Bat Activity in a Forest Landscape of Central Massachusetts

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Abstract - Nine species of bat are known to occur across the six New England states, but most aspects of their natural history, such as foraging habitat use, are poorly understood. Recent published research has documented the importance of still-water habitats as foci of bat flight activity. To better understand and document habitat use in southern New England, we used the AnaBat II acoustical monitoring system to assess species composition and relative levels of summer flight activity. Active acoustic surveys were conducted in six habitat types on the Quabbin Reservation in central Massachusetts in 2003 and 2004. Bat flight activity, as measured by numbers of echolocation call sequences, was high, with an average of 24 search-phase and 4 feeding-buzz calls per 20-minute survey period. *Myotis lucifugus* (little brown bat) was the most commonly recorded species. Bat flight activity was high over all still-water habitats, but greatest over large ponds. Large-bodied bats, such as *Eptesicus fuscus* (big brown bat), were recorded more often in open, structurally uncluttered habitats. Of the small-bodied bats, little brown bats were ubiquitous, whereas *Myotis septentrionalis* (northern myotis) was most common in structurally cluttered habitats of seasonal forest (vernal) pools and along forest streams. Generalized habitat associations among the bat species we recorded are similar to those reported for other New England forest sites. The Quabbin Reservation is an excellent site to continue examining bat-habitat relationships because of the abundance and diversity of aquatic habitats, in both cluttered closed-canopy and uncluttered open-canopy settings.

Introduction

Within New England, the Canadian Maritime Provinces, and elsewhere, bats are a faunal group of high conservation interest, yet our knowledge of life histories and ecologies of most species are often limited to anecdotal accounts or observational studies (Arnett 2003). Data on day-roost selection and foraging-habitat use, necessary for guiding and assessing forest and watershed management decisions, are particularly lacking (Arnett 2003). However, the recent widespread use of acoustical monitoring systems to survey and assess bat communities in forested landscapes has provided great insights into bat foraging-habitat use by individual species and a better understanding of bat community assemblages (Broders et al. 2003, Krusic et al. 1996, Zimmerman and Glanz 2000).

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In the mid-Atlantic and southeastern United States, researchers have sought to use acoustical monitoring, in conjunction with an understanding of species-specific morphological attributes and echolocation call characteristics, to explain foraging patterns and examine bat responses to forest management impacts (Johnson et al. 2002, Menzel et al. 2005, Owen et al. 2004). The relative ease and efficiency of active acoustical sampling with AnaBat® equipment are useful for examining the relationships of bat flight activity to habitat conditions (Johnson et al. 2002).

Data derived from these studies, and others using passive acoustical sampling, have shown that, for most bat species, flight activity is concentrated over riparian and wetland habitats (Francl et al. 2004; Grindal et al. 1999; Menzel et al., in press; Owen et al. 2004; Zimmerman and Glanz 2000). Passive acoustic surveys by Menzel (2003) and Owen et al. (2004) have additionally noted that when bats foraged in upland habitats, there was a high degree of predictability of how bats used forest successional stage and structure, or clutter, relative to their morphology.

In general, bat species with high wing loadings and large bodies are less maneuverable in flight, have lower frequency echolocation calls, and tend to forage over less structurally cluttered, open environments. Species with low wing loadings and smaller bodies are more maneuverable, have higher frequency echolocation calls, and utilize more cluttered, closed-canopy forest habitats (Aldridge and Rautenback 1987, Broders et al. 2004, Nowak 1994). For example, relative flight activity levels of larger species, such as *Lasiurus cinereus* Palisot de Beauvois (hoary bats), *Eptesicus fuscus* Palisot de Beauvois (big brown bats), and *Lasionycterus noctivigans* Le Conte(silver-haired bats), are highest in open habitats such as recent clearcuts or directly above forest canopies, whereas smaller bats, such as the *Myotis* species (e.g., *M. septentrionalis* Troussart [northern myotis] or *M. sodalis* Miller and G.M. Allen [Indiana bat]), have higher flight activity levels in more closed forest stands (Ford et al. 2003; Menzel et al. 2000, 2005; Owen et al. 2004).

Of the nine bat species occurring in New England (DeGraaf and Yamasaki 2001, King 1993), all but *M. leibii* Audobon and Bachman (small-footed bat) and the Indiana bat are either known or could be expected to occur in central Massachusetts east of the Connecticut River. Unlike many of the forested landscapes in southern New England, forests of the Quabbin Reservation are actively managed to promote diverse and vigorous stands capable of resisting catastrophic disturbance and protecting water quality (O'Connor et al. 1995). Accordingly, with a potentially rich bat fauna, ongoing active forest management, and numerous riparian and wetland habitats, the Quabbin provides a template to examine bat foraging ecology from which to develop management guidelines that promote bat conservation.

