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ORIGINAL PAPER

Habitat-associated and temporal patterns of bat activity in a diverse forest landscape of southern New England, USA

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Abstract The development and use of acoustic recording technology, surveys have revealed the composition, relative levels of activity, and preliminary habitat use of bat communities of various forest locations. However, detailed examinations of acoustic surveys results to investigate temporal patterns of bat activity are rare. Initial active acoustic surveys of bat activity on the Quabbin Reservoir watershed in central Massachusetts recorded high numbers of call sequences by five bat species. The results showed the importance of aquatic and open habitats for bats in this diverse forest landscape. Because the preliminary surveys were restricted in extent (habitats), number (replicates), and duration (active surveys only, limited number of repeated surveys), the authors strongly recommended more comprehensive and extensive surveys of bat activity on the area. This paper reports the results of active (manual) and passive (automated) acoustic bat activity surveys in three replicates of ten habitats, conducted three to four times per year over the course of the study between 2004 and 2006. Over the full study, 2,800 actively-recorded 37,632 passively-recorded call sequences were examined and identified to species when possible. General patterns in activity did not differ by habitat between the two survey methods. Call sequences were recorded more often in open, especially aquatic habitats than in cluttered habitats. The use of passive surveys allowed for the assessment of temporal patterns of activity and an analysis of the relationship between ambient temperature and activity.

Keywords Acoustic survey · AnaBat · Aquatic habitats · Bat survey · Forest management · Linear habitats · Timber harvest

Introduction

A preliminary acoustic survey of bat flight activity identified the Quabbin Reservoir watershed of northeastern United States as an excellent site for continued bat research due to the

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abundance and diversity of the bat community (Brooks and Ford 2005). This preliminary, 2-year effort, using active surveys in a limited number of habitats, identified flight activity levels of five bat species, with much greater levels of activity in open, uncluttered habitats, especially over large ponds. The paper concluded with the recommendation for continued and more extensive bat activity surveys.

Bat research in the northeastern United States and adjacent Canada has grown over the recent past, but much of the work has focused on either the federally-listed Indiana bat (*Myotis sodalis* Miller and G. M. Allen) or on the potential impacts of wind power development (Brooks and Ford 2006). The most recently published bat community research from the northeast re-emphasized the importance of aquatic habitats as reported in earlier bat research from the region (Krusic et al. 1996; Zimmerman and Glanz 2000; Broders et al. 2006). While it is clearly recognized that bats are an important component of the natural world, specific questions about the composition and relative levels of activity by the bat community in forest habitats remain unaddressed due to the relative paucity of bat research (Parsons et al. 2007). This basic information about bat ecology needs to be available before questions about the effects of forest management, land use change, or other environmental disturbances on bats can be addressed.

The aim of this paper is to summarize the results of 3 years (2004–2006) of active (time-constrained, hand-held operation (manual), searching) and passive (open-ended (sunset to sunrise), programmed operation (automated), stationary placement) acoustic surveys (Parsons et al. 2007) conducted at three sites in each of 10 habitats on the Quabbin, including partially and clearcut forest and woods roads, habitats which were not included in the preliminary surveys (Brooks and Ford 2005). Surveys across the complex landscape of the Quabbin forest, with its various types of aquatic habitats, permanent forest openings, maintained and gated roads, and long timbering history, allows for the examination of specific habitat-related questions about bat activity such as the impacts of timber harvesting, the use of linear habitats, and the importance of embedded aquatic habitats (species conservation surveys; Parsons et al. 2007). The use of passive surveys allows for the exploration of temporal patterns of nightly activity. During the second half of 2005 and all of 2006, temperature and relative humidity were recorded continuously during the passive acoustic surveys, allowing for the examination of the influence of these weather factors on bat activity. Lastly the results from active and passive surveys that are concurrent in time and space are compared.

Methods

Study area and sites

The study was completed on the Prescott peninsula, a Management Block on the watershed of the Quabbin Reservoir (Fig. 1). Access to the peninsula is restricted, allowing for the use of remotely-activated equipment with reduced concern for theft or disturbance. The 48,500 ha Quabbin Reservoir watershed, surrounding the 9,700 ha Reservoir, is mostly a working forest (Massachusetts Department of Conservation and Recreation (MA DCR) 2007). The centrally located Prescott peninsula is predominantly forested, but with significant areas of stream, wetland, and pond habitats, forest roads, and maintained open fields. The forests are actively managed, principally by uneven-aged single-tree and group selection, but with larger openings where plantations of red pine (*Pinus resinosa* Ait.) or Norway spruce (*Picea abies* (L.) Karst) have been harvested to restore native tree species.

