Measuring habitat use by bats using acoustic methods in northeastern Minnesota

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Dedication

This thesis is dedicated to my husband Matt, who is constantly supportive and always available to discuss bats and biology.

Abstract

Baseline data on bat distribution and habitat use is essential for bat conservation. Little information exists on bats in the southern boreal forests of the Midwest. We measured summer bat habitat use and foraging activity at aquatic, linear corridor, and interior forest sites with bat detectors in deciduous, mixed-wood, and coniferous forests in northeastern Minnesota. We used the number of files saved, the acoustical activity index, and the file size index to quantify acoustic bat data and we compared the results of each index. We further examined the acoustic activity index and the file size index to determine how differences among activity indices influence statistical inferences from analysis of bat activity. We determined the effects of relative insect abundance and vegetation density on bat activity. All seven resident bat species were detected across the study area. Bat activity, dominated by *Myotis* species (*Myotis lucifugus* and *M. septentrionalis*) and *Lasionycteris noctivagans* was concentrated at aquatic and linear corridor microsites, regardless of forest cover type. However, bats foraged at similar rates in each microsite type. Bat activity and foraging activity occurred earlier at interior forest sites relative to aquatic and linear corridor sites, suggesting that interior forest is also used by bats as they leave day roosts. The acoustic activity index resulted in a loss of data for clutter-adapted species and the file size index was biased towards all small-bodied bats with higher kilobytes per second recorded in acoustic files. Despite clear biases, bat activity indices resulted in similar statistical inferences of habitat use of northeastern Minnesota bat species.

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Introduction

Over the past decade two new threats to bat populations have emerged. White-nose syndrome has caused many bat fatalities in eastern North America and has spread to new bat hibernacula every year since its discovery in 2006 (Blehert *et al*. 2009, Boyles and Willis 2010). Increased bat mortality can also be attributed to the growing wind power industry. Migrating bats are killed at utility-scale wind turbines (Kunz *et al*. 2007*a*, Kunz *et al*. 2007*b*, Baerwald *et al.* 2008). Bat fatality estimates for utility-scale wind turbines are projected based on installed turbine capacity and results of previous bat fatality studies (Arnett *et al*. 2008), whereas fatalities caused by white-nose syndrome have often been directly measured.

White-nose syndrome is spreading west in North America while large utility-scale wind farms have regional distribution and are present in many Midwest states and the Pacific Northwest. Another development with the potential to affect local bat populations is the installation of small household- or community-size wind turbines (≤ 100 kilowatt capacity). Small wind turbines could potentially affect resident populations of bats foraging at low altitudes. Small wind turbines have lower tower height and smaller blades (AWEA 2009), and would be more spatially dispersed than utility-scale wind turbines. The effect of small wind turbines on bats is unknown.

Baseline data on bat distribution and habitat use would help estimate the potential effects of threats to bat populations in North America. Some parts of North America still have little baseline data on bat habitat use even though it has been the subject of many bat studies over the past two decades (Patriquin and Barclay 2003, Menzel *et al.* 2005). For example, there have been few studies of bats in the southern boreal forest of the upper Midwest. Recently, seven species of bats were acoustically detected at three sites in northeastern Minnesota during the spring and autumn (Nordquist 2006). Six species of bats were acoustically detected and four species were captured in mist-nets at three sites in northeastern Minnesota during the summer (Kruger and Peterson 2008). Habitat use was not addressed although species presence was confirmed.

Among the factors affecting bat habitat use are prey availability (Grindal and Brigham 1999) and the ease of flight (Loeb and O'Keefe 2006, Hayes and Loeb 2007). Insectivorous bats use aquatic, edge, and corridor features for foraging and commuting in forested habitats. Clutter-adapted insectivorous bat species can navigate through interior forest but forage in either open or dense forest habitats (Norberg and Rayner 1987, Sleep and Brigham 2003). Open-adapted insectivorous bat species are restricted to foraging in open habitats above the forest canopy, over water, or along linear corridors (Norberg and Rayner 1987).

Emergence periods of adult aquatic insects occur at different intervals throughout the summer (Judd 1962). These adult aquatic insects swarm above water bodies and provide bats with a higher density of prey (Grindal *et al.* 1999, Fukui *et al.* 2006). Forest edges created by corridors and streams are easier for bats to fly through than the forest interior and are more suitable than open spaces because they also provide shelter from the wind and predators (Krusic *et al.* 1996, Sleep and Brigham 2003, Hayes and Loeb 2007).

