints of most researchers, and the difficulty of obtaining reliable triangulation points on highly vagile animals capable of covering long distances in short periods. Because telemetry studies tend to target single species, they often are unable to generate ecologically interesting bat community assemblage or foraging niche differentiation data. For the rugged and heavily forested central Appalachian Mountains of the eastern United States, actual radio-telemetry studies of bat foraging habitat have been relatively limited in number and scope (Adam et al., 1994; Kiser and Elliot, 1996; Hurst and Lacki, 1999; Hutchison and Lacki, 1999; Butchkoski and Hassinger, 2002; Gumbert et al., 2002; Owen et al., 2003). Accordingly, science-based conservation of whole bat communities including endangered or sensitive species such as *M. sodalis*, *M. leibii*, or *Corynorhinus townsendii* on public and private lands in the central Appalachians is difficult because of our poor understanding of regional and local foraging habitat relationships.

Although subject to both real and perceived bias (Fenton, 2000; Sherwin et al., 2000; Fenton et al., 2001), zero-crossing period meter (Anabat) acoustical surveys can be used for rapidly assessing bat community structure and membership (Murray et al., 1999; O'Farrell and Gannon, 1999) with proper caveats accounted for (Sherwin et al., 2000; Corben and Fellers, 2001; Gannon et al., 2003). Anabat surveys are useful particularly when the local bat fauna has been documented by prior mist-netting and the development of a regional or local echolocation call library has occurred. Acoustical sampling has also been used successfully to show how bat activity differs by species or guild-group among managed and unmanaged forest stands and riparian conditions (Krusic et al., 1996; Zimmerman and Glanz, 2000; Seidman and Zabel, 2001; Broders et al., 2003; Tibbels and Kurta, 2003; Owen et al., 2004). Continent-wide, most bat species rely heavily on riparian areas. On the other hand, bat utilization of older, mature forest habitats, recently harvested stands or mid-successional forests for foraging areas and travel corridors varies depending on geographic location, bat community composition, bat species' morphological adaptations to structural clutter, insect prey abundance, and proximity to day-roost habitat (Sherwin et al., 2000; Estrada and Coates-Estrada, 2002).

Landscape-level Anabat surveys incorporating wider gradients of environmental conditions have been fewer in number than local inventories or defined habitat comparisons (Erickson and West, 2003; Gehrt and Chelsvig, 2003; Gehrt and Chelsvig, 2004) partially due to the inability to sample numerous sites over wide areas with passive surveys. However, the use of active-acoustical sampling transects that cover numerous locations has been widely employed in Europe and Australia (Walsh et al., 1993; Gjerde and Kovacic, 1999; de Wijs, 1999; Milne et al., 2004) and has been modified with Anabat recorders in the southeastern United States (Johnson et al., 2002; Francl et al., 2004). Such efforts have proven very effective at both quickly describing bat community membership and highlighting species-specific habitat associations across larger, landscape-level gradients. These types of data can help to elucidate fairly specific niche-separation and guild memberships and provide insights for conservation and management needs at larger scales (Menzel et al., 2003; Johnson et al., 2006). By recording bat species as solely detected or not detected to avoid problems relating numbers of echolocation passes to bat abundance, these data can be used to model the distribution of bats relative to habitat and landscape parameters in a generalized fashion similar to those using capture records, museum records, and hibernacula counts as is done in Europe (Jaberg and Guisan, 2001).

The objective of our study was to relate patterns of bat presence (measured acoustically) to simple forest habitat metrics on the Fernow Experimental Forest (FEF) that would be (1) useful for characterizing generalized foraging habitat associations by bat species in central Appalachian forests, and (2) capable of being collected quickly over a wide area akin to point-count surveys used in regional songbird research (Weakland et al., 2002). We hypothesized that the activity for all bat species would be highest along riparian zones and species-specific activity among cluttered or open habitats would be partially predictable based on species body morphology and echolocation call characteristics. We predicted that small-bodied obligate forest species with high frequency echolocations such as *M. septentrionalis* and *M. sodalis* would predominate in cluttered forest and closed riparian habitats on the FEF (Menzel et al., 2001; Owen et al., 2004; Menzel et al., 2005a), whereas small-bodied generalists such as *M. lucifugus* and *Pipistrellus subflavus* would be primarily associated with riparian habitat regardless of the presence of structural clutter (Fenton and Barclay, 1980; Fujita and Kunz, 1984; Ratcliffe and Dawson, 2003). We also predicted that large-bodied bats with lower frequency echolocation characteristics such as *Eptesicus fuscus* and *Lasiurus cinereus* would occur mainly in open habitats, including recently harvested forest areas or wide riparian areas with open water. Finally, we predicted that *Lasiurus borealis*, a medium-bodied bat with medium-to high-frequency echolocation characteristics, would occur equally in cluttered and open habitats (Menzel et al., 2005b).

2. Methods

Our study was conducted in north-central West Virginia on the FEF in Tucker County (Fig. 1). The FEF is a 1900 ha experimental forest that has been maintained by the USDA Forest Service Northeastern Research Station for long-term silvicultural and forest ecology research since 1949 (Schuler and Gillespie, 2000). Located within the Unglaciated Allegheny Mountains subsection of the Appalachian Plateau Physiographic Province, the topography at the FEF is characterized by steep slopes, broad ridge tops, narrow valleys, and high-gradient streams. Elevations range from >500 m to approximately 1200 m. The climate is cool and moist with annual precipitation exceeding 155 cm. Upland forest cover is primarily a second-growth (>80 years) mixed mesophytic type consisting of sugar maple (*Acer saccharum*), red maple (*A. rubrum*), northern red oak (*Quercus rubra*), chestnut oak (*Q. prinus*), yellow-poplar (*Liriodendron tulipifera*), American beech (*Fagus grandifolia*), sweet birch (*Betula lenta*), black cherry (*Prunus serotina*), and basswood (*Tilia Americana*). Overstories of eastern hemlock (*Tsuga canadensis*) and dense shrub layers of rosebay rhododendron (*Rhododendron maximum*) dominate riparian areas. Although the FEF exists largely in a lightly managed ''core'' forest landscape of the larger Monongahela National Forest, younger forest stands (<15 years) originating from clearcuts and deferment harvests and older

forest stands altered by selection cutting are numerous (Schuler, 2004). Underlain by the Greenbrier Limestone formation, the FEF contains several small and one large cave system. The large system, Big Springs Cave, is a winter hibernacula for approximately 200 male and female *M. sodalis*. Throughout the spring and summer, males of this endangered bat remain on the FEF to day-roost and forage (Ford et al., 2002).

We used Anabat II ultrasonic detectors linked to laptop computers using Anabat 6.3e software to determine the presence of foraging bats at 63 locations on the FEF during May–June of 2001–2003. We chose this short time period at the height of maternity activity of resident bats in part to minimize the confounding factors such as seasonal migration to and from wintering grounds or hibernacula (Whitaker and Hamilton, 1998) and because that period currently is of the greater ecological interest in the central Appalachians. The composition of the bat community on the FEF and surrounding area has been well established by prior mist-netting efforts to study day-roosting ecology and food habits (Edwards et al., 2001; Owen et al., 2001; Ford et al., 2002; Madarish et al., 2002; Menzel et al., 2002; Owen et al., 2002; Carter et al., 2003) and winter hibernacula counts (C. Stihler, West Virginia Dept. Natural Resources, unpubl. data), therefore inferences from data generated by acoustical sampling can be used with a higher degree of confidence than would occur without netting (Murray et al., 1999; O'Farrell and Gannon, 1999; Britzke et al., 2002; Gannon et al., 2003). As documented by the aforementioned studies, bat species that day-roost and forage during late spring and summer on the FEF include: *E. fuscus*, *L. borealis*, *L. cinereus*, *M. lucifugus*, *M. septentrionalis*, *M. sodalis*, and *P. subflavus*. *C. townsendii* and *M. leibii* have been detected during winter cave counts but are not present locally in the spring and summer. *Lasionycteris noctivagans* on the FEF is restricted primarily to early spring and late summer through early fall during its migration through the region.