The objectives of this study were: (1) determine species composition and relative flight activity levels of bats at a variety of riparian, wetland, and open-area habitat within the forested landscape of the Quabbin Reservation, central Massachusetts, using active acoustical sampling techniques; and (2) determine the importance of seasonal forest (vernal) pool habitats for bat foraging. Although little bat survey work has been conducted in central Massachusetts, we predicted that abundance of species such as the generalist *Myotis lucifigus* Le Conte (little brown bat) and big brown bats, and the closed-forest riparian and wetland specialist, the northern myotis, would be high because of the abundance of good foraging habitats (e.g., still water) and the large, intact, and diverse forested areas for day-roost habitats. We also hypothesized that relative flight activity levels of bat species would be partitioned by habitat, based on whether or not survey sites were structurally open or cluttered.

Field Site Descriptions

Acoustical bat surveys were conducted at open or aquatic inclusions in the extensive, closed forest of the Quabbin Reservation (72°21'W, 42°17'N) in central Massachusetts (Fig. 1). The Quabbin watershed is in the Worcester-Monadnock Plateau Subsection of the Lower New England Section, Eastern Broadleaf Forest (Oceanic) Province (McNab and Avers 1994). Widespread glacial features and glacially derived soils characterize the Lower New England Section. Forest, predominantly oak-hickory

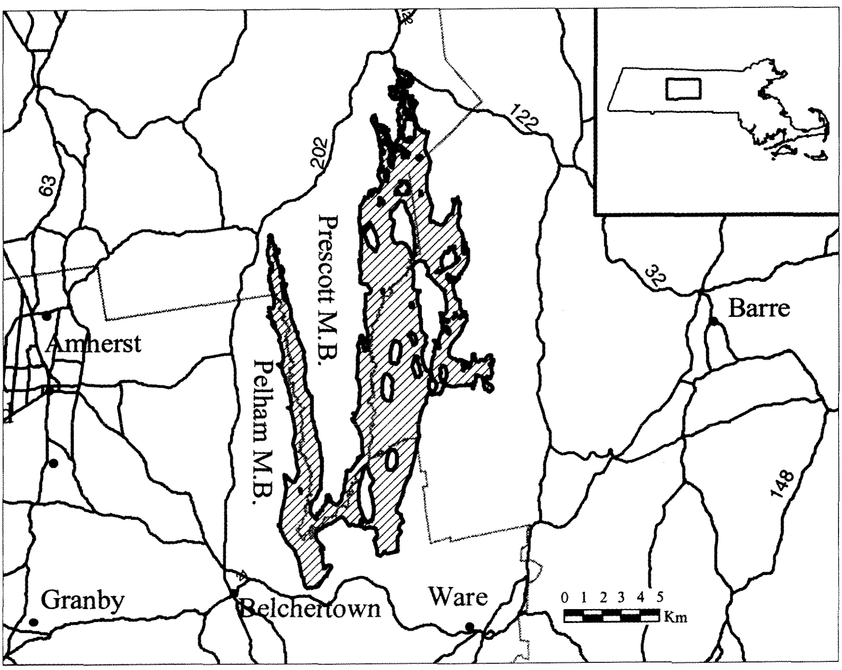

Figure 1. Location of Quabbin Reservation in central Massachusetts. Pelham and Prescott management blocks, where bat survey sites were located, are identified.

and northern hardwoods, is the dominant land cover of southern New England (Brooks et al. 1993).

The 48,500-ha Quabbin watershed surrounds the 9700-ha Quabbin Reservoir, the principal water source for greater Boston. The Massachusetts Department of Conservation and Recreation (MDCR) manages 64% of the watershed (Quabbin Reservation); the balance is in private or other public ownerships. The MDCR property is dominated by forestland (90.7% of upland area) of *Quercus* spp. (oak) and *Pinus strobus* L. (white pine) forest types. Embedded in the forest are over 2300 ha of wetlands and open water and approximately 212 km of streams (O'Connor et al. 1995). Open uplands include over 150 ha of cleared pine plantations, maintained as herbaceous fields, and of recently harvested forest stands.

The Quabbin Reservation is a working forest with an active timber-harvesting program. The goal of the forest management program is to create and maintain a vigorous forest that will withstand potential wind throw (O'Connor et al. 1995). The forest is principally managed using uneven-aged group selection with variable-sized openings (T. Kyker-Snowman, MDCR, pers. comm.). Remnant plantations, mostly of *P. resinosa* Ait. (red pine), are being regenerated to naturally occurring species using an even-aged shelterwood system that temporarily creates open-canopy, early-successional stands. Approximately 1600 acres (650 ha) on the Reservation are harvested each year (T. Kyker-Snowman, MDCR, pers. comm.).