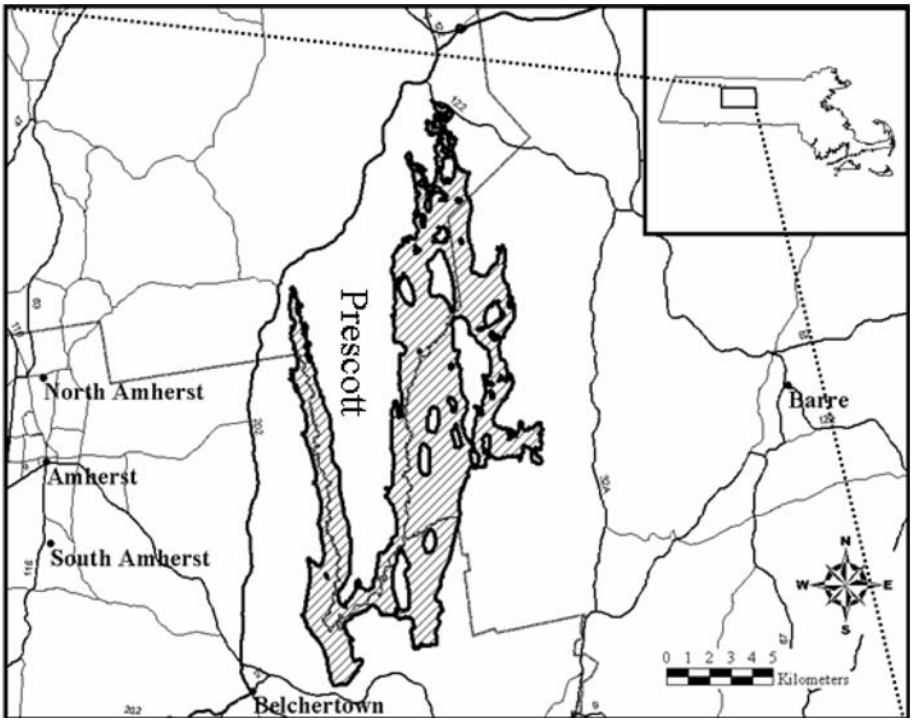

Fig. 1 Location of the Prescott Management Block on the Quabbin Reservoir watershed in central Massachetts

Bats activity was surveyed at three replicate sites (Sherwin et al. 2000) in each of 10 major habitats or habitat features of the study area, representing the major components of this predominantly forested watershed (Table 1). Habitat clutter has been shown to be an important factor affecting habitat selection and foraging behavior by bat species (Brigham et al. 1997; Sleep and Brigham 2003). In this study, clutter effects were addressed by surveying open-canopy sites, including both terrestrial (open fields and clear cuts) and aquatic habitats (beaver meadows, ponds, and reservoir) and closed-canopy sites (partial and uncut forests, woods roads, streams, and seasonal forest pools). One major habitat that was not surveyed was the air space above forest canopies (Menzel et al. 2000, 2005b). Individual survey sites were subjectively chosen to best represent the desired habitat.

Methods

Bat activity was surveyed acoustically, using AnaBat II detectors, connected to AnaBat CF Storage ZCAIMs (http://www.titley.com.au/products.htm), a remote bat detector record system (Parsons et al. 2007). Multiple active and passive surveys were conducted annually between 2004 and 2006 (Table 2). Passive surveys, which occurred over an entire evening, allowed for the assessment of temporal patterns in activity (Gannon et al. 2003; Parsons et al. 2007).

Three active acoustic survey rounds were conducted in 2004 and 2005 and two in 2006 in each of the three replicate sites of the ten habitats (Table 2). Active surveys were conducted by three people and scheduled to occur over two nights. Equipment malfunctions or

Table 1 Descriptions of habitat types or habitat features, Prescott peninsula, Quabbin Reservation, Massachusetts

Habitat type or feature	Habitat class	Description
Beaver meadow	Open	Abandoned beaver ponds, succeeded to herbaceous vegetation with scattered trees, little open water
Clear cut forest	Open	No or scattered mature trees, sapling-sized regeneration
Large ponds	Open	Open water; ~0.5, 2, and 9 ha
Open field	Open	Herbaceous vegetation, maintained by periodic mowing
Reservoir	Open	Open water
Control forest	Closed	Closed canopy, mature forest
Partial cut forest	Closed	Single-tree and group selection timber harvests
Stream	Closed	Closed canopy, perennial, 2nd-order
Vernal pool	Closed	Seasonal forest pools, mixed open water and shrubs; open forest canopy over center of pool
Woods road	Closed	Closed canopy, low use, low maintenance

Table 2 Inclusive dates of bat activity surveys by survey type, round, and year, Quabbin Reservoir watershed, Massachusetts

	2004	2005	2006
Passive surveys			
Round 1	12 May–21 Jun	28 Apr–13 May	18 Apr–14 Jun
Round 2	23 Jun–23 Jul	31 May–13 Jul	13 Jun–12 Jul
Round 3	3 Aug–11 Sep	21 Jul–8 Aug	13 Jul–3 Aug
Round 4	12 Sep–5 Oct	8 Aug–9 Sep	2 Aug–1 Sep
Active surveys			
Round 1	7–8 Jun	20–21 Jun	5–6 Jul
Round 2	25–26 Jul (4 Aug)	19–20 Jul	14–15 Aug
Round 3	23–24 Aug (26 Aug)	22–23 Aug	

other problems required resurveys of selected sites, especially the first year (2004), extending a survey beyond the two-night objective (Table 2). Survey sites were scheduled on a planned route to maximize efficiency. Surveys commenced when the first bat was observed or no later than sunset. Individual active site surveys were 20 min in length, whereupon an individual would travel to their next site for the 20-min survey. This continued for five active surveys per individual per night. All five surveys typically occurred within a 3-h period. During an active survey, an individual would hold the equipment and scan back and forth. If a bat was detected, the individual would attempt to follow its flight with equipment to obtain the maximum length call sequence.

