

Bat Activity in Harvested and Intact Forest Stands in the Allegheny Mountains

Sheldon F. Owen, Michael A. Menzel, and John W. Edwards, *Division of Forestry, West Virginia University, Morgantown, WV 26506*; W. Mark Ford, and Jennifer M. Menzel, *USDA Forest Service, Northeastern Research Station, Parsons, WV 26287*; Brian R. Chapman, *College of Arts and Sciences, Sam Houston State University, Huntsville, TX 77341*; Petra Bohall Wood, *USGS Biological Resources Division, West Virginia Cooperative Fish and Wildlife Research Unit and Division of Forestry, West Virginia University, Morgantown, WV 26506*; and Karl V. Miller, *Warnell School of Forest Resources, University of Georgia, Athens, GA 30602*.

ABSTRACT: We used Anabat acoustical monitoring devices to examine bat activity in intact canopy forests, complex canopy forests with gaps, forests subjected to diameter-limit harvests, recent deferment harvests, clearcuts and unmanaged forested riparian areas in the Allegheny Mountains of West Virginia in the summer of 1999. We detected eight species of bats, including the endangered Indiana bat (*Myotis sodalis*). Most bat activity was concentrated in forested riparian areas. Among upland habitats, activity of silver-haired bats (*Lasionycteris noctivagans*) and hoary bats (*Lasiurus cinereus*) was higher in open, less cluttered vegetative types such as recent deferment harvests and clearcuts. Our results suggest that bat species in the central Appalachians partially segregate themselves among vegetative conditions based on differences in body morphology and echolocation call characteristics. From the standpoint of conserving bat foraging habitat for the maximum number of species in the central Appalachians, special emphasis should be placed on protecting forested riparian areas. *North. J. Appl. For.* 21(3):154–159.

Key Words: Anabat, Appalachians, bat activity, riparian forests, timber harvest.

The use of ultrasonic acoustical monitoring devices such as the Anabat system has allowed ecologists to quickly and efficiently inventory bat communities (O'Farrell and Gannon 1999). Moreover, these techniques allow researchers to investigate differences in the relative activity of bats among habitat types across the landscape, as well as the effect of vegetative structure and condition on bat activity at a microhabitat scale (Brigham et al. 1997, Zimmerman and Glanz 2000). At the microhabitat scale, vertical structure or "clutter" in forest stands such as boles, branches, and foliage affect bat foraging by impeding detection and pursuit of prey (Findley 1976, Crome and Richards 1988, Findley 1993). Although modified greatly by arthropod prey abundance and the cost-benefit energetics of foraging efforts, the ranges of habitat scales that can be used by bat species are in part functions of wing morphology and echolocation call

structure (Sleep and Brigham 2003). Bats with high wing-loading and low-frequency calls tend to forage in open environments, whereas bats with lower wing-loadings and higher-frequency calls can use more cluttered environments (Aldridge and Rautenbach 1987, Nowak 1994).

Because the population and conservation status of many forest-dwelling bat species is unclear, recent research using acoustical sampling methods has focused on linkages between bat activity and common forest management practices such as clearcutting and group selection harvests (Krusic et al. 1996, Grindal and Brigham 1998, Menzel 1998) and the importance of riparian areas to foraging bats (Parker et al. 1996, Grindal et al. 1999, Seidman and Zabel 2001). In the heavily forested central Appalachians, permanently open habitats are uncommon and early-successional stands originating from clearcutting tend to be rare on public and nonindustrial private forests but are increasing in number on industrial forests. Regionally, most nonindustrial private forests and a large portion of industrial forests are routinely subjected to various selective harvests, such as diameter-limit cutting, that create small canopy gaps from the patchy removal of trees throughout harvested stands and leaves considerable portions of residual basal area and canopy

NOTE: W. Mark Ford can be reached at (304) 478-2000; Fax: (304) 478-8692; mford@fs.fed.us. Project funding was provided by USDA Forest Service Region 9 through the auspices of the Monongahela National Forest and by MeadWestvaco Corporation's Wildlife and Ecosystem Research Forest program. Field assistance was provided by Joshua Johnson, Dave Leput, Jane Rodrigue, and Brian Smith. Copyright © 2004 by the Society of American Foresters.

intact (Ford and Rodrigue 2001, Weakland et al. 2002). Because a wide range of forest conditions can be found with little or no permanently cleared land in agricultural or urban use, the central Appalachians provide a useful template to address research questions of bat activity from both a forest resource management and forest ecology perspective. The specific objectives of our study were to determine the importance of forested riparian areas to bat activity in the central Appalachians, how timber harvest methods influence bat activity, and whether activity levels can be predicted based on a species' body morphology and echolocation call characteristics and forest structural characteristics.