Methods

Acoustic bat surveys were conducted in six habitat types on the Quabbin Reservation. Based on the extent of overstory forest canopy cover, habitats were classified as uncluttered or open-canopy (beaver meadows, open uplands, large ponds, reservoir) and cluttered or closed-canopy (vernal pool, stream) habitat classes (Table 1). All habitats, with the exception of open uplands, were associated with still or running water. Open uplands were either mowed fields or early-successional forest stands that had recently been harvested. Beaver meadows were old beaver ponds that had filled with sediment and were dominated by herbaceous or shrub vegetation. Large-pond and reservoir habitats were open, still-water areas. Beaver-meadow and large-pond sites have been classified and mapped as palustrine wetland systems with interspersed forest, scrub-shrub, and emergent wetlands classes and open water (Cowardin et al. 1979). Streams were small, perennial, 3rd- or 4th-order systems. Vernal pools were seasonal to semi-permanent forest pools that have been monitored for many years (Brooks 2004, Brooks and Hayashi 2002, Brooks et al. 1998). Four to eight sites per habitat type were surveyed for bats; all sites were located in the western Pelham and central Prescott Management Blocks of the watershed (Fig. 1). We did not survey upland, closed-canopy forests because bat flight activity has been repeatedly shown to be low in these habitats, despite their known use for day-roost sites.

Bats were actively surveyed using AnaBat (Titley Electronics, Ballina, Australia) detection systems. AnaBat systems consisted of AnaBat II detectors attached to AnaBat CF (Compact Flash) data storage modules. Bat echolocation calls were actively recorded to maximize quality and quantity of bat calls (Johnson et al. 2002, O'Farrell et al. 1999). Surveys were conducted over three evenings in mid-July, 2003 and 2004.

To maximize the effectiveness of using echolocation data, we standardized our surveys and call-sequence analysis wherever possible (Barclay 1999). We started surveys 15–30 minutes after sunset each evening, when appreciable bat activity usually begins. To minimize as much as possible temporal variation due to seasonal and other environmental factors, we surveyed each habitat-site for 20 minutes following the methods of Francl et al. (2004), Johnson et al. (2002), and Menzel et al. (2003), with three or four AnaBats being used simultaneously, allowing for 15 to 20 sites to be surveyed each evening. The sensitivity of the AnaBat detectors had been investigated prior to this work, and it was determined that a sensitivity setting of 6 was optimal, excluding the majority of insect sounds and capturing most bat calls. Nevertheless, it is recognized that variation in sensitivity exists among AnaBat units as well as among habitats and even among days depending on air temperature and humidity.

Table 1. Mean (and range) of bat survey habitats' characteristics, Quabbin Reservoir watershed, MA.

	Open-canopy habitats				Closed-canopy habitats	
	Beaver meadows	Open uplands	Large ponds	Reservoir	Vernal pools	Streams
Number of locations	6	8	4	5	6	8
Elevation (m)	231 (183–273)	251 (183–318)	265 (244–302)	160	235 (168–301)	175 (161–195)
Slope (%)	1.5 (0–6)	2.5 (0–6)	0	0	0	1.4 (0–6)
Distance (m) to:						
Reservoir	1146 (700–1850)	1381 (200–2550)	1281 (625–1725)	0	800 (250–1400)	413 (150–975)
Stream	0	284 (200–2550)	125 (0–500)	365 (175–850)	229 (25–725)	0
Permanent pond	1938 (550–4075)	2003 (575–4800)	0	3210 (450–6150)	1163 (525–3400)	2119 (525–4900)
Canopy cover (%)						
Overstory	0.2 (0–10)	0	0	0	54.5 (21–85)	96.7 (73–100)
Midstory	38.6 (0–70)	16.3 (5–70)	2.4 (5–15)	0	71.2 (0–90)	7.1 (0–75)
Understory	81 (10–100)	89.1 (10–100)	17.1 (10–25)	0	1.1 (0–10)	23.6 (5–75)

After completing a survey at a site, each observer moved on to another site. The sequence of site surveys was not random; sites were surveyed along logistically efficient routes that minimized travel time and maximized our ability to visit numerous survey sites each evening. Surveys were ended at approximately midnight when the first bout of bat activity appeared to abate (Milne et al. 2004). There were neither high winds nor rainfall that would affect bat flight activity during the survey periods. Observers positioned themselves at each site so that the field of view was unobstructed by vegetation and so that the detection area was maximized and nearby clutter minimized (Johnson et al. 2002). Air temperature, humidity, and wind speed were recorded each evening.

Recorded echolocation call sequences were filtered prior to analysis (Britzke and Murray 2000) and qualitatively identified to species using information from Analook 4.7j and Analyze 2.0 software and a dichotomous call key based on frequency, curvature, and slope parameters of the calls. The key was developed using recorded echolocation sequences from bats in West Virginia, South Carolina, and Georgia (M.A. Menzel, West Virginia University, Morgantown WV, unpubl. data; Johnson et al. 2002, Menzel et al. 2003, Owen et al. 2004), supplemented with known northeastern calls from the University of New Mexico library (http://talpa.unm.edu/batcall/index2_old.html) and those provided with AnaBat-Analook software (http://users.lmi.net/corben/). Murray et al. (2001) found that while bat species call characteristics can vary geographically, the variation was comparatively small and that the accurate identification of species was possible using known calls from a few locations. Call sequences with fewer than three individual call pulses were excluded (Johnson et al. 2002).