Four passive acoustic survey rounds were conducted in all three replicates of the ten habitats in each of the 3 years (Table 2). Passive surveys were conducted by enclosing the AnaBat equipment in a small plastic container and suspending the container from a tripod, approximately 1.5 m from the ground and oriented at 45° towards the center of the site (Weller and Zabel 2002). A small diameter hole was cut in the container and the detector receiver extended slightly from the hole. The container was enclosed in a plastic shopping bag to protect it from dew or unexpected precipitation. AnaBats were programmed to record throughout the night (Hayes 2000), beginning at 0.5-h prior to sunset and recording until 0.5-h after sunrise the next day. The schedule of surveys was randomized by sites and habitats; one site from each habitat was surveyed before a survey of a second site was scheduled. Nightly passive surveys were completed if the forecast was for $\leq$30% chance of precipitation. Surveys were run continuously until all 30 sites were completed.

Starting in mid-2005, an iButton Hygrochron® (Dallas Semiconductor) was attached to the AnaBat installations of each passive survey. The iButtons were programmed to record ambient temperature and relative humidity every 15 min during the survey period.

Analysis

All recorded bat call sequences were individually examined using the program Analook 4.7j and Analzye 2.0 (http://www.titley.com.au/anabatsoftware.htm). Call sequences with three or more high quality cull pulses were classified to species (or occasionally genus (*Myotis*), if insufficient information were available for species identification) using a dichotomous key based on call frequency, curvature, and slope parameters (Brooks and Ford 2005; Menzel et al. 2005a; Ford et al. 2006). Classified calls sequences were recorded by date and time, site, and taxa. No identification was made for call sequences with less than three call pulses or call pulses of low quality.

Passive survey results were standardized by effort (hours of nightly survey), as the duration of surveys changed with time, and reported as call sequences per hour of survey. Assessments of the effects of habitats on bat activity levels were made using a repeated measures analysis of variance. Survey data were averaged over rounds within years to reduce the number of repeated measures. Analyses of active survey data for individual species or species groups (large-bodied bat and *Myotis* species) were made using ranked data because of large numbers of zero values. The separate analyses of large-bodied and *Myotis* species is based on the general identification of the groups as clutter-intolerant and clutter-tolerant, respectively, (Norberg and Rayner 1987; Sleep and Brigham 2003). The groups are morphologically distinct, with clutter tolerant species generally smaller, with lower wing loadings and aspect ratios making them capable of slower flight speed and able to make faster turns (Sleep and Brigham 2003).

Both seasonal and daily patterns in bat activity were assessed. Since activity surveys were not conducted during the same time periods in each of the 3 years, individual surveys were combined into sequential, but overlapping, 'sessions'. Passive surveys were combined into three sessions, roughly equivalent to late-spring (prior to June 15), early summer (June 15–August 15), and late summer (after August 15) and active surveys to three rounds of June, July, and August (Table 2). Passive survey results were summarized by hour following sunset for the assessment of hourly activity patterns. Average hourly ambient air temperatures were summarized for the 2006 passive survey periods to assess the relationship between air temperature and activity.

Chi-square was used to analyze categorical distributions (e.g., hour after sunset).

Results

Over all active surveys, 2800 call sequences were recorded and examined for identification to species. Big brown (*Eptesicus fuscus* Palisot de Beauvois) and little brown bat (*M. lucifugus* Le Conte) call sequences dominated the data, with one red bat sequence (*Lasiurus borealis* Muller), 87 hoary bat sequences (*L. cinereus* Palisot de Beauvois), and 13 eastern pipistrelle sequences (*Pipistrellus subflavus* F. Cuvier). Call sequences for red and hoary bats were combined with those of big brown bats in statistical analyses of large-bodied bat activity; call sequences for eastern pipistrelles were not statistically analyzed. Call sequence records for long-eared bats (*M. septentrionalis* Troussart) were infrequent (40) but the data were analyzed because of a special interest in the species. All six identified species were recorded only at the open field sites in the active surveys (Table 3a). Other sequences included those I was unable to identify because of too few individual calls or calls of poor quality and sequences that with no structured calls (noise). Across all surveys and habitats, an average of 8.7 call sequences was recorded per 20-min survey (Table 3a).

Over the study, 37,632 call sequences were recorded during passive surveys. As with the active surveys, call sequences of big brown and little brown bats predominated. An additional 33 red bat sequences and 335 hoary bat sequences were recorded but analyzed collectively with big brown bat sequences as large-bodied bat sequences. Eastern pipistrelles were recorded 57 times over the 3 years; no analyses were conducted on this data. In the passive surveys, all six identified species were recorded at the clearcut, large pond, open field, and reservoir sites (Table 3b). Even more than with active survey recordings, a large number of sequences could not be identified as there were too few individual calls or calls were of poor quality. There were also a number of sequences that were composed of static (noise), especially at open field sites. Over the 3 years of the study, an average of 5.6 call sequences per hour was recorded for all species and habitats (Table 3b).

Habitat-related patterns

Activity patterns by habitat class and species groups generally agreed between active and passive survey methods (Table 3). Differences in results were observed between the two survey methods with finer-scale analyses of individual species or habitats. Differences were also observed in statistical analyses of the two survey methods, with stronger associations (smaller P values) occurring with passive survey data. Unless otherwise noted, the following results are valid for both survey methods.