Study Design

Our study was conducted in northeastern West Virginia on the Mead-Westvaco Ecosystem Research Forest (MWERF) in Randolph County and the Fernow Experimental Forest (FEF) in Tucker County. The MWERF is a 3,360-ha working forest reserved for the study of industrial forestry impacts on ecosystems and ecological processes in an Appalachian setting (Ford and Rodrigue 2001). Moreover, the MWERF is located within a large matrix (>40,000 ha) of forest industry and coal company lands. The FEF is a 1,473-ha experimental forest that has been maintained for long-term forestry and ecological research by the USDA Forest Service Northeastern Research Station since 1951 (Madarish et al. 2002). Although some industry land is in close proximity, the FEF occurs in a more lightly managed landscape consisting of the Cheat Ranger District of the Monongahela National Forest including the adjacent Otter Creek Wilderness area. Because the MWERF and the FEF are designated as forestry research areas, younger forest stands (<10) originating from clear- and deferment cutting and older stands altered by diameter-limit and selection cutting are commonplace. Annual wood removals on the MWERF routinely exceed 24,000 m³, whereas annual removals on the FEF are approximately 7,000 m³. Elevations in this portion of the Allegheny Mountains subsection of the Appalachian Plateau Physiographic Province reach 1,300 m. The topography is characterized by steep slopes with broad ridge tops and narrow valleys. The climate is cool and moist with annual precipitation exceeding 155 cm. On high site index upland sites, second-growth (70–90 years) Allegheny-northern hardwood forests consisting of American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*), black cherry (*Prunus serotina*), northern red oak (*Quercus rubra*), yellow birch (*Betula alleghaniensis*), sweet birch (*B. lenta*), Fraser magnolia (*Magnolia fraseri*), and basswood (*Tilia americana*) are present. Upland understories beneath closed canopy stands are sparse, and those in forest gap areas generally consist of an American beech and striped maple (*A. pensylvanicum*) shrub layer. Overstories of eastern hemlock (*Tsuga canadensis*) and shrub layers of rosebay rhododendron (*Rhododendron maximum*) dominate riparian areas.

We used Anabat II ultrasonic detectors to compare bat foraging activity across three to four replicates in each of six Allegheny-northern hardwood stand conditions on the

MWERF and FEF during May–July 1999. The conditions were as follows: second-growth mature forest with intact canopy (three stands); mature forest with complex canopies and numerous gaps formed by wind throw or insect mortality (three stands); mature forests subjected to a 40-cm dbh diameter-limit harvest within the past 5 years (three stands); deferment stands within 5 years after harvest with 6–10 m²/ha sawtimber size residuals (three stands); silvicultural clearcuts within 5 years after harvest (three stands); and forested riparian zones along second- and third-order mountain streams (four areas). Sample site elevations ranged from approximately 800–1,015 m. Harvested areas were approximately 15 ha in size, whereas unharvested intact and complex canopy forest stands were approximately 30–40 ha (Ford and Rodrigue 2001, USDA Forest Service, unpublished data). All forested riparian areas were adjacent to mature forests. Each replicate of each type was surveyed for two or more nights between mid-May through late July except on nights where low temperatures fell below 10° C, the wind speed exceeded 8 km/hour or rain was falling. We placed Anabats in waterproof containers and suspended them at a height of 7–9 m on telescoping poles in harvested areas or suspended over tree limbs within the canopy in forested areas. All Anabats were placed in the center of each vegetation type replicate and >100 m from a hard edge to avoid detecting bat activity in adjacent habitats. Anabats placed in riparian areas were positioned so that the majority of the sampling cone encompassed space over the waterway. Each Anabat was linked to a remote-activated tape recorder with an Anabat delay switch that provided a calibration tone and time stamp after every recorded sequence (15 seconds). Longer continual sequences were recorded as two or more calls, although with passive Anabat sampling, that was an infrequent occurrence. Anabat detectors were equilibrated with an electronic, ultrasonic pest control device to sample distances of approximately 20 m without detecting constant extraneous noise from insects and Anurans (Menzel 1998). We defined an Anabat detector-night as a single night within a single replicate of a vegetative type.