Bat detection sites were not randomly selected on the FEF but were chosen a priori to encompass a wide variation of upland and riparian conditions ranging from closed, cluttered forested habitats to relatively open habitats such as newly clearcut regeneration sites as part of an onsite threatened, endangered, and sensitive species monitoring program in conjunction with the long-term silvicultural and watershed research on the FEF (Adams et al., 2000; Schuler, 2004). Following the survey methods described by O'Farrell et al. (1999) and Johnson et al. (2002), we actively monitored sites with Anabat detectors for 20-min periods between the end of twilight up to 2 h thereafter at 2–5 habitat types or conditions (Sherwin et al., 2000). Because between-night and between-site variation can be significant (Wickramasinghe et al., 2003), each site was sampled two times over different years. We slowly swept the detector back and forth
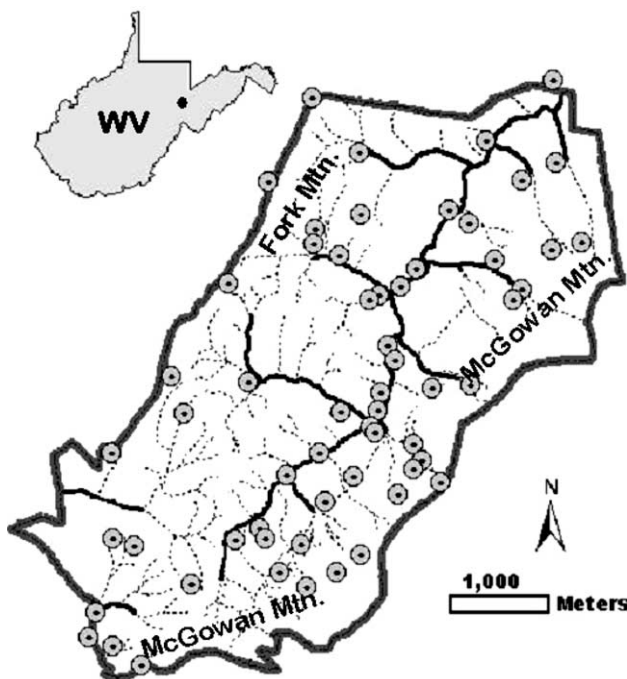

Fig. 1. Location of bat acoustical sampling sites along upland forest habitats and intermittent and perennial riparian forest habitats (*n* = 63), 2001–2003 on the Fernow Experimental Forest (1900 ha), Tucker County, West Virginia. Inset shows West Virginia, USA.

to scan for activity under a closed forest, within a forest canopy gap or forest harvest area, or along a stream. When bat activity was detected, we oriented the Anabat to capture as complete a call sequence as possible. We avoided acoustical sampling during evenings with low bat activity caused by high winds, precipitation or temperatures below 10 °C.

We filtered recorded echolocation passes prior to analysis (Britzke and Murray, 2000; Miller, 2001) and then identified species using Analook 4.7j and Analyze 2.0 software. To identify bat passes, we relied on a combination of quantitative (minimum and mean call note frequency) and qualitative (call note curvature and slope) metrics in a dichotomous key developed using a large bat echolocation call library from the eastern United States (M.A. Menzel, unpubl. data; Johnson et al., 2002; Owen et al., 2004; Wear, 2004). Whereas the echolocation sequences of non-*Myotis* bats that occur on the FEF can be identified with a high degree of certainty (Menzel et al., 2003), accurate identification of *M. lucifugus*, *M. septentrionalis*, and *M. sodalis* where all three species occur syntopically is not foolproof with a combined correct classification rates of 85% (Britzke et al., 2002). We only retained echolocation passes with ⩾3 calls appearing in close sequence for identification, thereby liberally assigning "no identification" to reduce our errors of commission (Betts, 1998). We further avoided other biases associated with using acoustical monitoring to assess relative abundance and relative use via number of passes recorded per unit area (Miller et al., 2003) or quantifying feeding activity (Weller et al., 1998) by merely assigning detection or non-detection of a bat species at a site once it was identified, regardless of number of passes or feeding buzzes recorded for each species.

At each echolocation sampling site, we recorded overstory canopy cover (%) with a spherical densiometer, overstory canopy height (m) and minimum forest canopy gap width (m) with a handheld laser rangefinder, and classification of stream condition and site elevation (m) within a GIS coverage of the FEF. We classified stream condition as either riparian (⩽30 m of stream) 1st, 2nd or 3rd order or upland (>30 m of stream). To determine if these simple habitat measures differed between acoustical survey sites by individual bat species' detection or non-detection, we used non-parametric Wilcoxon tests because these data were not normally distributed. We used a Fisher's Exact test for stream condition, a categorical variable (Stokes et al., 1995). For variables that differed between present and absent categories ($P < 0.1$), we used logistic regression to construct meaningful 1–2 variable models to further elucidate these relationships (Hosmer and Lemeshow, 2000; Odom et al., 2001) as well as to compute percent correct classification of observations using a jackknife procedure, and to assign probability of occurrence relative to habitat measures (SAS Institute, 1995; Teixeira

et al., 2001). Because we generated a priori hypotheses about bat species presence or absence across these habitat variables and because our study was exploratory, the use of Bonferroni adjustments to correct *P*-values generated by multiple pairwise comparisons not warranted (Perneger, 1998). To assess goodness-of-fit, we used Pearson tests rather than the Hosmer and Lemeshow goodness-of-fit test because the latter's inability to assess combination of categorical, ordinal and continuous variables in small (<100) samples (Hosmer et al., 1998; Kuss, 2002). We used both Spearman's rank correlation and Kruskall–Wallis test (Steel and Torrie, 1980) to examine the relationship of the proportion of non-identifiable bat echolocation sequences to the number identifiable to species as each survey site for each habitat variable. Canopy cover and minimum gap width were negatively correlated ($r_s = -0.73$, $n = 63$, $P = 0.0001$), as were elevation and stream condition (from upland to 2nd or 3rd order riparian; $r_s = -0.62$, $n = 63$, $P = 0.0001$), therefore to avoid autocorrelation biases we selected the more significant of the respective pairs for inclusion into logistic regression analyses by individual bat species.