Open versus cluttered habitat classes

The activity levels of all bats differed significantly between habitat classes (Table 4). Calls of all species were recorded more frequently in open habitats than in cluttered habitats in both active (10.8 vs. 6.5 sequences/20 min, respectively; Table 3a) and passive surveys (7.7 vs. 3.5 sequences/h; Table 3b). This effect was significant for both survey methods ($F_{df=1,20} = 3.652$, $P = 0.07$, $F_{df=1,20} = 6.94$, $P = 0.016$, respectively; Table 4). *Myotis* species were recorded more frequently than large-bodied bats in both habitat classes, but the difference was greater in cluttered than in open habitats (Table 3). A significant effect of habitat clutter was observed for large-bodied bats but not for *Myotis* species (Table 4). The little-brown bat was the single most frequently recorded species overall and in both habitat classes, but only marginally greater than big brown bats in open habitats. Red and hoary bats, the only other identified large-bodied bat species were recorded exclusively in open habitats with the exception of a single passively recorded sequence along woods roads (Table 3b). Long-eared bats were recorded less frequently than either dominant species with the exception of closed-canopy control forest and woods road sites, where they were more common than big brown bats in active surveys (Table 3a). Eastern pipistrelles were only recorded at open habitats and were most common at the large pond habitats.

Table 3 Mean number of (a) actively-recorded bat call sequences per 20-min session and (b) passively-recorded sequences per hour by species and species group and habitat, Quabbin Reservoir watershed, Massachusetts, 2004–2006

Habitat/Habitat class	Big brown bat	Red bat	Hoary bat	All large bodied bats	Little brown bat	Long-eared bat	All Myotis species	Eastern pipistrelle	All bat species
(a) Actively-recorded sequences per 20 min									
Beaver meadow	0.7	0.0	0.4	1.2	2.2	0.0	3.1	0.0	4.3
Clearcut forest	2.9	0.0	0.2	3.0	1.3	0.1	3.2	0.0	6.2
Large pond	3.5	0.0	2.5	4.9	7.4	0.2	10.7	0.4	15.9
Open field	7.1	0.1	0.9	8.0	2.5	<0.1	3.2	0.1	11.3
Reservoir	5.6	0.0	1.1	6.5	7.4	0.0	9.6	0.0	16.1
All open habitats	4.0	<0.1	1.1	4.7	4.1	0.1	6.0	<0.1	10.8
Control forest	0.0	0.0	0.0	0.0	0.4	0.1	1.4	0.0	1.3
Partial cut forest	1.3	0.0	0.0	1.3	0.9	0.1	1.8	0.0	3.1
Stream	3.4	0.0	0.0	3.4	2.7	0.4	8.4	0.0	11.8
Vernal pool	4.0	0.0	0.0	4.0	4.4	0.5	8.7	0.0	10.3
Woods road	0.2	0.0	0.0	0.2	2.5	0.3	6.1	0.0	6.3
All cluttered habitats	1.8	0.0	0.0	1.8	2.2	0.3	5.3	0.0	6.5
All habitats	2.9	<0.1	0.5	3.3	3.2	0.2	5.6	<0.1	8.7
(b) Passively-recorded sequences per hour									
Beaver meadow	0.9	0.0	0.03	0.9	0.6	0.2	1.8	0.0	2.7
Clearcut forest	0.9	<0.01	0.02	0.9	0.5	0.1	0.9	<0.01	1.8
Large pond	2.8	0.01	0.32	3.1	6.9	0.9	13.1	0.03	16.3
Open field	3.3	0.02	0.11	3.5	2.5	0.2	4.9	0.01	8.4
Reservoir	2.0	0.04	0.28	2.3	3.0	0.4	6.6	0.12	9.0
All open habitats	2.0	0.02	0.15	2.2	2.7	0.3	5.5	0.03	7.7
Control forest	<0.1	0.0	0.0	<0.1	0.5	0.03	1.2	0.0	1.2
Partial cut forest	0.3	0.0	0.0	0.3	0.9	0.1	2.0	0.0	2.3
Stream	0.1	0.0	0.0	0.1	0.5	0.4	3.3	0.0	3.4
Vernal pool	0.2	0.0	0.0	0.2	0.3	0.1	2.7	0.0	2.8
Woods road	0.5	0.01	0.0	0.5	4.9	0.05	7.4	0.03	7.9
All cluttered habitats	0.2	<0.01	0.0	0.2	1.4	0.1	3.3	0.01	3.5
All habitats	1.1	0.01	0.08	1.2	2.1	0.2	3.6	0.02	5.6

Table 4 Results of analysis of variance numbers of call sequences, by survey type, dependent variable, and habitat and temporal effects, Quabbin Reservoir watershed, Massachusetts, 2004–2006