We transferred bat echolocation recordings from tape to computer using a Zero-Crossing Analysis Interface Module. We identified bat species using Anabat 6.3e (Titley Electronics, Ballina NSW, Australia), Analook 4.8i (Corben Scientific, Rohnert Park, CA), and Analyze 2.1 software (members.ozemail.com.au/~jollys/analyze95.htm) using a combination of quantitative (minimum and mean call note frequency) and more qualitative (call note curvature and slope) metrics in a dichotomous key format developed by using an extensive call library from the Southeast and Mid-Atlantic (M.A. Menzel, West Virginia Univ., unpublished data). All call sequences were filtered before analysis (Britzke and Murray 2000). The ability of researchers to identify sequences using Anabat, of North American bats, including the ability to discriminate among *Myotis*, has improved substantially in recent years (O'Farrell et al. 1999, Britzke and Murray 2000, Gannon et al. 2001, Murray et al. 2001). We counted the number of bat passes (including

feeding buzzes) among species recorded per site, per individual night sampled, as defined by Krusic et al. (1996). However, our method was more conservative in that we only attempted to identify bat passes to species with ≥ 5 echolocation calls appearing in close sequence. The use of activity indices as a quantification of bat activity as proposed by Miller (2001) was impractical owing to the low overall level of bat activity in all but the forested riparian areas we surveyed. Because we recorded bat echolocations from fixed points and on tape, an accurate distinction and count of feeding buzzes relative to other search-phase calls was unreliable (Weller et al. 1998, Johnson et al. 2002). All bat-pass identifications were confirmed by the senior author to reduce potential bias from multiple observers, and all echolocation recordings were saved as vouchers.

Because our bat echolocation data were not normally distributed based on Kolomogorov's Test (SAS Institute 1985a), we used ranked data of bat species for all comparisons of passes (SAS Institute 1985b). We analyzed numbers of bat passes across the six forest stand conditions using a nested analysis of variance (ANOVA) design with vegetative type as the treatment effect and with individual nights at each replicate site as a nested effect (Petersen 1985). We made a priori hypotheses about how activity would differ among bat species based on body morphology (the higher the wing loading, the more open the foraging habitat selected), echolocation call characteristics (the lower the mean call frequency, the more open the foraging habitat selected), and feeding strategies among forest condition. We performed linear orthogonal contrasts (SAS Institute 1985b) rather than traditional mean separation tests to determine effects differing habitat structure across the forest treatments on bat activity. We used the following contrasts: forested riparian zones versus all upland habitats; open habitats (deferment and clearcut harvests) versus cluttered habitats (intact canopy forest, complex canopy forest, and diameter-limit harvests); and forests with gaps (complex canopy forest and diameter-limit harvests) versus intact

canopy forest. Statistical significance for all contrasts was accepted at $\alpha = 0.05$.

Results

We monitored bat activity over 49 Anabat detector-nights and recorded 1,477 bat passes during 1999. Because of equipment malfunctions and frequent rain events, sampling effort was not equal among treatments, and we sometimes failed to get simultaneous detector-nights across each treatment type within a night (Table 1). Numbers of detector-nights ranged from a low of 6 in the intact canopy and clearcut harvest sites to a high of 11 in the complex canopy stands (Table 1). We recorded eight bat species: little brown bat (*Myotis lucifugus*), $n = 224$ passes; northern myotis (*M. septentrionalis*), $n = 4$ passes; Indiana bat (*M. sodalis*), $n = 70$ passes; silver-haired bat (*Lasionycteris noctivagans*), $n = 19$ passes; eastern pipistrelle (*Pipistrellus subflavus*), $n = 17$ passes; big brown bat (*Eptesicus fuscus*), $n = 123$ passes; eastern red bat (*Lasiurus borealis*), $n = 47$ passes; and hoary bat (*L. cinereus*), $n = 22$ passes. Because we chose a conservative approach of only identifying high-quality calls, we classified 361 echolocation sequences to *Myotis*, but did not attempt to identify the call to species. We recorded an additional 590 calls that were not identifiable to genus or species. Away from riparian areas, mean numbers of calls per night for most bat species were minimal (Table 1).