3. Results

During our survey on the FEF, we recorded 1974 echolocation passes of the following species: 486 *M. lucifugus* at 39 sites, 382 *L. borealis* at 36 sites, 216 *E. fuscus* at 38 sites, 189 *M. septentrionalis* at 31 sites, 181 *L. cinereus* at 23 sites, 76 *M. sodalis* at 22 sites, and 35 *P. subflavus* at 14 sites. Excluded from analyses due to small sample size, we recorded 15 passes of *L. noctivagans* at two sites. The remaining 394 passes at 52 sites that were not identifiable to species were mostly echolocation passes from bats in the genus *Myotis*. The proportion of non-identifiable echolocation passes to identifiable passes exceed the number expected for 1st order riparian to 2nd or 3rd order riparian sites, whereas the opposite was true for upland survey sites (Kruskall–Wallis test, $\chi^2 = 11.28$, df = 2, $P = 0.004$). Albeit weakly, the proportion of non-identifiable echolocation passes was positively correlated to increasing forest canopy cover ($r_s = 0.27$, $n = 63$, $P = 0.03$) and negatively correlated with increasing elevation ($r_s = -0.38$, $n = 63$, $P = 0.002$). Non-identifiable echolocation passes were not correlated with minimum canopy gap width ($r_s = -0.17$, $n = 63$, $P = 0.18$), or forest canopy height ($r_s = 0.17$, $n = 63$, $P = 0.18$). *L. cinereus*, *M. lucifugus*, *M. sodalis*, and *P. subflavus* detections occurred more than expected along riparian categories; whereas, the detection of *M. septentrionalis*, *E. fuscus*, and *L. borealis* was similar between upland and riparian sites (Table 1).

Of the small-bodied bats, the detection of *M. septentrionalis* and *M. sodalis* was related to greater canopy

Table 1
Frequency of distribution of the presence and absence along with expected values of seven bat species on the Fernow Experimental Forest, West Virginia, 2001–2003 among upland, riparian 1st order and riparian 2nd or 3rd order acoustical survey sites

Species	Upland ($n = 34$)	1st Order ($n = 18$)	2nd or 3rd Order ($n = 11$)	P[a]
Eptesicus fuscus				
Present	17 (21)[b]	13 (11)	8 (7)	0.224
Absent	17 (13)	5 (7)	3 (4)	
Lasiurus borealis				
Present	16 (19)	13 (10)	7 (6)	0.228
Absent	18 (15)	5 (8)	4 (5)	
Lasiurus cinereus				
Present	8 (12)	10 (7)	5 (4)	0.004
Absent	26 (12)	10 (7)	5 (4)	
Myotis lucifugus				
Present	14 (21)	14 (11)	11 (7)	<0.001
Absent	20 (13)	4 (7)	0 (4)	
Myotis septentrionalis				
Present	14 (17)	12 (9)	5 (5)	0.226
Absent	20 (17)	6 (9)	6 (6)	
Myotis sodalis				
Present	8 (12)	7 (6)	7 (4)	0.048
Absent	26 (22)	11 (12)	4 (7)	
Pipistrellus subflavus				
Present	2 (8)	6 (4)	6 (2)	<0.001
Absent	32 (26)	12 (14)	5 (9)	

[a] Fisher's exact test.
[b] Expected value.

cover; whereas, *M. lucifugus* was related to larger minimum canopy gap width (Table 2). Sites where *P. subflavus* and *M. lucifugus* were detected were lower in elevation than sites where they were not (Table 2). Also, canopy height was greater where *P. subflavus* was detected than where it was not (Table 2). The logistic regression model for *M. lucifugus* was a strong predictor of presence (Nagelkerke's $R^2 = 0.41$; Pearson Goodness-of-Fit = 48.86, df = 46, $P = 0.36$; 73% correct classification), showing an increased probability of presence at a site as minimum gap size increased and stream classification went from upland to 1st order riparian to 2nd or 3rd order riparian (Table 3, Fig. 2(a)). Models for *M. septentrionalis*, *M. sodalis*, and *P. subflavus* were less strong, but still reasonable predictors of each species' presence. Increasing probability of *M. septentrionalis* occurrence was predicted by increasing canopy cover (Nagelkerke's $R^2 = 0.12$; Pearson Goodness-of-Fit = 54.27, df = 52, $P = 0.39$; 65% correct classification; Table 3, Fig. 2(b)), whereas *M. sodalis* probability of occurrence increased both with increasing canopy cover and with proximity to 1st order riparian and 2nd or 3rd order riparian conditions (Nagelkerke's $R^2 = 0.23$; Pearson Goodness-of-Fit = 59.15, df = 56, $P = 0.36$; 70% correct classification; Table 3, Fig. 2(c)). The logistic regression model for *P. subflavus* was overfit with the inclusion of stream condition, a significant contributor

towards predicting *P. subflavus* presence with overstory canopy height (Nagelkerke's $R^2 = 0.31$; Pearson Goodness-of-Fit = 53.44, df = 58, $P = 0.65$; 77% correct classification; Table 3, Fig. 2(d)).

For large-bodied bats, sites where *L. cinereus* was detected had larger minimum canopy gap widths than sites where it was not (Table 2). For *E. fuscus* and *L. borealis*, sites where both species were detected had greater minimum canopy gap width and lower canopy cover (Table 2). Elevation also was lower at sites where *E. fuscus* was detected (Table 2). Logistic regression showed that the probability of occurrence of *E. fuscus* increased with decreasing elevation and increasing minimum canopy gap width, though with a poor fit (Nagelkerke's $R^2 = 0.20$; Pearson Goodness-of-Fit = 122.96, df = 60, $P = 0.0001$; 73% correct classification; Table 3, Fig. 3(a)). Increased probability of occurrence of *L. cinereus* was associated with increasing minimum canopy gap width and proximity to 1st and 2nd or 3rd order riparian areas, but the model was weak (Nagelkerke's $R^2 = 0.14$; Pearson Goodness-of-Fit = 49.78, df = 46, $P = 0.33$; 62% correct classification; Table 3, Fig. 3(b)). Despite being a significant variable in the univariate analyses, minimum canopy gap width failed to produce a significant logistic regression model to predict the presence of *L. borealis* although the fit was good and the correct classification rate was moderate (Nage-

Table 2
Mean forest canopy metrics and site elevations for presence and absence values among seven bat species on the Fernow Experimental Forest, West Virginia, 2001–2003 at 63 acoustical monitoring sites

Variable	n	Mean	SE	P[a]
Eptesicus fuscus				
Canopy cover[b] (present)	38	73.6	3.2	0.009
Canopy cover (absent)	25	81.7	3.7	
Canopy height[c] (present)	38	21.7	1.3	0.828
Canopy height (absent)	25	21.4	1.2	
Min. gap width[c] (present)	38	32.9	5.4	0.003
Min. gap width (absent)	25	16.6	4.1	
Elevation[c] (present)	38	709.2	14.6	0.073
Elevation (absent)	25	761.7	19.1	
Lasiurus borealis				
Canopy cover (present)	36	73.9	3.0	0.007
Canopy cover (absent)	27	80.5	4.1	
Canopy height (present)	36	22.3	1.3	0.308
Canopy height (absent)	27	20.6	1.2	
Min. gap width (present)	36	30.9	5.1	0.003
Min. gap width (absent)	27	19.7	5.3	
Elevation (present)	36	718.2	16.4	0.218
Elevation (absent)	27	746.0	17.2	
Lasiurus cinereus				
Canopy cover (present)	23	74.0	4.0	0.124
Canopy cover (absent)	40	78.4	3.1	
Canopy height (present)	23	21.5	1.4	0.954
Canopy height (absent)	40	21.6	1.2	
Min. gap width (present)	23	35.1	7.8	0.045
Min. gap width (absent)	40	21.0	3.6	
Elevation (present)	23	721.3	19.9	0.634
Elevation (absent)	40	735.2	15.1	
Myotis lucifugus				
Canopy cover (present)	39	75.6	3.2	0.114
Canopy cover (absent)	24	78.7	4.0	
Canopy height (present)	39	22.7	1.2	0.118
Canopy height (absent)	24	19.7	1.3	
Min. gap width (present)	39	31.8	5.4	0.016
Min. gap width (absent)	24	16.9	3.5	
Elevation (present)	39	710.2	15.3	0.057
Elevation (absent)	24	762.4	17.7	
Myotis septentrionalis				
Canopy cover (present)	31	82.7	2.8	0.019
Canopy cover (absent)	32	71.1	3.8	
Canopy height (present)	31	21.6	1.4	0.118
Canopy height (absent)	32	21.5	1.2	
Min. gap width (present)	31	20.1	4.8	0.853
Min. gap width (absent)	32	32.1	5.6	
Elevation (present)	31	742.0	15.5	0.398
Elevation (absent)	32	718.5	18.1	
Myotis sodalis				
Canopy cover (present)	22	84.9	2.4	0.048
Canopy cover (absent)	41	72.4	3.4	
Canopy height (present)	22	23.2	1.4	0.309
Canopy height (absent)	41	20.7	1.1	
Min. gap width (present)	22	18.2	2.9	0.174
Min. gap width (absent)	41	30.4	5.4	
Elevation (present)	22	721.9	18.1	0.745
Elevation (absent)	41	734.4	15.7	
Pipistrellus subflavus				
Canopy cover (present)	14	78.4	5.1	0.497
Canopy cover (absent)	49	76.4	2.8	
Canopy height (present)	14	24.4	1.8	0.045
Canopy height (absent)	49	20.8	1.0	