The numbers of search-phase and feeding-buzz call sequences per 20-minute survey were tallied by habitat. Call rates were compared between and within open- and closed-canopy habitat types using repeated measures, analysis of variance by ranks (Zar 1974). Pairwise comparisons of call rates were performed among open-canopy habitats using Bonferroni's procedure and two-sample t-tests performed for the two closed-canopy habitats. Pairwise comparisons were performed separately for 2003 and 2004, as repeated measures methods are not available for these procedures. We performed all statistical analyses using SYSTAT® v. 11.1 (SPSS Inc., Chicago, IL).

Results

Five species of bat were identified with an average of 23.9 search-phase and 4.4 feeding-buzz call sequences per 20-minute survey over both years and all habitats on the Quabbin watershed (Table 2). The little brown bat was the most frequently recorded species, with an average rate of 8.8 search-phase and 3.5 feeding-buzz call sequences per survey across all habitat-sites. Other species included *Lasiurus borealis* Müller (red bat), big brown bat,

Table 2. Average number of search phase and feeding buzz echolocation call sequences per 20-minute ultrasonic survey by species and habitat and analysis of variance results comparing call activity between open- and closed-habitat types, Quabbin Reservoir watershed, MA, 2003 and 2004. SC = search call; FB = feeding buzz.

		Open-canopy habitats					Closed-canopy habitats			Analysis of variance[1]	
Bat species	Call activity	Open uplands	Reservoir	Large pond	Beaver meadow	Mean	Vernal pool	Stream	Mean	F	p
Big brown bat	SC	9.7	4.6	9.6	4.0	6.5	0.1	2.0	1.1	8.4	0.092
	FB	0.6	0.1	0.9	0.8	0.6	0.0	0.1	0.1	5.6	0.168
Eastern red bat	SC	1.7	4.6	8.7	3.8	4.7	0.7	0.7	0.6	87.4	< 0.001
	FB	0.1	0.5	1.1	0.4	0.5	0.1	0.0	0.1	4.0	0.261
Hoary bat	SC	1.3	9.5	3.2	1.7	3.9	0.1	0.6	0.4	88.4	< 0.001
	FB	0.0	0.1	0.0	0.0	< 0.1	0.0	0.0	0.0	[2]	
All large-bodied bats	SC	12.7	18.9	21.0	9.4	15.5	0.6	3.3	2.0	29.2	0.012
	FB	0.7	0.7	2.0	1.3	1.2	0.1	0.1	0.1	17.2	0.033
Little brown bat	SC	0.5	5.0	19.2	13.3	9.5	13.5	1.0	7.3	< 1.0	> 0.500
	FB	0.3	0.7	7.1	6.6	3.7	5.8	0.1	3.0	1.3	> 0.500
Northern myotis	SC	0.4	0.0	0.2	0.0	0.2	0.8	0.5	0.7	11.6	0.057
	FB	0.1	0.0	0.0	0.0	< 0.1	0.1	0.1	0.1	10.0	0.075
Unidentified *Myotis*	SC	0.2	0.4	0.6	1.0	0.6	3.8	1.8	2.8	3.3	0.336
	FB	0.0	0.0	0.0	0.1	< 0.1	0.4	0.3	0.4	8.0	0.097
All *Myotis*	SC	1.0	5.4	19.9	14.3	10.2	18.0	3.3	10.7	< 1.0	> 0.500
	FB	0.3	0.7	7.1	6.7	3.7	6.3	0.5	3.4	< 1.0	> 0.500
All species	SC	15.9	29.4	46.8	24.8	29.2	19.0	7.7	13.4	10.1	0.073
	FB	1.0	1.4	9.1	7.9	4.9	6.3	0.6	3.5	5.3	0.177

[1]Repeated measures (years), analysis of ranks; comparison of closed-versus open-canopy habitat classes.
[2]No analysis performed, no observations in one habitat class.

and hoary bat, with call sequence numbers generally less than half of those of the little brown bats. Northern myotis were the least frequently recorded identified species. Call sequences that were clearly a *Myotis,* but unidentifiable as either a little brown bat or a northern myotis, were classified as unidentified *Myotis* calls (Table 2).

Bat flight activity was recorded at 33 of the 37 survey sites during the three successive survey nights in 2003. No bats were recorded at one beaver meadow site, two stream sites, and one vernal pool site. Activity was recorded at all 37 sites during the 2004 surveys. Average numbers of call sequences for all species were greatest at large pond habitats, with an average of 46.8 search-phase and 9.1 feeding-buzz call sequences per 20-minute survey (Table 2). Numbers of search-phase call sequences were high at all other still-water sites as well (> 25 per survey); feeding-buzz sequences were low at reservoir sites (1.4 per survey). The average numbers of both search-phase and feeding-buzz sequences were much lower at upland open-area sites (15.9 and 1.0 per survey respectively) and least at stream sites (7.7 and 0.6 per survey).