We detected significantly more little brown bat passes (contrast $F = 172.3$, $df = 1$, $P < 0.001$), northern myotis passes (contrast $F = 21.2$, $df = 1$, $P < 0.001$), Indiana bat passes (contrast $F = 16.59$, $df = 1$, $P < 0.001$), silver-haired bat passes (contrast $F = 4.7$, $df = 1$, $P = 0.04$), eastern pipistrelle passes (contrast $F = 18.8$, $df = 1$, $P = 0.002$), big brown bat passes (contrast $F = 7.5$, $df = 1$, $P = 0.01$) and eastern red bat passes ($F = 12.1$, $df = 1$, $P = 0.002$) in riparian forests than in upland habitats. We detected significantly more silver-haired bat passes (contrast $F = 5.42$, $df = 1$, $P = 0.03$) and hoary bat passes (contrast

Table 1. Mean numbers and standard errors of bat echolocation search-phase passes per detector-night across six forest conditions (see text) on the Mead-Westvaco Ecosystem Research Forest and Fernow Experimental Forest, WV, 1999.

	Intact canopy, ^{a,b} $n = 6$		Complex canopy, $n = 11$		Diameter-limit, $n = 7$		Deferment, $n = 9$		Clearcut, $n = 6$		Forested riparian, $n = 10$	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Little brown bat	0.0	0.0	0.0	0.0	0.1	0.1	0.6	0.4	0.0	0.0	21.8	6.3
Northern myotis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.2
Indiana bat	0.5	0.3	0.0	0.0	1.1	0.4	0.1	0.1	0.0	0.0	5.8	2.3
<i>Myotis</i> spp.	12.0	5.4	5.4	3.4	4.4	1.5	1.7	0.5	0.0	0.0	18.4	7.7
Silver-haired bat	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.3	0.2	0.2	1.4	1.3
Eastern pipistrelle	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	1.0
Big brown bat	1.0	0.8	1.4	0.4	0.3	0.2	2.0	1.6	0.5	0.3	7.9	3.6
Eastern red bat	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.7	3.3
Hoary bat	0.0	0.0	0.1	0.1	0.1	0.1	1.2	0.7	1.2	0.6	0.3	0.2
Unknown to genus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	59.0	11.7

^a For purpose of orthogonal contrasts, "upland" = intact canopy, complex canopy, diameter-limit, deferment, and clearcut; "riparian" = forested riparian; "open habitats" = deferment and clearcut; "cluttered forests" = intact canopy, complex canopy, and diameter-limit; "forests with gaps" = complex canopy and diameter-limit (see text for comparisons).

^b Anabat detector-nights per forest condition type.

$F = 11.9$, $df = 1$, $P < 0.002$) in open forests than in cluttered habitats. The opposite was true for unidentified *Myotis* (contrast $F = 9.84$, $df = 1$, $P < 0.004$), as we detected significantly higher activity levels in cluttered than in open habitats. Bat activity did not differ between forests with gaps and intact canopy forests for all species ($P > 0.05$) and was low in forests with gaps and intact canopies (Table 1).

Discussion

Bat activity levels in nonriparian upland forests and harvested forests were low relative to forested riparian areas. The different activity levels between upland and riparian areas for most species from our contrast analyses were similar to what has been reported in the Southeast (Menzel 1998), New England (Krusic et al. 1996, Zimmerman and Glanz 2000) and the Pacific Northwest (Grindal et al. 1999, Seidman and Zabel 2001). High levels of bat activity observed in riparian areas elsewhere often were related to the increased foraging efficiency associated with foraging in areas where insect abundances are greater (Barclay 1991, Grindal et al. 1999). We speculate that the same is true in the Allegheny Mountains. Krusic et al. (1996) observed higher levels of bat activity along edge and linear landscape elements. It could be that these protected, corridor-like settings as found along riparian areas at our study sites reduce energetic demands associated with flight during travel and foraging. Whether or not this same level of activity occurred at the edges of harvested and unharvested stands or along forest roads on our study sites was not tested by our design and it remains an important question. Regardless, our research reasserts the biological importance of forested riparian habitats in the Appalachians, a biological contention that has been widely assumed (Murray and Stauffer 1995), but rarely tested (Ford and Rodrigue 2001). Further emphasis on the protection of forested riparian areas in the central Appalachians seems warranted by the presence of the endangered Indiana bat in the region during the nonhibernation period (Hobson and Holland 1995, Owen et al. 2001). Although Indiana bats have been documented foraging in upland habitats in many parts of their range (Easterla and Watkins 1969, LaVal et al. 1977, Brack 1983), most foraging observations have been made in forested riparian habitats throughout their distribution (Humphrey et al. 1977, Kessler et al. 1981, Menzel et al. 2001) and locally on the FEF (Ford et al. 2003).