Flying insects also use the habitat and shelter from the wind provided by forest edges and streams (Brittain 1982, Grindal and Brigham 1999).

The relationship between forest cover type and bat activity is less well-understood. Forest management that creates heterogeneous forest types and multiple age classes is thought to satisfy habitat requirements of most North American bat species (Krusic *et al.*1996, Jung *et al.* 1999, Patriquin and Barclay 2003, Menzel *et al.* 2005, Loeb and O'Keefe 2006), but different habitats are often found to be preferred. For example, male *M. lucifugus* preferred deciduous forest over coniferous forest in New Brunswick, Canada (Broders *et al.* 2006). *M. lucifugus* and *M. septentrionalis* activity was higher in aspen (*Populus tremuloides*) -white birch (*Betula papyrifera*) mixed-wood forest than either aspen or jack pine (*Pinus banksiana*) forest cover types in Saskatchewan, Canada (Kalcounis *et al.* 1999). *Myotis* species were more active in coniferous forests but foraged more in deciduous forest than mixed-wood or coniferous forests in Alberta, Canada (Patriquin and Barclay 2003). Finally, temperate bat species are more active in deciduous forest than coniferous forest cover types in Britain (Walsh and Harris 1996). Use seems to depend on the study and the location, with bats using most forest cover types to some extent.

Acoustic monitoring with bat detectors is the method most commonly used to study bats over large areas (Kunz *et al.* 2007*a*, Fischer *et al.* 2009). Bat detectors record high frequency sounds that bats emit and write a file each time a bat call is detected. The simplest index to measure bat activity is the number of files saved (NFS) per unit time, which is equivalent to the number of bat passes per unit time (Britzke *et al.*1999). The acoustic activity index (AAI) and the file size index (FSI) have also been used to quantify bat activity. The AAI converts the number of bat passes to the number of minutes bats are present per unit time (Miller 2001). Files of the same species that are recorded within a one minute period are discarded in the AAI to reduce the possible bias of the same bats being detected repeatedly (Miller 2001). The FSI is the total file size per unit time and is calculated from the sum of the file size of each bat pass (Broders 2003). In addition to the number of bat passes, the FSI accounts for the variability in the length of the call sequence and any variability in the file due to bat orientation or the type of echolocation signal (Broders 2003). There are positive linear correlations between the AAI and NFS (Miller 2001) and the FSI and NFS (Broders 2003), but all three indices have yet to be directly compared.

We measured bat activity with bat detectors placed at aquatic, linear corridor, and interior forest microsites within mixed-wood, deciduous, and coniferous forest cover types in northeastern Minnesota. We measured the spatial distribution of bat species along the north-south gradient of the study area. We examined the effects of estimated vegetation volume on bat activity and we also examined temporal patterns of bat activity. We used light traps to estimate insect density at aquatic and linear corridor sites and we counted feeding buzzes in call files to determine foraging activity at each microsite type. Finally, we used the NFS, AAI, and FSI to quantify bat activity in microsite and forest cover types and tested the AAI and FSI for potential bias.

Methods

The study area encompasses portions of St. Louis, Lake, and Cook Counties along the North Shore of Lake Superior and includes the Minnesota Lake Superior Coastal Program (MLSCP) boundary (Figure 1). The Lake Superior watershed has numerous streams, lakes and wetlands. Elevation ranges from 180 to 580 meters. The climate is continental, with precipitation ranging from 71 to 76 cm of rainfall and 152 to 163 cm of snowfall annually. The region consists almost entirely of the North Shore Highlands land type (Albert 1995). Dominant deciduous tree species are quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and maple (*Acer* spp.) along the shore. Coniferous tree species include jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), tamarack (*Larix laricina*), balsam fir (*Abies balsamea*), northern white cedar (*Thuja occidentalis*), and Red pine (*Pinus resinosa*) is present in plantations (Albert 1995). Alder (*Alnus* spp.), willow (*Salix* spp.), and beaked hazel (*Corylus cornuta*) are often present in the understory.