Dependent variable	Effect	*df*	Active surveys		Passive surveys	
			F	*P*(*F*)	*F*	*P*(*F*)
All bats	Habitat class (HC)	1, 20	3.652	0.07	6.94	0.016
	Habitat type: HC	8, 20	2.023	0.096	3.318	0.014
	Open habitats	4, 10	1.762	0.213	3.346	0.055
	Cluttered habitats	4, 10	2.571	0.103	3.18	0.063
	Forest habitats	2, 6	3.434	0.101	0.473	0.645
	Aquatic versus upland	1, 20	12.846	0.002	5.784	0.026
	Aquatic habitats	3, 8	0.313	0.816	2.979	0.096
	Round/Session	2, 40	4.209	0.022	8.859	0.001
Large-bodied bats	Habitat class (HC)	S	49.719	<0.001	37.818	<0.001
	Habitat type: HC	a	2.451	0.05	2.983	0.023
	Open habitats	m	2.299	0.13	3.045	0.07
	Cluttered habitats	e	2.647	0.097	1.523	0.268
	Forest habitats		6.559	0.031	4.155	0.074
	Aquatic versus upland		1.231	0.28	1.666	0.212
	Aquatic habitats		4.909	0.032	4.759	0.035
	Round/Session		47.9	0.021	7.227	0.002
Myotis species	Habitat class (HC)	S	0.114	0.739	2.657	0.119
	Habitat type: HC	a	2.502	0.046	3.365	0.013
	Open habitats	m	1.906	0.186	3.404	0.053
	Cluttered habitats	e	2.976	0.074	3.218	0.061
	Forest habitats		0.607	0.575	0.751	0.512
	Aquatic versus upland		14.727	<0.001	6.309	0.021
	Aquatic habitats		0.285	0.835	2.471	0.136
	Round/Session		2.98	0.062	6.892	0.003

Habitat types

Numbers of call sequences of all species differed among the 10 habitat types, but the effect was less apparent in active ($F_{df=8,20} = 2.023$, $P = 0.096$) than in passive surveys ($F_{df=8,20} = 3.318$, $P = 0.014$; Table 4). Activity differed significantly between aquatic and upland habitats. Activity levels were greatest at the open, reservoir and large-pond habitats, but large numbers of call sequences were also recorded at cluttered, stream and vernal pool habitats (Table 3). Differences in activity levels among aquatic habitats did not differ significantly (Table 4). While activity levels were greater in the harvested forest sites, compared to the uncut, control forest, these differences were not significant (Table 4). Activity levels along linear habitats were mixed, with numbers of call sequences along streams greater than the overall average and those along woods roads less than the average in the active surveys (Table 3a) and vice versa in the passive surveys (Table 3b).

For individual species and species groups, big-brown bats and other large-bodied bats were most active at open-field, large-pond, and reservoir habitats and, among the cluttered habitats, at vernal pools and streams (Table 3). Hoary and red bat activity was exclusively recorded at these habitats with the previously noted exception. The effect of habitat clutter on large-bodied bat activity was observed in the significant difference in large-bodied bat activity among forest habitats, with higher numbers of call sequences in the open clearcuts and lesser numbers in the cluttered partial cut and control forest habitats (Tables 3, 4). Large-bodied bat activity was not different between upland and aquatic habitats, but differed significantly among aquatic habitats, with greater numbers recorded at the open, large-pond and reservoir habitats and fewer at the more cluttered stream and vernal pool habitats. Activity levels of large-bodied bats were generally low at both the linear stream and woods road habitats, with the exception of active survey recordings at stream sites (Table 3a).

Activity levels of all *Myotis* species, and little-brown bats specifically, were greatest at open, large-pond and reservoir habitats and cluttered, stream, vernal pool, and woods road habitats (Table 3). Activity levels of *Myotis* species were not significantly different between open and cluttered habitat classes nor among the three forest or four aquatic habitat types (Table 4). Differences in *Myotis* activity between aquatic and upland habitats were significant. The strength of this effect was less than observed for large bodied bats (Table 4). Long-eared bats, the only other individually identified *Myotis* species, were recorded most frequently in cluttered habitats, especially at vernal pools in active surveys (Table 3a). In passive surveys, long-eared bats were also recorded at open pond and reservoir sites as well as at vernal pool habitats (Table 3b). Eastern pipistrelles were mostly recorded in open habitats, with a few recordings along woods roads.

Temporal patterns

Seasonal patterns

Seasonal patterns of bat activity were the same for both active and passive surveys, with highest levels of activity in the early summer surveys, lowest in the late summer surveys, and intermediate levels in the late spring surveys (Tables 5 and 6). These results were observed for both large-bodied and *Myotis* bats. The effects of season (round or session) on activity levels were significant ($P(F) < 0.05$) for all analyses with the exception of active survey, *Myotis* results ($F_{df=2,40} = 2.98$, $P = 0.062$; Table 4). Seasonal patterns of bat activity were most noticeable in open habitats, with over twice as many call sequences recorded per 20-min survey in early-summer active surveys than in late-spring or late summer-surveys (Table 5). This comparison was less dramatic for passive surveys (Table 6).

Hourly patterns

In the passive surveys, activity levels peaked in the second hour after sunset, especially in open habitats, and declined with every hour thereafter (Fig. 2). Activity levels were less in cluttered habitats and the hourly pattern of activity was slightly but not significantly different from that observed in open habitats ($X^2 = 16.3$, $df = 11$, $0.25 < P(X^2) < 0.1$).