Although we detected few silver-haired bat and hoary bat passes, the higher numbers in open habitats, such as recent clearcuts and deferment harvests, than in closed forests was expected based on the morphological traits of these species (Barclay 1985). Both of these bat species have lower wing-aspect ratios, higher wing-loadings, and lower call frequencies than most species of *Myotis*. Accordingly, these two species are better suited for foraging in open areas away from forest structure and clutter, where highly maneuverable flight is less critical. Moreover, both species use low-frequency echolocation calls to navigate and locate prey. Low-frequency calls are attenuated less than high frequency

calls and provide less target resolution and accordingly are more suited for foraging in open habitats (Griffin 1971, Fenton 1999).

Within the heavily forested central Appalachian region, timber harvest probably increases the amount of usable upland foraging habitat for bat species typified by high wing loadings and low call frequencies. Consequently, upland foraging habitat for silver-haired bats and hoary bats probably is more abundant on industrial forest areas such as the MWERF, where the percentage of early-successional forests and recently harvested stands is greater than on less used national forest lands in the central Appalachians. Whether or not the amount of open area in the industrial forest landscape exceeds that required of the two bat species or is detrimental to these in terms of roost availability or other bat species' foraging or roosting needs is unknown. Similarly, it is not entirely clear what the value or extent of foraging habitat above the canopy at the intact forest sites were for these species or any other bat species on the MWERF and FEF. Based on Anabat positioning, our sampling would have been able to detect considerable above-canopy activity (if present) in diameter-limit harvests and complex canopy forests, although less so within intact canopy forests. Although few studies have addressed above-canopy bat activity in the East or elsewhere, Menzel et al. (2000) found considerably less low- and medium-frequency and no high-frequency echolocation activity at 1 and 21 m above the forest canopy than beneath the forest canopy near ground level in a mixed loblolly pine (*Pinus taeda*)-mesic hardwood forest in the Georgia Piedmont.

Because the big brown bat is a large bat with a low-frequency echolocation call, we expected higher levels of big brown bat activity in open habitats than in closed forest habitats. Contrary to our expectations, we found no differences in big brown bat use among the upland vegetation types, perhaps supporting the view that this species has generalized, opportunistic foraging habits (Brigham 1991, Whitaker and Hamilton 1998) despite what could be predicted based on its morphology and echolocation patterns.

We found the opposite habitat-use pattern for the species of *Myotis*. Their activity was lower in open (harvested) upland forests and higher in closed canopy forests. These spatial activity patterns are consistent with their small body size, lower wing loading, and higher echolocation call frequency. Our inability to detect differences in call activity between forest stands with gaps (complex canopy and diameter-limit harvest) and stands without canopy breaks (intact forest canopy), might suggest that stands subjected to diameter-limit harvest where 12–20 m²/ha of the basal area is retained still approximate usable foraging habitat for *Myotis* species in the central Appalachians. Grindal and Brigham (1998) noted a similar inability to detect threshold levels of forest disturbance impacts to bats among small-scale canopy openings and harvest areas in Canadian forests. Nonetheless, before recommending diameter-limit timber harvest, we would note that this system fails to regenerate shade-intolerant mast-producing tree species that are

valuable to many wildlife species in the central Appalachians (Miller and Smith 1993, Miller and Kochenderfer 1998). Additionally, these harvests do not promote the retention of large diameter trees that could serve as day-roosts for species such as Indiana bat (Menzel et al. 2001, Ford et al. 2002). It is important to note that forests are the primary day-roost habitats in the central Appalachians for each of the species we detected in this study (Menzel et al. 2002).

The use of zero-crossing analysis acoustical detection systems such as Anabat to positively identify species, inventory bat communities, and examine relative habitat use has come under recent criticism (Barclay 1999, O'Farrell et al. 1999, Sherwin et al. 2000, Corbin and Fellers 2001, Fenton et al. 2001). We acknowledge that absolute data about bat habitat use cannot be obtained using Anabats or any acoustical monitoring devices alone. Furthermore, the inability to distinguish gender of bats emitting echolocation calls limits inferences that can be drawn from these data, particularly with regard to the endangered Indiana bat and the need to delineate maternity habitat areas. However, within these limits, many researchers recognize the efficacy of using Anabat detection systems to complement mist-netting efforts to survey bat communities within an area and to provide commentary on relative bat activity among habitats (Betts 1998, Murray et al. 1999, O'Farrell et al. 1999).