(continued on next page)

Table 2 (*continued*)

Variable	n	Mean	SE	P[a]
Min. gap width (present)	14	33.5	9.8	0.179
Min. gap width (absent)	49	24.0	3.9	
Elevation (present)	14	680.8	12.6	0.027
Elevation (absent)	49	744.2	28.2	

[a] Wilcoxon test.
[b] Percent value.
[c] Meters.

Table 3
Logistic regression analyses of habitat variables influencing the presence and absence of seven bat species on the Fernow Experimental Forest, West Virginia, 2001–2003 as determined by acoustical sampling at 63 sites

Variable[a]	Parameter estimate	SE	Wald χ^2	$P > \chi^2$	Odds ratio
Eptesicus fuscus					
Intercept	4.74	2.56	3.41	0.065	–
Min. gap width	0.03	0.02	3.10	0.078	1.03
Elevation	−0.01	0.003	3.87	0.049	0.99
Lasiurus borealis					
Intercept	−0.10	0.36	0.08	0.779	–
Min. gap width	0.02	0.01	1.92	0.165	1.02
Lasiurus cinereus					
Intercept	−1.46	0.47	9.57	0.002	–
Riparian type[b]	0.66	0.36	3.37	0.066	1.92
Min. gap width	0.02	0.01	2.92	0.087	1.02
Myotis lucifugus					
Intercept	−1.13	0.53	4.57	0.032	–
Riparian type[b]	1.94	0.58	11.10	0.001	6.95
Min. gap width	0.04	0.02	2.95	0.085	1.03
Myotis septentrionalis					
Intercept	−2.67	1.21	4.84	0.028	–
Canopy cover	0.03	0.02	5.12	0.023	1.04
Myotis sodalis					
Intercept	−4.52	1.70	7.08	0.008	–
Riparian type[b]	0.82	0.38	4.69	0.030	2.28
Canopy cover	0.04	0.02	4.45	0.034	1.04
Pipistrellus subflavus					
Intercept	−3.76	1.34	7.94	0.005	–
Riparian type[b]	1.37	0.45	9.36	0.002	3.93
Canopy height	0.06	0.06	1.28	0.257	0.96

[a] df = 1 for each intercept and parameter estimate.
[b] Ordination of riparian type for analysis: upland (0), 1st order (1), and 2nd or 3rd order (2).

lkerke's $R^2 = 0.06$; Pearson Goodness-of-Fit = 35.70, df = 33, $P = 0.34$; 68% correct classification; Table 3, Fig. 3c).

4. Discussion

Our acoustical survey data conformed moderately well to our predictions of generalized habitat structure associations for several of the bat species present on the FEF landscape. Based solely on body size, *M. lucifugus* and *P. subflavus* detections should have been more restricted to structurally cluttered environments (Menzel et al., 2003; Menzel et al., 2005b). However, the feeding ecology and habitat use of these species in forested landscapes typically favors larger watercourses at lower elevations with open spaces and is probably more related to overall prey abundance and foraging ease than morphological adaptations fully would suggest (Broders et al., 2003; Patriquin and Barclay, 2003). Except for *L. borealis*, the remaining species were distributed more or less along measures of forest clutter or openness as their body size and echolocation call characteristics would indicate. The failure to link to any habitat measure to the presence of *L. borealis* is indicative of its very generalist nature in the central Appalachians (Hutchison and Lacki, 1999). Consistent with the findings of other bat researchers in North America and elsewhere, 4 of the 7 species we analyzed were more likely to be present around riparian areas than upland forests underscoring
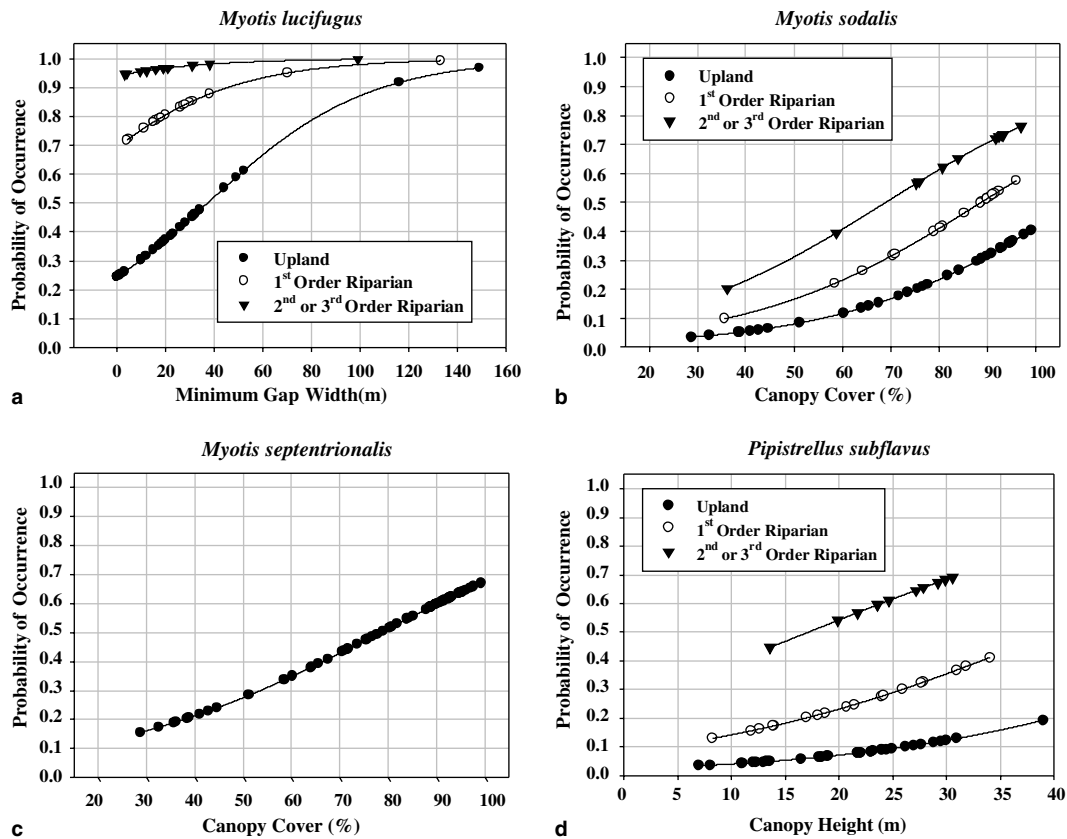
Fig. 2. Predicted probabilities of occurrence across simple habitat measures (see text) as determined by logistic regression analysis for *Myotis lucifugus*, *M. sodalis*, *M. septentrionalis*, and *Pipistrellus subflavus* on the Fernow Experimental Forest, Tucker County, West Virginia, 2001–2003.
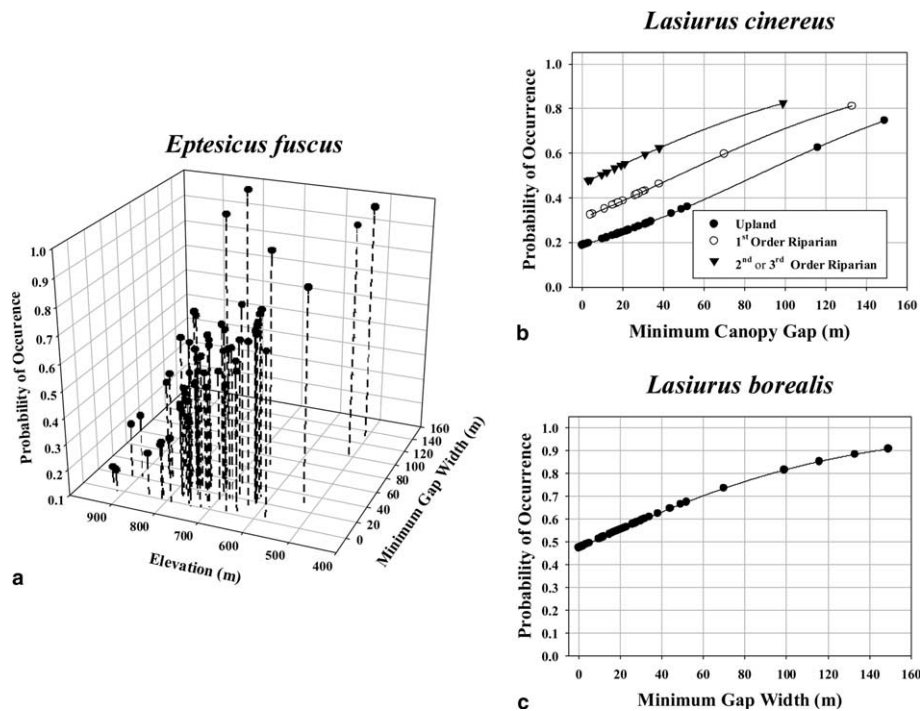