Over both years, all five species were recorded at least once in all habitats, but activity levels of species groups (i.e., large-bodied vs. small-bodied bats, *Myotis* species) and individual species differed between open- and closed-canopy habitats. Search-phase call sequences of the large-bodied species were recorded significantly more often at open-canopy habitats, primarily because of significantly ($p < 0.001$) higher numbers of call sequences of red bats and hoary bats at these habitats (Table 2). Big brown bats were also recorded significantly more often in open-canopy habitats, but the differences between habitat classes was less than for the *Lasiurus* species. The smaller-bodied little brown bat was ubiquitous, occurring commonly in all habitats (Table 2). The northern myotis was recorded significantly more often in closed-canopy vernal pool and stream habitats than in open-canopy habitats ($p = 0.057$).

No significant species-specific differences in search-phase or feeding-buzz call sequences were found among open-canopy or between closed-canopy habitat types within habitat classes except for little brown bat search-phase sequences in open habitats and feeding-buzz sequences in closed habitats. The numbers of search-phase sequences for the species were less in open uplands than in other open-canopy habitats; the numbers of feeding-buzz sequences over vernal pools were significantly greater than over streams ($p = 0.015$).

Discussion

The AnaBat II bat detection system has been criticized as being less sensitive or reliable than detector systems using time-expansion technology (Fenton 2000), or as inappropriate technology for the definitive study of habitat preference by bats (Miller et al. 2003). However, ultrasonic detectors have been successfully used and recommended for assessing foraging and flight activity patterns and for indexing habitat use (Duffy et al. 2000; Gerht and Chelsvig 2003, 2004; Kunz and Brock 1975). Although the use of bat detectors in general and the AnaBat system specifically may be less than an ideal research methodology for some aspects of bat biology (Barclay 1999), the system can accurately characterize the composition of bat faunas among various habitats (Duffy et al. 2000, Kunz and Brock 1975, Menzel et al. 2005, O'Farrell and Gannon 1999, O'Farrell et al. 1999).

The bat fauna of the Quabbin Reservation in central Massachusetts was similar in composition to that reported elsewhere in New England, but relative levels of flight activity were much greater. Krusic and Neefus (1996) and Krusic et al. (1996) reported five species and a combined *Myotis* species group from AnaBat acoustic surveys of forest interior and edges sites on the White Mountain National Forest (WMNF), NH. Two species, silver-haired bats and *Pipistrellus subflavus* F. Cuvier (eastern pipistrelles), were recorded at the WMNF, but not in the Quabbin surveys. Zimmerman and Glanz (2000) conducted a survey of bats in and near Acadia National Park (ANP), ME, that included active-sampling acoustic surveys with AnaBat detectors. Species were not identified in their published call survey data, but from concurrent mist-net surveys, and were principally little brown bats and northern myotis. They also captured one eastern small-footed bat, another species not recorded in the Quabbin surveys, but they did not capture red bats at ANP, recorded at the Quabbin.

Of the species documented from the WMNF or ANP, and not recorded in this study, Brooks (unpubl. data) subsequently recorded eastern pipistrelles at large pond, reservoir, and clear-cut habitats in a separate study of temporal patterns of bat activity on the Quabbin Reservation. The silver-haired bat may have been present during the Quabbin surveys, although southern New England is probably at the extreme southern periphery of its summer distribution (Whitaker and Hamilton 1998). The eastern small-footed bat is generally uncommon throughout its distribution and is listed as a species of special concern in Massachusetts. Based on limited, often anecdotal information, the species is associated with emergent rock, cliffline, and karst formations (Best and Jennings 1997, DeGraaf and Yamasaki 2001). Given the known occurrence and distributions of silver-haired and small-footed bats in New England (DeGraaf and Yamasaki 2001), there is reason to believe that they may occur on the Reservation even though they were not recorded in these surveys.

All WMNF species/species groups were recorded at all of their surveyed habitats, including forest-interior sites, although at significantly different levels of flight activity (Krusic and Neefus 1996). Overall, *Myotis* species were most common on the WMNF, as was observed on the Quabbin watershed (Table 2). However, average flight activity for *Myotis* species on the WMNF was approximately 22 search-phase calls per detector per full night at the more productive forest edge sites, while on the Quabbin, an average of 10.4 *Myotis* search-phase call sequences were recorded in 20-minute surveys across all habitats, and nearly 20 sequences were recorded per 20 minutes at the most productive large-pond habitats (Table 2). Overall levels of flight activity for the large-bodied big brown, red, and hoary bats were similarly greater on the Quabbin than at the WMNF. Some of these differences in activity levels between the two areas are likely due to the use of active acoustic sampling in this study, whereas Krusic and Neefus (1996) used passive sampling from a fixed position (e.g., Johnson et al. 2002). However, not all differences in activity levels can be attributed to differing survey methodologies.