One noticeable bias attributed to the use of Anabat acoustical sampling is the reduced ability to detect the low-intensity calls of northern myotis (Faure et al. 1993, Murray et al. 1999). Similar to the research of Krusic et al. (1996) in New England, we rarely detected northern myotis with Anabat at settings optimized to detect other bat species, despite it being the most numerous bat encountered in concurrent mist-net surveys (Owen et al. 2001, Menzel et al. 2002). Without discounting the importance of forested riparian areas, our low sample size of northern myotis calls severely limits the inferences we can draw about the species' habitat selection. Concurrent research on the MWERF utilizing radio-telemetry has shown that northern myotis use unharvested forest stands and diameter-limit harvest areas while avoiding clearcut and deferment harvests (Owen et al., in 2003). Our ability to positively identify *Myotis* to species was hindered by our recording calls to tape rather than directly to a computer (O'Farrell and Gannon 1999, Johnson et al. 2002). The use of Anabat sampling recording directly to a computer or compact flash card with a researcher present akin to songbird point count surveys (Weakland et al. 2002) has shown great promise in overcoming such deficiencies and will allow for better resolution of bat activity among habitat types (White and Gehrt 2001, Johnson et al. 2002).

Literature Cited

- ALDRIDGE, H.D.N., AND I.L. RAUTENBACH. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. *J. Animal Ecol.* 56:763-778.
- BARCLAY, R.M.R. 1985. Long- versus short-range foraging strategies of hoary (*Lasiurus cinereus*) and silver-haired (*Lasionycteris noctivagans*) bats and the consequences for prey selection. *Can. J. Zool.* 63:2570-2575.
- BARCLAY, R.M.R. 1991. Population structure of temperate zone insectivorous bats in relation to foraging behavior and energy demand. *J. Animal Ecol.* 60:165-178.
- BARCLAY, R.M.R. 1999. Bats are not birds—A cautionary note on using echolocation calls to identify bats: a comment. *J. Mammal.* 80:290-296.
- BETTS, B.J. 1998. Effects of inter-individual variation in echolocation calls on identification of big brown and silver-haired bats. *J. Wildl. Manage.* 62:1003-1010.
- BRACK, V.W. 1983. The nonhibernating ecology of bats in Indiana with emphasis on the endangered Indiana bat, *Myotis sodalis*. Ph.D. dissertation, Purdue Univ., West Lafayette, Indiana. 280 p.
- BRIGHAM, R.M. 1991. Flexibility in foraging and roosting behavior by the big brown bat (*Eptesicus fuscus*). *Can. J. Zool.* 69:117-121.
- BRIGHAM, R.M., S.D. GRINDAL, M. C. FIRMAN, AND J.L. MORISSETTE. 1997. The influence of structural clutter on activity patterns of insectivorous bats. *Can. J. Zool.* 75:131-136.
- BRITZKE, E.R., AND K.L. MURRAY. 2000. A quantitative method for selection of identifiable search-phase calls using the Anabat system. *Bat Res. News.* 41:33-36.