Table 5 Average number of active survey call sequences per 20-min survey by round, habitat class, and species group, Quabbin Reservoir watershed, Massachusetts, 2004–2006

Habitat class	Round 1 (June)			Round 2 (July)			Round 3 (August)		
	Large-bodied	All Myotis	All	Large-bodied	All Myotis	All	Large-bodied	All Myotis	All
Open	4.0	4.0	7.9	7.9	9.0	16.9	3.3	4.2	6.8
Cluttered	0.6	6.9	7.5	0.5	6.0	6.5	0.3	4.3	6.2
All	2.3	5.4	7.7	4.2	7.5	11.7	1.8	4.9	6.5

Table 6 Average number of passive survey call sequences per hour by session, habitat class, and species group, Quabbin Reservoir watershed, Massachusetts, 2004–2006

Habitat class	Session 1 (Prior to 16 June)			Session 2			Session 3 (After 14 August)		
	Large-bodied	All Myotis	All	Large-bodied	All Myotis	All	Large-bodied	All Myotis	All
Open	1.9	5.3	7.3	3.5	7.3	10.9	0.6	1.5	2.1
Cluttered	0.1	3.4	3.6	0.4	5.6	6.0	0.1	2.0	2.1
All	1.1	4.4	5.4	2.0	6.4	8.4	0.3	1.8	2.1

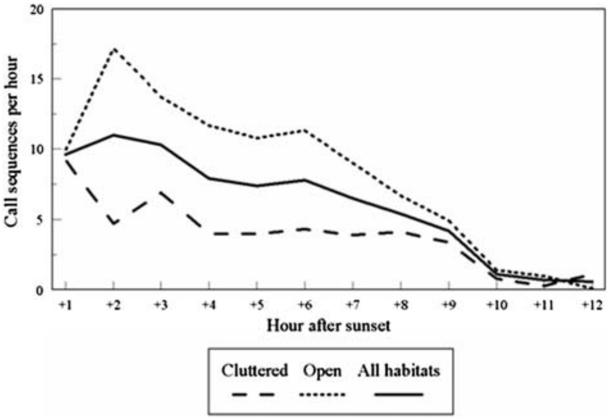

Fig. 2 Average numbers of call sequences per hour by habitat class and hour after sunset, Quabbin Reservoir watershed, Massachusetts, 2004–2006

Temperature effects

Bat activity increased with increasing ambient temperature to a maximum between 17 and 21°C, and then declined as temperatures increased above 21°C (Fig. 3). A second peak was observed at 26°C, but this was based on only 8 h of survey data, so these may be spurious results. Over the range of recorded temperatures, no calls were recorded when temperatures were below 5°C, and activity was low at temperatures below 15°C. The distribution of call sequences by temperature was significantly different than expected by survey effort ($X^2 = 2{,}141.8$, $df = 14$, $P(X^2) < 0.001$).

Discussion

Over the 3 years (2004–2006) of the study, multiple active and passive acoustic surveys of bat activity were conducted at three replicate sites of ten major habitats of the Quabbin Reservoir watershed. The surveys were designed to address questions about the composition of the bat community, relative use of uncut and harvested forests, the use of linear habitats (streams, woods roads) as possible travel corridors, the use of various aquatic habitats, and about seasonal and nightly patterns of bat activity.

Overall, the results reinforce the findings of the previous bat activity surveys at the study area (Brooks and Ford 2005); with large numbers of bats of all species recorded at open

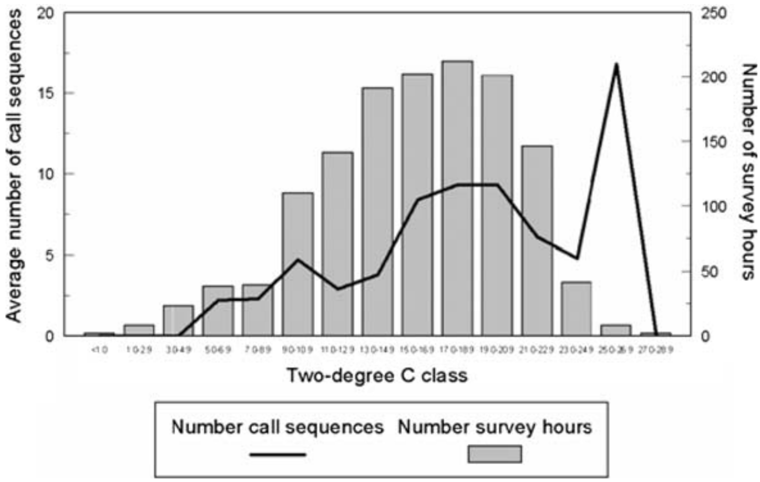

Fig. 3 Average number of call sequences per hour and number of bat survey hours by two-degree Centigrade class, Quabbin Reservoir watershed, Massachusetts, 2006

habitats in general and at reservoir and large pond habitats specifically (Table 3). This result was most strongly seen for the large-bodied bat species, species not adapted for flight in cluttered habitats (Aldridge and Rautenbach 1987; Norberg and Rayner 1987; Fenton 1990; Sleep and Brigham 2003). This effect is commonly observed in community-scale bat surveys (Owen et al. 2004; Menzel et al. 2005a; Ford et al. 2005, 2006). Even within cluttered habitats, activity was greatest at those that are open beneath the forest canopy (i.e., vernal pool, stream, and woods road) and less in closed and partially-closed canopy forests.