We submit that the greater numbers of recorded bat call sequences on the Quabbin Reservation are due to differences in the extent and richness of aquatic habitats compared to the WMNF (Bat Conservation International 2001). Krusic and Neefus (1996) and Krusic et al. (1996) did not describe land cover composition of the WMNF, but the area's mountainous terrain presumably contains proportionally fewer still-water habitats. Still-water habitats are abundant on the Quabbin Reservation with its relatively gentle terrain and historically abundant beaver populations (P. Lyons, MDCR, pers. comm.).

Unlike the WMNF, wetland occurrence on the Quabbin Reservation is more similar to the ANP, where wetlands constitute 20% of the park area and ponds and streams are numerous (Zimmerman and Glanz 2000). Bat flight activity in ANP was greatest at lake and pond habitats, with mean numbers of approximately 30 search-phase call passes per 15-minute survey at each habitat, and with considerably less flight activity at streams (12 passes/survey) and wetlands (7 passes/survey) (Zimmerman and Glanz 2000). Bat activity at ANP lakes was similar to the Quabbin survey results, where an average of 29.4 call sequences were recorded per 20-minute survey (Table 2). The Quabbin pond results, with an average of 46.8 sequences per survey, were considerably greater than for ANP ponds. Bat flight activity at Quabbin streams was less than at ANP streams, but activity was three times greater at Quabbin beaver meadow (i.e., wetland) habitats than at ANP wetlands. Still, without direct structural and compositional comparisons between "similar" habitats on the Quabbin and ANP, it would be speculative to further analyze the differences in levels of bat activity between the two areas.

The location of the Quabbin Reservation, considerably south of either the WMNF or ANP, is another consideration in assessing the differences in bat activity levels between the studies. The difference in latitude results in a longer warm season with higher average summer temperatures. Thirty-year average July temperatures in central Massachusetts (21.8 °C) are greater than in the White Mountains of New Hampshire (20.5 °C) or coastal Maine

(20.3 °C) (Climatological Data, National Climatic Data Center, Asheville, NC). For thermoregulatory reasons, nightly bat activity is highly correlated with ambient temperatures (Hayes 1997, O'Donnell 2000, Vaughn et al 1997). Cooler average temperatures in northern New England should result, in general, in less bat activity. Warmer minimum summer temperatures in southern New England could also result in a greater diversity and abundance of insect prey and, consequently, in greater bat populations and flight activity (O'Donnell 2000, Willig and Selcer 1989).

The results of this study generally agree with theories on the effects of species morphology on the structure of foraging bat communities and habitat use (Fenton 1990, Menzel et al. 2005, Norberg and Rayner 1987, Saunders and Barclay 1992). Flight activity levels of large-bodied bat species, with faster but less maneuverable flight (e.g., big brown, red, and hoary bats), was significantly less in closed-canopy, cluttered habitats (e.g., streams, vernal pools), compared to less-cluttered, open-canopy habitats ($p = 0.012$; Table 2). Overall, there was no significant difference in call sequence numbers between open- and closed-canopy habitat classes for the smaller bodied, more maneuverable *Myotis* species. Little brown bats were equally prevalent at open-canopy, large pond, and beaver meadow habitats as they were at closed-canopy vernal pools. However, northern myotis were recorded significantly more at closed-canopy vernal pools and streams, and more of the unidentified *Myotis* call sequences were recorded at these habitats as well (Table 2). This pattern of habitat use by the northern myotis corresponds to findings that the species readily uses cluttered habitats for foraging and roost-tree selection (Owen et al. 2002, 2004). The preference for vernal pool habitats was also observed by Owen et al. (2002), who recorded the majority of northern myotis specimens at ephemeral pools in West Virginia, and by Huie (2002) in Kentucky, where the northern myotis was the most abundant species at constructed woodland ponds located within the large, forested landscapes.

Large numbers of unidentified *Myotis* species (Table 2) were recorded on the Quabbin Reservation. Many (57%) of these call sequences had characteristics (i.e., minimum call slopes between 110 and 200) that would be indicative of the endangered Indiana bat in survey locations where they have been positively documented by both mist-net and acoustical surveys (Britzke et al. 2002; Murray et al. 1999; M.A. Menzel,pers. comm.). These calls were most common at vernal pool sites, but were also recorded at all other habitats. There are five listed observations of Indiana bats in Massachusetts, most recently in Hampshire County in 1976 and in the 1930s in Berkshire and Worcester Counties (http://www.state.ma.us/dfwele/dfw/nhesp/nhspeices/htm). In the Northeast, Indiana bats are known from hibernacula in West Virginia, Pennsylvania, Vermont, New Jersey, and New York (US Fish and Wildlife Service 1999). Our study area in central Massachusetts is located within migration radii for the species (i.e., 410–532 km [Kurta and Murray 2002]) using known hibernacula in eastern New York and Vermont. Based on the habitat modeling of Gardner and Cook (2002) and the warmer summer temperatures for the study site relative to the environments surrounding known hibernacula in the Northeast, the possible presence of Indiana bats throughout portions of southern New England, such as on the Quabbin, seems a reasonable expectation. Definitive proof of the presence of the Indiana bat requires mist-netting and in-hand collection (Britzke et al. 2002).