- CORBIN, C., AND G.M. FELLERS. 2001. Choosing the "correct" bat detector—A reply. *Acta Chiropt.* 3:253-256.
- CROME, F.H.J., AND G.C. RICHARDS. 1988. Bats and gaps: Microchiropteran community structures in a Queensland rainforest. *Ecology* 69:1960-1969.
- EASTERLA, D.A., AND L.C. WATKINS. 1969. Pregnant *Myotis sodalis* in northwestern Missouri. *J. Mammal.* 50:372-373.
- FAURE, P.A., J.H. FULLARD, AND J.W. DAWSON. 1993. The gleaning attacks of the northern long-eared bat, *Myotis septentrionalis*, are relatively inaudible to moths. *J. Exp. Biol.* 178:173-189.
- FENTON, M.B. 1999. Describing the echolocation calls and behavior of bats. *Acta Chiropt.* 1:127-136.
- FENTON, M.B., S. BOUCHARD, M.J. VONHOF, AND J. ZIGOURS. 2001. Time-expansion and zero-crossing period meter systems present significantly different views of echolocation calls of bats. *J. Mammal.* 82:721-727.
- FINDLEY, J.S. 1976. The structure of bat communities. *Am. Nat.* 110:129-139.
- FINDLEY, J.S. 1993. Bats: A community perspective. Cambridge Univ. Press, Cambridge, MA. 167 p.
- FORD, W.M., J.M. MENZEL, M.A. MENZEL, AND J.W. EDWARDS. 2002. Summer roost-tree selection by a male Indiana bat on the Fernow Experimental Forest. USDA For. Serv. Res. Note NE-378. 7 p.
- FORD, W.M., M.A. MENZEL, J.M. MENZEL, AND J.L. RODRIGUE. 2003. Hearing bat habitat: Anabat surveys on the the Fernow Experimental Forest. Abstracts of the 13th Ann. Coll. Cons. of Mammals in the Southeast 13:15-16.
- FORD, W.M., AND J.L. RODRIGUE. 2001. Soricid abundance in partial overstory removal harvests and riparian areas in an industrial forest landscape of the central Appalachians. *For. Ecol. Manage.* 152:159-168.
- GANNON, W.L., R.E. SHERWIN, T.N. DECARVALHO, AND M.J. O'FARRELL. 2001. Pinnae and echolocation call differences between *Myotis californicus* and *M. ciliolabrum* (Chiroptera: Vespertilionidae). *Acta Chiropt.* 3:77-91.
- GRIFFIN, D.R. 1971. The importance of atmospheric attenuation for the echolocation of bats (Chiroptera). *Animal Behav.* 19:55-61.
- GRINDAL, S.D., AND R.M. BRIGHAM. 1998. Short-term effects of small-scale habitat disturbance on activity by insectivorous bats. *J. Wildl. Manage.* 62:996-1003.
- GRINDAL, S.D., J.L. MORRISSETTE, AND R.M. BRIGHAM. 1999. Concentration of bat activity in riparian habitats over an elevational gradient. *Can. J. Zool.* 77:972-977.
- HOBSON, C.S., AND J.N. HOLLAND. 1995. Post-hibernation movement and foraging habitat of a male Indiana bat, *Myotis sodalis* (Chiroptera: Vespertilionidae), in western Virginia. *Brimleyana* 23:95-101.
- HUMPHREY, S.R., A.R. RICHTER, AND J.B. COPE. 1977. Summer habitat and ecology of the endangered Indiana bat, *Myotis sodalis*. *J. Mammal.* 58:334-346.
- JOHNSON, J.B., M.A. MENZEL, J.W. EDWARDS, AND W.M. FORD. 2002. A quantitative comparison between two acoustical bat survey techniques. *Wildl. Soc. Bull.* 30:931-936.