Fig. 3. Predicted probabilities of occurrence across simple habitat measures (see text) as determined by logistic regression analysis for *Eptesicus fuscus*, *Lasiurus cinereus*, and *L. borealis* on the Fernow Experimental Forest, Tucker County, West Virginia, 2001–2003.

the importance of these habitats as feeding substrates (Vaughn et al., 1997; Grindal et al., 1999; Zimmerman and Glanz, 2000; Seidman and Zabel, 2001; Russo and Jones, 2003; Wickramasinghe et al., 2003; Menzel et al., 2005b) and as travel corridors (Verboom and Huitema, 1997; Law and Chidel, 2002; Russ and Montgomery, 2002; Owen et al., 2003; Murray and Kurta, 2004). This contrasts with neotropical migratory songbirds and small mammals in the central Appalachians where few species actually are riparian forest dependent (Murray and Stauffer, 1995; Pagels et al., 1998; Ford and Rodrigue, 2001). Bat community conservation could be used to provide a more compelling argument for the value of streamside management zones in managed forests beyond those established for aesthetics, soil erosion, water quality, or stream temperature (Kochenderfer et al., 1997; Warren et al., 2000).

Within the heavily forested central Appalachians, less cluttered habitats such as recently harvested forest stands or meadows, pastures and wildlife openings comprise a very small percentage of the landscape (Owen et al., 2004). For species such as *E. fuscus*, *L. borealis*, or *L. cinereus*, open habitats probably provide additional foraging opportunities that are at a premium in these forested landscapes relative to more agricultural or suburban-dominated landscapes (de Jong, 1995; Gehrt and Chelsvig, 2003; Gehrt and Chelsvig, 2004; Owen et al., 2004). Linkages of canopy openness (as measured by canopy cover or minimum canopy gap width) and riparian area associations provide a great framework for illustrating the foraging habitat niche-separation of the three extant summer-resident species of Myotis on the FEF. Despite the considerable degree of monitoring site overlap, this separation is aptly illustrated by the predicted probability curves for *M. septentrionalis*, *M. sodalis*, and *M. lucifugus* that describe each species' respective occurrences along a closed to open forest canopy gradient and from upland sites to larger 2nd and 3rd order streams. Variation in micro-habitat features where each of these species foraged on the FEF is important from the perspective of interspecific competition minimization. Whitaker (2004) noted that these three species of Myotis showed remarkable dietary overlap of arthropod prey at local scales in west-central Indiana. For endangered species such as *M. sodalis*, full understanding of these habitat-use and interspecific competition relationships could be important from a conservation management standpoint as has been identified for European bat communities (Arlettaz et al., 2000).

Despite being among the most numerous bats in mist-net surveys in the northeastern United States and southeastern Canada, many researchers have found that the low-intensity echolocation of *M. septentrionalis* often causes the species to be less frequently recorded (Faure et al., 1993; Broders et al., 2003; Owen et al., 2004) lead-

ing to erroneous conclusions of rarity and an assumed preference for non-forested habitats (Gannon et al., 2003). Our use of active rather than passive sampling, along with surveying across a wide variety of conditions including closed-canopy upland forest conditions overcame these shortfalls to some extent and allowed us to acoustically confirm the forest-obligate habits congruent with the acoustical surveys in Canada (Patriquin and Barclay, 2003) along with radio-telemetry studies of the *M. septentrionalis* near the FEF landscape (Owen et al., 2002; Owen et al., 2003). Still, our data show that there is some bias inherent in using acoustical sampling as the number of unidentifiable echolocation sequences was proportionally more numerous in the cluttered, closed forest canopy habitats. Whether or not these calls represented unidentified M. septentrionalis or were above-canopy passes of that or other species of Myotis (Kalcounis et al., 1999) is unknown and merits further investigation.

The relationship we show between closed canopy (>70%) riparian areas and the detection of *M. sodalis* allows us to better assess its critical habitat components in the central Appalachians. Additionally, our acoustical survey data show a high degree of congruence with the limited foraging habitat observations made by Butchkoski and Hassinger (2002) on *M. sodalis* in Pennsylvania, the only telemetry-derived foraging habitat data available for the region during the summer months. Although female *M. sodalis* typically are not present around winter hibernacula sites in the late spring through late summer in the central Appalachians in appreciable numbers (Brack et al., 2002), most males remain as summer residents within close proximity of hibernacula using forested habitats for day-roosting and foraging (Menzel et al., 2001; Ford et al., 2002). Because of the wooded nature of the FEF, the generalized habitat relationships between resident male *M. sodalis* and forest structure and riparian condition probably more closely approximate the habitat relationships that would have occurred prior to European settlement and land conversion than does the species' current distribution in much of the agricultural Midwest. Although not as biologically important as maternity foraging and roosting habitat in the core of *M. sodalis* range (Menzel et al., 2002; Murray and Kurta, 2004; Menzel et al., 2005a), protection of male foraging habitat around hibernacula in the central Appalachians is still critical from a regulatory standpoint. Being able to quantify potential *M. sodalis* foraging habitat structurally should help managers protect and retain existing habitat as well as give measurable targets for the enhancement of forested riparian areas for *M. sodalis* suitability.