Given the success of this preliminary survey, we believe additional bat research in central Massachusetts is warranted. Continued and more extensive acoustic surveys, in both time and space, are needed to affirm these findings and to determine if and where additional species occur on the Quabbin Reservation. Expanded research to more closely examine the influence of timber harvesting on foraging and day-roosting ecology should be a priority on the Quabbin (Campbell et al. 1996; Grindal and Brigham 1999; Owen et al. 2002, 2004; Tibbels and Kurta 2003; Waldien and Hayes 2001). The Quabbin is a working forest in a landscape protected from development, with an abundance of water-associated habitats and diverse forest conditions. These conditions would appear to support an abundant and rich bat community (Fenton 1997), which provides a unique opportunity for a broad and rigorous program of research on habitat use by forest bat species in southern New England forests.

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Literature Cited

Aldridge, H.D.N., and I.L. Rautenbach. 1987. Morphology, echolocation, and resource partitioning in insectivorous bats. Journal of Animal Ecology 56:763–778.

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

Barclay, R.M.R. 1999. Bats are not birds: A cautionary note on using echolocation calls to identify bats: A comment. Journal of Mammalogy 80:290–296.

Bat Conservation International, Inc. 2001. Bats in Eastern Woodlands. Austin, TX. 310 pp.

Best, T.L., and J.B. Jennings. 1997. *Myotis leibii*. Mammalian Species no. 547, American Society of Mammalogists, Lawrence, KS.

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

Britzke, E.R., K.L. Murray, J.S. Heywood, and L.W. Robbins. 2002. Acoustic identification. Pp. 221–225, *In* A. Kurta, and J. Kennedy (Eds.). The Indiana Bat: Biology and Management of an Endangered Species. Bat Conservation International, Austin, TX. 253 pp.

Broders, H.G., G.M. Quinn, and G.J. Forbes. 2003. Species status, and the spatial and temporal patterns of activity of bats in southwest Nova Scotia, Canada. Northeastern Naturalist 10:383–398.

Broders, H.G., C.S. Findlay, and L. Zheng. 2004. Effects of clutter on echolocation call structure of *Myotis septentrionalis* and *M. lucifugus*. Journal of Mammalogy 85:273–281.

Brooks, R.T. 2004. Weather-related effects on woodland vernal pool hydrology and hydroperiod. Wetlands 24:104–114.

Brooks, R.T., and M. Hayashi. 2002. Depth-area-volume and hydroperiod relationships of ephemeral (vernal) forest pools in southern New England. Wetlands 22:247–255.

Brooks, R.T., D.B. Kittredge, and C.L. Alerich. 1993. Forest Resources of Southern New England. Resource Bulletin NE-127. USDA Forest Service, Northeastern Forest Experiment Station, Radnor, PA. 71 pp.

Brooks, R.T., J. Stone, and P. Lyons. 1998. An inventory of seasonal forest ponds on the Quabbin Reservoir watershed, Massachusetts. Northeastern Naturalist 5:219–230.

Campbell, L.A., J.G. Hallett, and M.A. O'Connell. 1996. Conservation of bats in managed forests: Use of roosts by *Lasionycteris noctivagans*. Journal of Mammalolgy 77:976–984.

Cowardin, L.M., V. Carter, F.C. Golet, and E.T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. US Department of the Interior, US Fish and Wildlife Service, Office of Biological Services, Biological Services Program, Washington, DC. FWS/OBS-79/31. 103 pp.

DeGraaf, R.M., and M. Yamasaki. 2001. New England Wildlife: Habitat, Natural History, and Distribution. University Press of New England, Hanover, NH. 482 pp.

Duffy, A.M., L.F. Lumsden, C.R. Caddle, R.R. Chick, and G.R. Newell. 2000. The efficacy of AnaBat ultrasonic detectors and harp traps for surveying microchiropterans in south-eastern Australia. Acta Chiropterologica 2:127–144.

Fenton, M.B. 1990. The foraging behaviour and ecology of animal-eating bats. Canadian Journal of Zoology 68:411–422.

Fenton, M.B. 1997. Science and the conservation of bats. Journal of Mammalogy 78:1–14.

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

Ford, W.M., M.A. Menzel, J.M. Menzel, and J.L. Rodrigue. 2003. Hearing bat habitat: AnaBat surveys on the Fernow Experimental Forest. Abstracts of the 13th Annual Colloquium of Conservation of Mammals in the Southeast. 13:15–16.

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

Gardner, J.E., and E.A. Cook. 2002. Seasonal and geographic distribution and quantification of potential summer habitat. Pp. 9–20, *In* A. Kurta, and J. Kennedy (Eds.). The Indiana Bat: Biology and Management of an Endangered Species. Bat Conservation International, Austin, TX.