- KESSLER, J.S., W.M. TURNER, AND L. MORGAN. 1981. A survey for the Indiana bat, *Myotis sodalis*, on Knob Creek, Bullitt County, Kentucky. *Trans. Kentucky Acad. Sci.* 44:38–40.
- KRUSIC, R.A., M. YAMASAKI, C.D. NEEFUS, AND P.J. PEKINS. 1996. Bat habitat use in White Mountain National Forest. *J. Wildl. Manage.* 60:625–631.
- LAVAL, R.K., R.L. CLAWSON, M.L. LAVAL, AND W. CLAIRE. 1977. Foraging behavior and nocturnal activity patterns of Missouri bats with emphasis on the endangered species *Myotis grisecens* and *Myotis sodalis*. *J. Mammal.* 58:592–599.
- MADARISH, D.M., J.L. RODRIGUE, AND M.B. ADAMS. 2002. Vascular flora and macroscopic fauna on the Fernow Experimental Forest. USDA For. Serv. Gen. Tech. Rep. NE-291. 37 p.
- MENZEL, J.M., M.A. MENZEL, G.F. MCCracken, AND B.R. CHAPMAN. 2000. Notes on bat activity above the forest canopy in the eastern United States. *Ga. J. Sci.* 58:212–216.
- MENZEL, M.A. 1998. The effects of group selection timber harvest in a southeastern bottomland hardwood community on the roosting and foraging behavior of tree-roosting bats. M.S. thesis, Univ. of Georgia, Athens, GA. 160 p.
- MENZEL, M.A., J.M. MENZEL, T.C. CARTER, W.M. FORD, AND J.W. EDWARDS. 2001. Review of the forest habitat relationships of the Indiana bat (*Myotis sodalis*). USDA For. Serv. Gen. Tech. Rep. NE-284. 21 p.
- MENZEL, M.A., S.F. OWEN, W.M. FORD, B.R. CHAPMAN, K.V. MILLER, J.E. EDWARDS, AND P.B. WOOD. 2002. Roost tree selection by maternity colonies of northern long-eared bats (*Myotis septentrionalis*) in an industrial forest of the central Appalachian Mountains. *For. Ecol. Manage.* 155:107–114.
- MILLER, B.W. 2001. A method for determining relative activity of free flying bats using a new activity index for acoustical monitoring. *Acta Chiropt.* 3:93–105.
- MILLER, G.W., AND J.N. KOCHENDERFER. 1998. Maintaining species diversity in the central Appalachians. *J. For.* 96:28–33.
- MILLER, G.W., AND H.C. SMITH. 1993. A practical alternative to single-tree selection? *North. J. Appl. For.* 10:32–38.
- MURRAY, K.L., E.R. BRITZKE, B.M. HADLEY, AND L.W. ROGGINS. 1999. Surveying bat communities: A comparison between mist nets and the Anabat II bat detector system. *Acta Chiropt.* 1:105–112.
- MURRAY, K.L., E.R. BRITZKE, AND L.W. ROBBINS. 2001. Variation in search-phase calls of bats. *J. Mammal.* 82:728–737.
- MURRAY, N.L., AND D.F. STAUFFER. 1995. Nongame bird use of habitat in central Appalachian riparian forests. *J. Wildl. Manage.* 59:78–99.
- NOWAK, R.M. 1994. *Walker's bats of the world*. Johns Hopkins Univ. Press, Baltimore, MD. 287 p.
- O'FARRELL, M.J., AND W.L. GANNON. 1999. A comparison of acoustic versus capture techniques for the inventory of bats. *J. Mammal.* 80:24–30.
- O'FARRELL, M.J., B.W. MILLER, AND W.L. GANNON. 1999. Qualitative identification of free-flying bats using the anabat detector. *J. Mammal.* 80:11–23.
- OWEN, S.F., M.A. MENZEL, W.M. FORD, B.R. CHAPMAN, K.V. MILLER, J.W. EDWARDS, AND P.B. WOOD. 2001. First summer record of a female Indiana bat, *Myotis sodalis*, in West Virginia. *J. Elisha Mitchell Sci. Soc.* 117:132–134.
- OWEN, S.F., M.A. MENZEL, W.M. FORD, B.R. CHAPMAN, K.V. MILLER, J.W. EDWARDS, AND P.B. WOOD. 2003. Home-range size and habitat use of the northern myotis (*Myotis septentrionalis*). *Am. Mid. Nat.* 150:352–359.
- PARKER, D.I., J.A. COOK, AND S.W. LEWIS. 1996. Effects of timber harvest on bat activity in southeastern Alaska's temperate rainforests. P. 277–292. *in* Proc. of the Bats and Forest Symposium, Barclay, R.M.R., and R.M. Brigham (eds.). Victoria, BC, Canada. 292 p.
- PETERSEN, R.G. 1985. *Design and analysis of experiments*. Marcel Dekker Press, Inc., New York, NY. 429 p.
- SAS INSTITUTE. 1985a. *SAS user's guide—Basics: Version 5.0*. SAS Institute, Cary, NC. 1,290 p.
- SAS INSTITUTE. 1985b. *SAS user's guide—Statistics: Version 5.0*. SAS Institute, Cary, NC. 956 p.
- SEIDMAN, V.M., AND C.J. ZABEL. 2001. Bat activity along intermittent streams in northwestern California. *J. Mammal.* 82:738–747.
- SHERWIN, R.E., W.L. GANNON, AND S. HAYMOND. 2000. The efficacy of acoustical techniques to infer differential use of habitat by bats. *Acta Chiropt.* 2:145–153.
- SLEEP, D.J.H., AND R.M. BRIGHAM. 2003. An experimental test of clutter tolerance in bats. *J. Mammal.* 84:216–224.
- WEAKLAND, C.A., P.B. WOOD, AND W.M. FORD. 2002. Responses of songbirds to diameter-limit cutting in the central Appalachians of West Virginia, USA. *For. Ecol. Manage.* 155:115–129.
- WELLER, T.J., V.M. SEIDMAN, AND C.J. ZABEL. 1998. Assessment of foraging activity using Anabat II: A cautionary note. *Bat Res. News* 39:61–65.
- WHITAKER, J.O., AND W.J. HAMILTON. 1998. *Mammals of the eastern United States*. Cornell Univ. Press, Ithaca, New York, NY. 583 p.
- WHITE, E.P., AND S.D. GEHRT. 2001. Effects of recording media on echolocation data from broadband bat detectors. *Wildl. Soc. Bull.* 29:974–978.
- ZIMMERMAN, G.S., AND W.E. GLANZ. 2000. Habitat use by bats in eastern Maine. *J. Wildl. Manage.* 64:1032–1040.