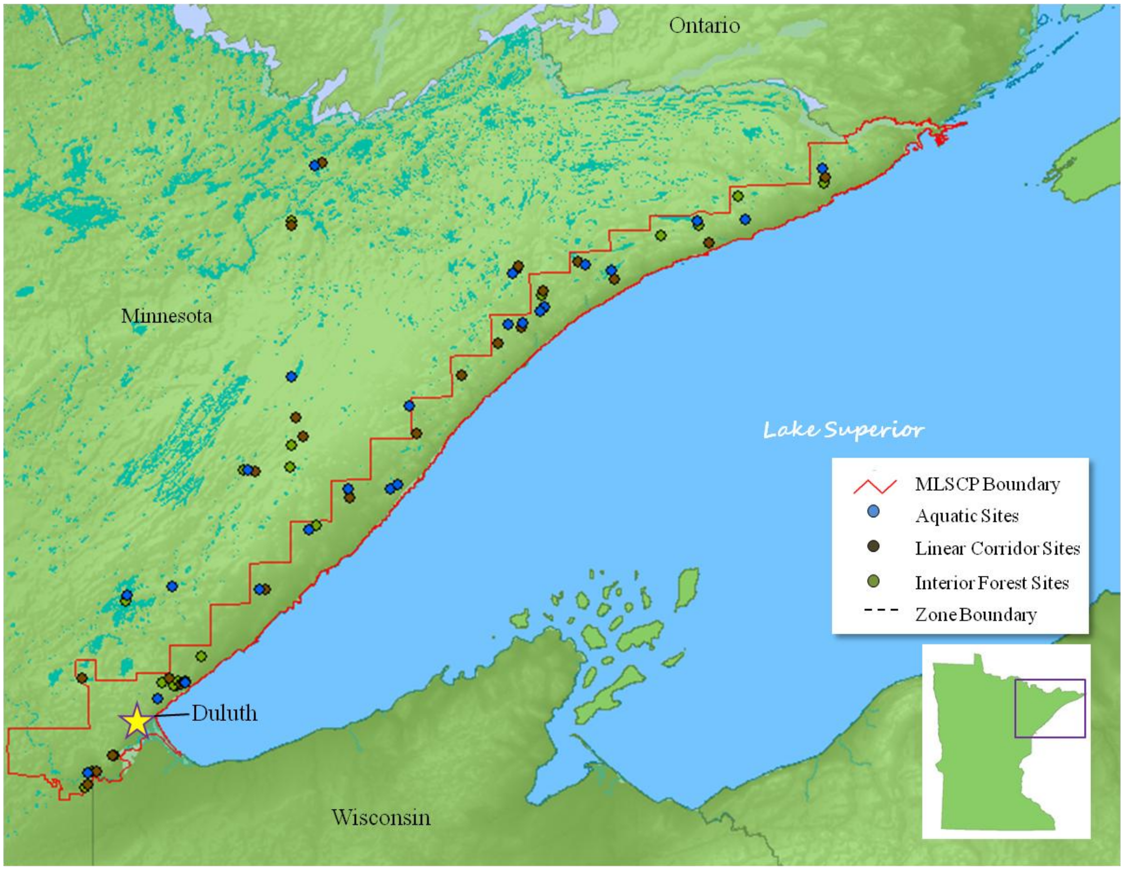


Figure 1. Study area and acoustic survey sites in northeastern Minnesota during the summer months of 2009 and 2010. Most survey sites were located within the Minnesota Lake Superior Coastal Program (MLSCP) boundary.

Forested habitats were identified in landsat-based satellite imagery land cover classifications. The Gap Analysis Program (GAP) Level I land cover classification (MDNR 2007*a*) and the Land Use Land Cover (LULC) data set (MDNR 2007*b*) were used to identify deciduous, coniferous, and mixed-wood forest cover types. A restricted randomized sampling design was used to choose bat detector sites. We buffered aquatic features and linear corridor features 500 m with ArcGIS. Aquatic features were streams or inland lakes and linear corridors were trails, roads, or transmission line corridors. Random points were placed within the 500 m buffer in mixed-wood, coniferous, or deciduous forest cover types using ArcGIS. Points that were not accessible and points that were on private land were discarded.

Acoustic monitoring was conducted from May to September in 2009 and April through August in 2010. We used three Anabat II bat detectors with the Anabat Zero Crossings Analysis Interface Module (ZCAIM) (Titley Scientific, Australia). The Anabat system records bat passes until >1 second passes between successive pulses. If the maximum file length of 15 seconds is reached the system begins recording the next file. We standardized the sensitivity of each Anabat detector with the Bat Chirp Board (Nevada Bat Technology, Las Vegas, NV) (Larson and Hayes 2000). Bat detectors were placed at one linear corridor site and one aquatic site. We also placed a detector at an interior forest site that was ≥ 100 and ≤ 500 meters from any trail, road, or stream. Detectors at aquatic sites, linear corridors, and interior forest sites were separated by at least 1 km. We oriented detector microphones to point along the axis of the stream or corridor, or toward a forest gap at the interior forest sites.