Activity was generally greatest in the early-summer surveys (Table 5), when female bats would be foraging more actively to support the energy costs of lactation. Activity peaked in the first hour after sunset in closed-canopy (cluttered) habitats and in the second hour after sunset in open habitats (Fig. 2). A second, minor peak in activity preceding sunrise was not observed. Activity peaked between 17 and 21°C, from no recorded activity below 5°C (Fig. 3).

Habitat effects

Aquatic habitats

All aquatic habitats, with the exception of beaver meadows, were highly used on the Quabbin (Table 3) and their abundance and diversity are most likely a major factor in the area having a diverse and abundant bat community (Krusic et al. 1996; Zimmerman and Glanz 2000; Owen et al. 2004; Menzel et al. 2005a; Ford et al. 2005). Still-water habitats are preferred sites for foraging and drinking (Krusic et al. 1996) and flowing-water habitats are used for foraging, but especially commuting (Krusic et al. 1996). The size of aquatic habitat is important, as activity at the larger reservoir and large pond habitats was greater than at the vernal pool and stream habitats. Since this result was observed for both open-adapted large-bodied and clutter-adapted *Myotis* species, it would seem that the larger aquatic habitats are superior by size alone. The smaller aquatic habitats were used most preferentially by long-eared bats, the most clutter-adapted bat species of the northeast (Caceres and Barclay 2000; Broders et al. 2003, 2004; Francl 2008).

The low levels of activity recorded at beaver meadow sites (Table 3) were unexpected (Brooks and Ford 2005). Zimmerman and Glanz (2000) recorded low levels of activity at wetlands in Maine, which they suggested may be due to lower air temperatures at these sites. The beaver meadow sites in this study are mature, with luxuriant herbaceous vegetation, including dense *Phragmites australis* at one site, early woody-stemmed succession, and little remaining open water. These conditions may be less favorable for insects and, hence, offer poorer foraging conditions.

Harvested and uncut forests

The full (clearcut) or partial removal of the forest canopy by timber harvests clearly resulted in increased bat activity, but the impact of the effect differed between forest-harvesting intensity and by clutter- and open-adapted bat species. The difference in bat activity between harvested and uncut forest was most clearly seen in active acoustic surveys of large-bodied (open adapted) species, with larger numbers of bats recorded per unit time in the harvested sites and with the numbers increasing with cutting intensity (Table 3a). These results support the suggestion that the opening of the forest canopy creates additional uncluttered foraging habitat (Grindal and Brigham 1998; Owen et al. 2004; Menzel et al. 2005b). The effect was less apparent for clutter-adapted *Myotis* species. It may be that the any potential foraging opportunity benefits were offset by the costs of increased exposure to aerial predation. Insect surveys (Kunz 1988) would be required to ascertain the quality of the open habitat for the insectivorous bats of the northeast (Carter et al. 2003; Whitaker 2004) created by timber harvesting, as compared to known high-quality open habitat such as large ponds.

Linear habitat use

Bat activity was frequently recorded at stream and woods road habitats (Table 3). These linear features, along with hard forest edges, have been identified as commuting habitat, linking day-roost and foraging sites (Krusic et al. 1996; Grindal and Brigham 1998; Verboom and Spoelstra 1999; Zimmerman and Glanz 2000; Downs and Racey 2006). During the early evening, in the active surveys, activity levels were greater at stream habitats, while over the entire night (passive surveys), activity was greater at woods road habitats. This likely indicates that, while both habitats were used for commuting between roosts and foraging sites, stream sites may have also been used as foraging sites, an early evening activity. During the active surveys, it was common to be able track bats with the AnaBat, flying in a single direction as if heading towards a destination. Tracking flight patterns with the AnaBat at other habitats showed less directionality. It would be worthwhile to further investigate the directionality and timing of flight activity along linear habitats by using two AnaBats, facing in opposing directions, for passive surveys. Comparisons of time-specific results might reveal if flight activity was predominantly in one direction.

Temporal patterns

Seasonal patterns

Activity levels were consistently greatest during early summer surveys, with the exception of active surveys in cluttered habitats (Table 5). Similar early-summer peaks in activity were reported by Zimmerman and Glanz (2000). High levels of activity during this period could be a reflection of the additional foraging activity by females to meet the energy requirements of lactation (Kunz 1973; Fenton and Barclay 1980; Anthony et al. 1981). Both the big and little brown bats, the most common species in the surveys, would have given birth and be lactating during the early summer period (Fenton and Barclay 1980; Kurta and Baker 1990). Low activity levels in the early fall could be attributable to migration to regional winter hibernacula (Davis and Hitchcock 1965; Veilleux 2007).

Nightly patterns

Overall activity levels increased slightly shortly after sunset and then generally declined as the night progressed (Fig. 2). This same pattern in activity was reported by Broders et al. (2003) for little brown bats at a national park in Nova Scotia and in central Iowa by Kunz (1973). Unlike some analyses of nightly patterns in activity, I did not observe a second peak of activity (biphasic) immediately before dawn as reported by Hayes (1997), but rather I observed a peak in activity immediately after dusk and then a gradual decline as time progressed (Fig. 2) similar to that reported by Broders et al. (2003). While Hayes noted this second, late evening period of increased activity, he cautioned that there was substantial variation in activity among nights, and the second period of activity was often missing. Hayes (1997) explained that the reasons for this variability in activity patterns was not clear and could be related to changes in abundances in prey (insects), meteorological conditions (temperature, precipitation), social factors, energetic needs, or some other unexplained factor. My surveys occurred between mid-spring and mid-fall (Table 2). Late evening (dawn) temperatures in the early and late season surveys would typically be low, with lower expected levels of bat activity (Fig. 3). Agosta et al. (2005), Milne et al. (2005), Kuenzi and Morrison (2003), and Ciechanowski et al. (2007) report a positive correlation between bat activity and ambient temperature from temporal surveys.