From an overall bat conservation and biodiversity monitoring standpoint, we believe our use of active acoustical sampling in a manner similar to that of songbird point-count methodologies could have great utility

in areas where general bat fauna is already documented from mist-netting but many details on habitat association and use are lacking. This will become particularly apparent as species identification using the Anabat or other acoustical systems improves. In no way discounting attempts of others to use acoustical monitoring to ascertain relative-use indices to compare habitat types, detection and non-detection data analyzed over a large area with methods such as logistic regression can be very robust and quite amenable to predictive habitat mapping within a geographic information system (Jaberg and Guisan, 2001; Odom et al., 2001; Ford et al., 2006; but see also Sherwin et al., 2000). In addition to being much more logistically feasible for providing bat species and generalized habitat association information, widespread efforts such as ours could aid researchers in determining where to target mist-netting efforts for species-specific collections for radio-telemetry research.

However, we certainly agree with Sherwin et al. (2000) that great caution should be used in extending inferences beyond the type and scope of data collected in this or any acoustical survey study. Further work refining the use of Anabat and its evolving analytical protocols will be necessary for full acceptance within the natural resource community as a robust bat research tool (Miller, 2001; Miller et al., 2003; Gannon et al., 2003; Milne et al., 2004). For example, problems such as the inability to distinguish sex of bats using acoustical methods may be biases impossible to overcome. Temporally, our focus on summer activity also may present an incomplete picture of generalized habitat associations of bats in the central Appalachians, particularly with respect to migratory species such as *L. noctivagans* that are more common locally in spring or early fall. For endangered species such as *M. sodalis*, information on their distribution within this landscape pre-hibernation and immediately post-emergence from hibernation is still unclear. To illustrate, Kiser and Elliot (1996) showed that as temperatures cooled in the central Appalachians in Kentucky during the early to mid-fall, *M. sodalis* foraging activity shifted to forested habitats on upper slopes and ridgelines away from the cold-air drainage areas that were similar to where we recorded summer *M. sodalis* activity on the FEF. Therefore to track complete bat activity on the landscape, acoustical monitoring efforts should be more inclusive over the year, from the spring through the fall. Lastly, recent research in the southeastern United States indicates that above-forest canopy activity in upland sites for large-bodied bats such as *E. fuscus* and *L. cinereus* can be considerably greater than that below the forest canopy (though still far lower than activity levels associated with riparian areas), thereby lowering the perceived value of upland forest stands to those species by researcher conducting acoustical surveys beneath forest canopies (Menzel et al., 2000; Menzel et al., 2005b).

References

Adams, M.B., Knibbs, J., Rodrigue, J.L., Edwards, P.J., Wood, F., Ford, W.M., Kochenderfer, J.A., Schuler, T.M., Crews, J., 2000. Fernow Experimental Forest: environmental impact state. Final Report. U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA.

Adam, M.D., Lacki, M.J., Barnes, T.G., 1994. Foraging areas and habitat use of the Virginia big-eared bat in Kentucky. Journal of Wildlife Management 58, 462–469.

Arlettaz, R., Godat, S., Meyer, H., 2000. Competition for food by expanding pipistrelle bat populations (*Pipistrellus pipistrellus*) might contribute to the decline of lesser horseshoe bats (*Rhinolophus hipposideros*). Biological Conservation 93, 55–60.

Arnett, E.B., 2003. Advancing science and partnerships for the conservation of bats and their habitats. Wildlife Society Bulletin 31, 2–5.

Betts, B.J., 1998. Effects of interindividual variation in echolocation calls on identification of big brown and silver-haired bats. Journal of Wildlife Management 62, 1003–1010.

Brack, V., Stihler, C.W., Reynolds, R.J., Butchkoski, C.M., Hobson, C.S., 2002. Effect of climate and elevation on distribution and abundance in the mideastern United States. In: Kurta, A., Kennedy, J. (Eds.), The Indiana Bat: Biology and Management of an Endangered Species. Bat Conservation International, Austin, TX, pp. 21–28.

Britzke, E.R., Murray, K.L., 2000. A quantitative method for selection of identifiable search-phase calls using the Anabat system. Bat Research News 41, 33–36.

Britzke, E.R., Murray, K.L., Heywood, J.S., Robbins, L.W., 2002. Acoustic identification. In: Kurta, A., Kennedy, J. (Eds.), The Indiana Bat: Biology and Management of an Endangered Species. Bat Conservation International, Austin, TX, pp. 221–227.

Broders, H.G., Quinn, G.M., Forbes, G.J., 2003. Species status, and the spatial and temporal patterns of activity of bats in southwest Nova Scotia, Canada. Northeastern Naturalist 10, 235–241.

Butchkoski, C.M., Hassinger, J.D., 2002. Ecology of a maternity colony roosting in a building. In: Kurta, A., Kennedy, J. (Eds.), The Indiana Bat: Biology and Management of an Endangered Species. Bat Conservation International, Austin, TX, pp. 130–142.

Carter, T.C., Menzel, M.A., Owen, S.F., Edwards, J.W., Menzel, J.M., Ford, W.M., 2003. Food habits of seven species of bats in the Allegheny Plateau and Ridge and Valley of West Virginia. Northeastern Naturalist 10, 83–88.

Corben, C., Fellers, G.M., 2001. Choosing the 'correct' bat detector – a reply. Acta Chiropterologica 3, 253–256.

Edwards, J.W., Ford, W.M., Wood, P.B., Menzel, M.A., Johnson, J.B., Owen, S.F., Menzel, J.M., Chapman, B.R., Miller, K.V., 2001. Survey of forest bat communities on the Monongahela National Forest and Westvaco Wildlife and Ecosystem Research Forest with emphasis on the Indiana Bat. U.S. Department of Agriculture Forest Service Final Report. Monongahela National Forest, Elkins, WV, 119p.

Erickson, J.L., West, S.D., 2003. Associations of bats with local structure and landscape features of forested stands in western Oregon and Washington. Biological Conservation 109, 95–102.

Estrada, A., Coates-Estrada, R., 2002. Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlas, Mexico. Biological Conservation 103, 237–245.

Faure, P.A., Fullard, J.H., Dawson, J.W., 1993. The gleaning attacks of the northern long-eared bat, *Myotis septentrionalis*, are relatively inaudible to moths. Journal of Experimental Biology 178, 173–189.

Fenton, M.B., 2000. Choosing the 'correct' bat detector. Acta Chiropterologica 2, 215–224.

Fenton, M.B., Barclay, R.M.R., 1980. *Myotis lucifugus*. Mammalian Species 142, 1–8.

Fenton, M.B., Bouchard, S., Vonhof, M.J., Zigouris, J., 2001. Time-expansion and zero-crossing period meter systems present significantly different views of echolocation calls of bats. Journal of Mammalogy 82, 721–727.