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

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

Grindal, S.D., and R.M. Brigham. 1999. Impacts of forest harvesting on habitat use by foraging insectivorous bats at different scales. Ecosciences 6:25–34.

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

Hayes, J.P. 1997. Temporal variation in activity of bats and the design of echolocation-monitoring studies. Journal of Mammalogy 78:514–524.

Huie, K.M. 2002. Use of constructed woodland ponds by bats in the Daniel Boone National Forest. M.Sc. Thesis. Eastern Kentucky University, Moorhead, KY. 69 pp.

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

King, M.A. 1993. A field identification key to New England's present-day bats. Maine Naturalist 1:33–34.

Krusic, R.A., and C.D. Neefus. 1996. Habitat associations of bat species in the White Mountain National Forest. Pp. 185–198, *In* R.M.R. Barclay, and R.M. Brigham (Eds.). Bats and Forests Symposium. Ministry of Forests Research Branch, Victoria, BC, Canada. 292 pp.

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

Kunz, T.H., and C.E. Brock. 1975. A comparison of mist nets and ultrasonic detectors for monitoring flight activity of bats. Journal of Mammalogy 56:907–911.

Kurta, A., and S.W. Murray. 2002. Philopatry and migration of banded Indiana bats (*Myotis sodalis*) and effects of radio transmitters. Journal of Mammalogy 83:585–589.

McNab, W.H., and P.E. Avers. 1994. Ecological subregions of the United States: Section descriptions. USDA Forest Service, Ecosystem Management, Washington, DC. Administrative Publication WO-WSA-5.

Menzel, M.A. 2003. An examination of factors influencing the spatial distribution of foraging bats in pine stands in the southeastern United States. Ph.D. Dissertation. West Virginia University, Morgantown, WV.

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. Georgia Journal of Science 58:212–216.

Menzel, M.A., J.M. Menzel, J.C. Kilgo, W.M. Ford, T.C. Carter, and J.W. Edwards. 2003. Bats of the Savannah River Site and vicinity. USDA Forest Service, Southern Research Station, Asheville, NC. General Technical Report GTR-SRS-68.

Menzel, J.M., M.A. Menzel, J.C. Kilgo, W.M. Ford, J.W. Edwards, and G.F. McCracken. 2005. Effects 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., M.A. Menzel, W.M. Ford, J.W. Edwards, and J.C. Kilgo. In press. A comparison of bat activity levels in and surrounding Carolina Bays prior to and after bay restoration. Wetlands.

Miller, D.A., E.B. Arnett, and M.J. Lacki. 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., M. Armstrong, A. Fisher, T. Flores, and C.R. Pavey. 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., E.R. Britzke, B.M. Hadley, and L.W. Robbins. 1999. Surveying bat communities: A comparison between mist nets and the AnaBat II bat detector system. Acta Chiropterologica 1:105–112.

Murray, K.L., E.R. Britzke, and L.W. Robbins. 2001. Variation in search-phase calls of bats. Journal of Mammalogy 82:728–737.

Norberg, U.M., and J.M.V. Rayner. 1987. Ecological morphology and flight in bats: Wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London Series B Biological Sciences 316:335–427.

Nowak, R.M. 1994. Walker's Bats of the World. John Hopkins University Press, Baltimore, MD. 287 pp.

O'Connor, R., T. Kyker-Snowman, P. Lyons, and B. Spencer. 1995. Quabbin watershed: MDC land management plan 1995–2004. Commonwealth of Massachusetts, Metropolitan District Commission, Boston, MA.

O'Donnell, C.F.J. 2000. Influence of season, habitat, temperature, and invertebrate availability on nocturnal activity of the New Zealand long-tailed bat (*Chalinolobus tuberculatus*). New Zealand Journal of Zoology 27:207–221.

O'Farrell, M.J., and W.L. Gannon. 1999. A comparison of acoustic versus capture techniques for the inventory of bats. Journal of Mammalogy 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. Journal of Mammalogy 80:11–23.

Owen, S.F., M.A. Menzel, W.M. Ford, J.W. Edwards, B.R. Chapman, K.V. Miller, and P.B. Wood. 2002. Roost tree selection by maternal colonies of northern long-eared myotis in an intensively managed forest. USDA Forest Service, Northeastern Research Station, General Technical Report NE-292. 6 pp.

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

Saunders, M.B., and R.M.R. Barclay. 1992. Ecomorphology of insectivorous bats: A test of predictions using two morphologically similar species. Ecology 73:1335–1345.

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

US Fish and Wildlife Service. 1999. Agency draft Indiana Bat (*Myotis sodalis*) revised recovery plan. Region 3, Fort Snelling, MN. 53 pp.

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

Waldien, D.L., and J. P. Hayes. 2001. Activity areas of female long-eared myotis in coniferous forests in western Oregon. Northwest Science 75:307–314.

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

Willig, M.R., and K.W. Selcer. 1989. Bat species density gradients in the New World: A statistical assessment. Journal of Biogeography 16:189–195.

Zar, J.H. 1974. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, NJ. 620 pp.

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