The nightly activity patterns I recorded, when separated by habitat class, reflect known behaviors. The early peak in activity in cluttered, linear habitats immediately after sunset could reflect commuting between day roosts and open, foraging habitats (Downs and Racey 2006). This conclusion is supported by the high levels of activity at the linear stream and woods road sites, known commuting habitats (Krusic et al. 1996; Grindal and Brigham 1998; Zimmerman and Glanz 2000; Downs and Racey 2006). The slightly later peak in activity at open habitats is readily explained as activity was concentrated on large-pond sites, where bats could drink and forage after commuting from day-roost sites (Hayes 1997). Finally, the second peak in activity in cluttered habitats (3-h after sunset; Fig. 2) could be explained by clutter-adapted species returning to forage in forest habitats after drinking and preliminary foraging at open-pond sites.

Temperature effects

I recorded little bat activity at temperatures below 5°C, a peak in activity at temperatures between 15 and 20°C, and an apparent decline in activity above 20°C (Fig. 3). A positive correlation between bat activity and air temperature is commonly reported (Hayes 1997; Broders et al. 2006) but a decline in activity above a maximum temperature is less commonly reported (e.g., Hayes 1997; Agosta et al. 2005; Ciechanowski et al. 2007). A reduction in activity above some maximum temperature could be a behavioral response to avoid overheating (Reeder and Cowles 1951) or reduced energy demands for thermoregulation. Behavioral changes by bats in response to low temperatures, including entering torpor, are widely reported (Audet and Fenton 1988; O'Donnell 2000; Milne et al. 2005; Arbuthnott and Brigham 2007). However, the cessation of bat activity below 5°C, and the increase in activity with increasing temperature above 5°C, may be as much an effect of air temperature on the activity of potential insect prey as on bat activity directly (Hayes 1997; Arbuthnott and Brigham 2007; Ciechanowski et al. 2007).

Passive versus active surveys

While not an intended objective of the study, the concurrent use of active (manual) and passive (automated) acoustic surveys allows for a comparison of the two survey methods (Johnson et al. 2002; Parsons et al. 2007). Automated, passive surveys (1) achieve a greater level of survey intensity than manual, active surveys with minimal to no additional survey effort, (2) allow for multiple points to be surveyed simultaneously, allowing for time-comparable results, and (3) allow for a more flexible survey schedule (Parsons et al. 2007). Average activity levels (numbers per equivalent unit time) were less for passive surveys than for active surveys (Table 3). However, active surveys occurred during the early evening (approximately 3 h following sunset), when bat activity was the greatest (Fig. 2). Additionally, active surveys, by definition, involve searching for bat activity while passive surveys are limited to recordings from a relatively small, fixed volume of air space. Relative patterns of activity among habitats for all bat taxa were not significantly different for the two types of surveys ($X^2 = 13.5$, $df = 9$, $0.25 < P(X^2) < 0.1$). The necessity of using analysis of variance by ranks for the analysis of active survey data, due to the large number of zeros, reduced the power of the analyses of these data. The general quality (number of calls per sequence, complete call structure) of recorded call sequences from active surveys was frequently superior to those of passive recorded calls (Johnson et al. 2002).

Passive surveys allow for the evaluation of temporal patterns of activity. Active surveys are shorter in duration and a greater number of surveys can be completed within a fixed period of time. There are benefits to both types of surveys and a comprehensive acoustical bat survey program should include active and passive efforts.

Conclusions and recommendations

The richness, diversity, and abundance of the bat community on the Quabbin Reservoir watershed, together with the well-regulated management of the forest, create an ideal mosaic of high-quality bat habitat and provide an opportunity for continued and more focused bat research. Mist netting surveys would allow for verification the identity of the species that occur on Quabbin, especially of *Myotis* species which are more difficult to distinguish using AnaBat recordings. Radio-telemetry studies could be used with captured bats to address questions regarding specific patterns of habitat use and how bats, especially the forest specialist long-eared bat, respond to timber harvests.

Another topic that could be pursued is a specific assessment of the role of aquatic habitats in supporting the bat community. Other Management Blocks on the Quabbin are more rugged and have fewer large pond habitats or are more distant from the Reservoir than are locations on the peninsular Prescott Management Block. Additionally, does each of the different aquatic habitats provide unique invertebrate prey and how does the invertebrate community differ between aquatic habitats and upland habitats.

Additional acoustic surveys could be conducted to investigate the composition and activity patterns at more restricted habitats, such as talus slopes and rock outcrops for small-footed bats ([*M. leibii* Audubon and Bachman]; Best and Jennings 1997; Amelon and

Burhans 2006), to document activity above the forest canopy (Menzel et al. 2000), or for the timing of migratory species occurrence (Cryan 2003).

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