Ford, W.M., Menzel, J.M., Menzel, M.A., Edwards, J.W., 2002. Summer roost-tree selection by a male Indiana bat on the Fernow Experimental Forest (Research Note NE-378). U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA, 7p.

Ford, W.M., McCay, T.S., Menzel, M.A., Webster, W.D., Greenberg, C.H., Pagels, J.F., Merritt, J.F., 2006. Influence of elevation and forest type on shrew community assemblage and species distribution in the central and southern Appalachian Mountains. In: Merrit, J.F., Churchfield, S. (Eds.), Second International Congress on the Biology of the Soricidae. Carnegie Museum of Natural History Special Publication, Pittsburgh, PA.

Ford, W.M., Rodrigue, J.L., 2001. Soricid abundance in partial overstory removal harvests and riparian areas in an industrial forest landscape of the central Appalachians. Forest Ecology and Management 152, 159–168.

Francl, K.E., Ford, W.M., Castleberry, S.B., 2004. Bat activity in central Appalachian wetlands. Georgia Journal of Science 62, 87–94.

Fujita, M.S., Kunz, T.H., 1984. *Pipistrellus subflavus*. Mammalian Species 228, 1–6.

Gannon, W.L., Sherwin, R.E., Haymond, S., 2003. On the importance of articulating assumptions when conducting acoustic studies of habitat use by bats. Wildlife Society Bulletin 31, 45–61.

Gehrt, S.D., Chelsvig, J.E., 2003. Bat activity in a urban landscape: patterns at the landscape and microhabitat scale. Ecological Applications 13, 939–950.

Gehrt, S.D., Chelsvig, J.E., 2004. Species-specific patterns of bat activity in an urban landscape. Ecological Applications 14, 625–635.

Gjerde, L., Kovacic, D., 1999. Bat surveys by car transects in Luxembourg. In: Harbusch, C., Pir, J. (Eds.). Proceedings of the 3rd European Bat Detector Workshop, Larochette, Luxembourg, pp. 87–93.

Grindal, S.D., Morissette, J.L., Brigham, R.M., 1999. Concentration of bat activity in riparian habitats over an elevational gradient. Canadian Journal of Zoology 77, 972–977.

Gumbert, M.W., O'Keefe, J.M., MacGregor, J.R., 2002. Roost fidelity in Kentucky. In: Kurta, A., Kennedy, J. (Eds.), The Indiana Bat: Biology and Management of an Endangered Species. Bat Conservation International, Austin, TX, pp. 143–152.

Hosmer, D.W., Hosmer, T., Le Cessie, S., Lemeshow, S., 1998. A comparison of goodness-of-fit tests for the logistic regression model. Statistics in Medicine 16, 965–980.

Hosmer, D.W., Lemeshow, S., 2000. Applied Logistic Regression. Wiley–Interscience, New York, 373p.

Hurst, T.E, Lacki, M.J., 1999. Roost selection, population size and habitat use by a colony of Rafinesque's Big-eared bats (*Corynorhinus rafinesquii*). American Midland Naturalist 142, 363–371.

Hutchison, J.T., Lacki, M.J., 1999. Foraging behavior and habitat use of red bats in mixed mesophytic forests of the Cumberland Plateau, Kentucky. In: Stringer, J.W., Loftis, D.L. (Eds.), Proceedings of the 12th Central Hardwood Conference. (General Technical Report SRS-24). U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp. 171–177.

Jaberg, C., Guisan, A., 2001. Modeling the distribution of bats in relation to landscape structure in a temperate mountain environment. Journal of Applied Ecology 38, 1169–1181.

Johnson, J.B., Menzel, M.A., Edwards, J.W., Ford, W.M., 2002. A comparison of 2 acoustical bat survey techniques. Wildlife Society Bulletin 30, 931–936.

Johnson, J.B., Menzel, M.A., Edwards, J.W., Ford, W.M., Petty, J.T., 2006. Spatial and predictive foraging models for gray bats in northwest Georgia. Acta Chiropterologica (in review).

de Jong, J., 1995. Habitat use and species richness of bats in a patchy landscape. Acta Theriologica 40, 237–248.

Kalcounis, M.C., Hobson, K.A., Brigham, R.M., Hecker, K.R., 1999. Activity in the boreal forest: importance of stand type and vertical strata. Journal of Mammalogy 80, 673–682.

Kiser, J.D., Elliot, C.L., 1996. Foraging habitat, food habits and roost tree characteristics of the Indiana bat (*Myotis sodalis*) during autumn in Jackson County, Kentucky. Final Report to the Kentucky Department of Fish and Wildlife Resources, Frankfort, KY. 65pp.

Kochenderfer, J.N., Edwards, P.J., Wood, F., 1997. Hydrologic impacts of logging an Appalachian watershed using West Virginia's best management practices. Northern Journal of Applied Forestry 14, 207–218.

Krusic, R.A., Yamasaki, M., Neefus, C.D., Pekins, P.J., 1996. Bat habitat use in White Mountain National Forest. Journal of Wildlife Management 60, 625–631.

Kuss, O., 2002. Global goodness-of-fit tests in logistic regression with sparse data. Statistics in Medicine 21, 3789–3801.

Law, B., Chidel, M., 2002. Tracks and riparian zones facilitate the use of Australian regrowth forest by insectivorous bats. Journal of Applied Ecology 39, 605–617.

Madarish, D.M., Rodrigue, J.L., Adams, M.B., 2002. Vascular flora and macroscopic fauna on the Fernow Experimental Forest. (General Technical Report NE-291). U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA, 37p.

Menzel, J.M., Ford, W.M., Menzel, M.A., Carter, T.C., Gardner, J.E., Garner, J.D., Hoffman, J.E., 2005a. Summer habitat use and home-range analysis of the endangered Indiana bat. Journal of Wildlife Management 69, 430–436.

Menzel, J.M., Menzel, M.A., Kilgo, J.C., Ford, W.M., Edwards, J.W., McCracken, G.F., 2005b. Effect of habitat and foraging height on bat activity in the southeastern Coastal Plain of the United States. Journal of Wildlife Management 69, 235–245.

Menzel, J.M., Menzel, M.A., McCracken, G.F., Chapman, B.R., 2000. Note on bat activity above the forest canopy in the eastern United States. Georgia Journal of Science 58, 212–216.

Menzel, M.A., Carter, T.C., Menzel, J.M., Ford, W.M., Edwards, J.W., 2001. Review of the forest habitat relationships of the Indiana bat (*Myotis sodalis*). (General Technical Report NE-284). U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA, 21p.

Menzel, M.A., Menzel, J.M., Kilgo, J.C., Ford, W.M., Carter, T.C., Edwards, J.W., 2003. Bats of the Savannah River Site and vicinity. (General Technical Report SRS-68). U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, 69p.

Menzel, M.A., Owen, S.F., Ford, W.M., Chapman, B.R., Miller, K.V., Edwards, J.E., Wood, P.B., 2002. Roost tree selection by maternity colonies of northern long-eared bats (*Myotis septentrionalis*) in an

industrial forest of the central Appalachian Mountains. Forest Ecology and Management 155, 107–114.

Miller, B.W., 2001. A method for determining relative activity of free flying bats using a new activity index for acoutic monitoring. Acta Chiropterologica 3, 93–105.

Miller, D.A., Arnett, E.B., Lacki, M.J., 2003. Habitat management for forest-roosting bats of North America: a critical review of habitat studies. Wildlife Society Bulletin 31, 30–44.

Milne, D.J., Armstrong, M., Fisher, A., Flores, T., Pavey, C.R., 2004. A comparison of three survey methods for collecting bat echolocation calls for species accumulation rates from nightly Anabat recordings. Wildlife Research 31, 57–63.

Murray, K.L., Britzke, E.R., Hadley, B.M., Robbins, L.W., 1999. Surveying bat communities: a comparison between mist nets and the Anabat II detector system. Acta Chiropterologica 1, 105–112.

Murray, N.L., Stauffer, D.F., 1995. Nongame bird use of habitat in central Appalachian riparian forests. Journal of Wildlife Management 59, 78–88.

Murray, S.W., Kurta, A., 2004. Noctural activity of the endangered Indiana bat (*Myotis sodalis*). Journal of Zoology 262, 197–206.

Odom, R.H., Ford, W.M., Edwards, J.W., Stihler, C., Menzel, J.M., 2001. Modeling Virginia northern flying squirrel habitat in the central Appalachians. Biological Conservation 99, 245–252.

O'Farrell, M.J., Gannon, W.L., 1999. A comparison of acoustic versus capture techniques for the inventory of bats. Journal of Mammalogy 80, 24–30.

O'Farrell, M.J., Miller, B.W., Gannon, W.L., 1999. Qualitative identification of free-flying bats using the Anabat detector. Journal of Mammalogy 80, 11–23.

Owen, S.F., Menzel, M.A., Ford, W.M., Chapman, B.R., Miller, K.V., Edwards, J.W., Wood, P.B., 2001. First summer record of a female Indiana bat, *Myotis sodalis*, in West Virginia. The Journal of the Elisha Mitchell Scientific Society 117, 132–134.

Owen, S.F., Menzel, M.A., Ford, W.M., Chapman, B.R., Miller, K.V., Wood, P.B., 2002. Roost tree selection by maternal colonies of northern long-eared Myotis in an intensively managed forest. (General Technical Report NE-292). U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA. 6p.

Owen, S.F., Menzel, M.A., Ford, W.M., Chapman, B.R., Miller, K.V., Edwards, J.W., Wood, P.B., 2003. Home-range size and habitat used by the northern myotis (*Myotis septentrionalis*). American Midland Naturalist 150, 352–359.

Owen, S.F., Menzel, M.A., Edwards, J.W., Ford, W.M., Menzel, J.M., Chapman, B.R., Wood, P.B., Miller, K.V., 2004. Bat activity in harvested and intact forest stands in the Allegheny Mountains. Northern Journal of Applied Forestry 21, 154–159.

Pagels, J.F., Smock, L.A., Sklarew, S.H., 1998. The water shrew, *Sorex palustris* Richardson (Insectivora: Soricidae), and its habitat in Virginia. Brimleyana 25, 120–134.

Patriquin, K.J., Barclay, R.M.R., 2003. Foraging by bats in cleared, thinned and unharvested boreal forest. Journal of Applied Ecology 40, 646–657.

Perneger, T.V., 1998. What's wrong with Bonferroni adjustments. British Medical Journal 312, 1236–1238.

Ratcliffe, J.M., Dawson, J.W., 2003. Behavioral flexibility: the little brown bat, *Myotis lucifugus*, and the northern long-eared bat, *M. septentrionalis*, both glean and hawk prey. Animal Behavior 66, 847–856.

Russ, J.M., Montgomery, W.I., 2002. Habitat associations of bats in northern Ireland: implications for conservation. Biological Conservation 108, 49–58.

Russo, D., Jones, G., 2003. Use of foraging habitats by bats in a Mediterranean area determined by acoustic surveys: conservation implications. Ecography 26, 197–209.

SAS Institute, 1995. Logistic Regression Examples Using the SAS System. SAS Institute, Cary, NC, 163pp..

Schuler, T.M., 2004. Fifty years of partial harvesting in a mixed mesophytic forest: composition and productivity. Canadian Journal of Forest Research 34, 985–997.

Schuler, T.M., Gillespie, A.R., 2000. Temporal patterns of woody species in a central Appalachian forest from 1856 to 1997. Journal of the Torrey Botanical Society 127, 149–161.

Seidman, V.M., Zabel, C.J., 2001. Bat activity along intermittent streams in northwestern California. Journal of Mammalogy 82, 738–747.

Sherwin, R.E., Gannon, W.L., Haymond, S., 2000. The efficacy of acoustical techniques to infer differential use of habitat by bats. Acta Chiropterologica 2, 145–153.

Steel, R.G.D., Torrie, J.H., 1980. Principles and Procedures of Statistics: A Biometrical Approach. McGraw-Hill, New York, NY, 633pp..

Stokes, M.E., Davis, C.S., Koch, G.G., 1995. Categorical Data Analysis using the SAS System. SAS Institute Inc., Cary, NC, 499pp..

Teixeira, J., Ferrand, N., Arntzen, J.W., 2001. Biogeography of the golden-striped salamander *Chioglossa lusitanica*: a field survey and spatial modeling approach. Ecography 24, 618–624.

Tibbels, A.E., Kurta, A., 2003. Bat activity is low in thinned and unthinned stands of red pine. Canadian Journal of Forest Research 33, 2436–2442.

Vaughn, N., Jones, G., Harris, S., 1997. Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. Journal of Applied Ecology 34, 716–730.

Verboom, B., Huitema, H., 1997. The importance of linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. Landscape Ecology 12, 117–125.

Walsh, A.L., Hutson, T.M., Harris, S., 1993. UK volunteer bat groups and the British bat and habitats survey. In: Kapteyn, K. (Ed.), Proceedings of the 1st European Bat Detector Workshop, Amsterdam, Netherlands. pp. 113–123.

Warren, R.D., Waters, D.A., Altringham, J.D., Bullock, D.J., 2000. The distribution of Dauberton's bats (*Myotis daubentonii*) and pipistrelle bats (*Pipistrellus pipistrellus*) (Vespertilionidae) in relation to small-scale variation in riverine habitat. Biological Conservation 92, 85–91.

Weakland, C.A., Wood, P.B., Ford, W.M., 2002. Responses of songbirds to diameter-limit cutting in the central Appalachians of West Virginia. Forest Ecology and Management 155, 115–129.

Wear, M.S., 2004. Diversity and distribution of bat species on Chuck Swan Wildlife Management Area, Tennessee. M.S. Thesis, University of Tennessee, Knoxville, TN, USA. 68pp.

Weller, T.J., Seidman, V.M., Zabel, C.J., 1998. Assessment of foraging activity using Anabat II: a cautionary note. Bat Research News 39, 61–64.

Wickramasinghe, L.P., Harris, S., Jones, G., Vaughn, N., 2003. Bat activity and species richness on organic and conventional farms: impact of agricultural intensification. Journal of Applied Ecology 40, 984–993.

Wijs, W.J.R. de., 1999. Feasibility of monitoring bats on transects with ultrasound detectors. In: Harbusch, C., Pir, J. (Eds.), Proceedings of the 3rd European Bat Detector Workshop, Larochette, Luxembourg, pp. 95–105.

Whitaker, J.O., 2004. Prey selection in a temperate zone insectivorous bat community. Journal of Mammalogy 85, 460–469.

Whitaker, J.O., Hamilton, W.J., 1998. Mammals of the Eastern United States. Cornell University Press, Ithaca, NY, 583pp.

Zimmerman, G.S., Glanz, W.E., 2000. Habitat use by bats in eastern Maine. Journal of Wildlife Management 64, 1032–1040.