We surveyed each site for three nights and we programmed the Anabat system to operate from 7:00 p.m. until 5:00 a.m. in 2009 and 2010. We surveyed only on nights with low wind speeds (≤ 6 mph) and no precipitation. Each detector remained at a site until precipitation and wind criteria were met for three nights, and then each detector was transferred to a new site. The bat detector, ZCAIM, and a 12-volt sealed lead acid battery were housed in a weatherproof container measuring 30.5 cm x 15.2 cm x 15.2 cm. We attached the housing to a tree 3-4 meters above ground level with elastic tie-downs and a bicycle lock. We oriented detector microphones downward toward a reflection plate angled 22.5° below horizontal which sampled an area 45° upwards and protected the microphone from precipitation (Figure 2).

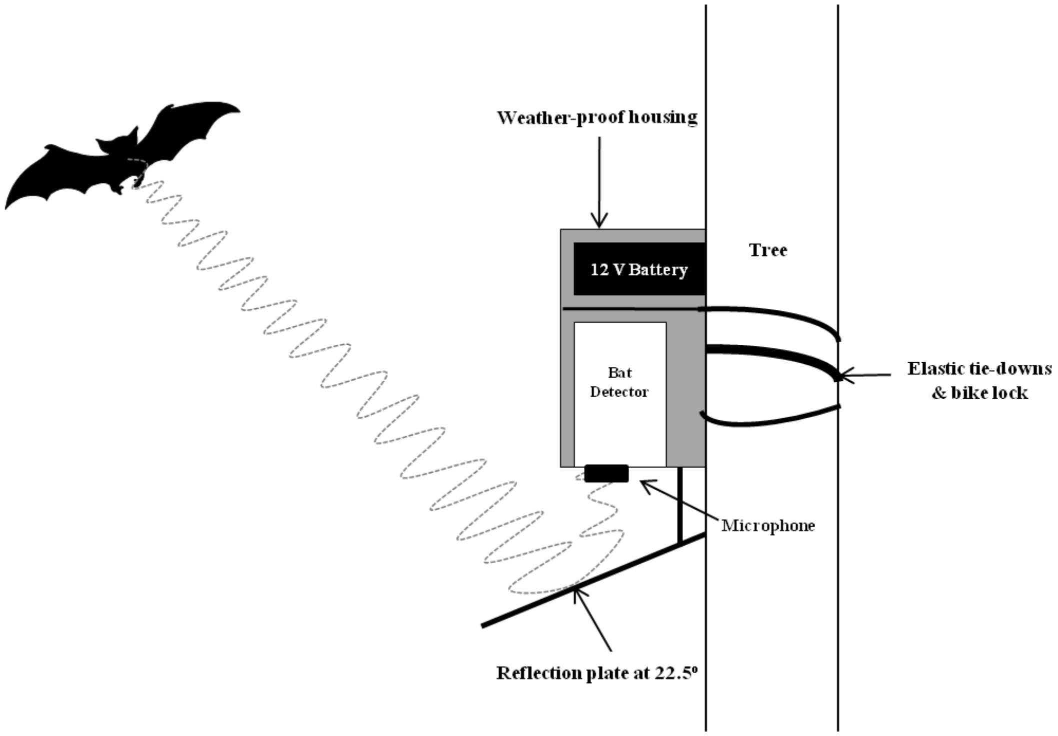


Figure 2. Weather-proof housing system designed for Anabat bat detectors. A 12 volt, 7.5 or 12 Amp-hour external battery, Anabat detector and Anabat ZCAIM with wiring is housed within the box and mounted to the trunk of a tree with elastic tie-downs and a bike lock for security. The microphone is protected from precipitation and debris by the reflection plate positioned 22.5 degrees below horizontal while still allowing ultra-sonic sounds to be reflected from the plate into the microphone.

We downloaded acoustical data from the detectors and visually identified each call to genus and species by comparing characteristics of the shape, duration, and frequency of the recorded calls. Fragmented calls or files with less than two echolocation pulses were not included in analysis. We distinguished *M. lucifugus* and *M. septentrionalis* to genus (Krusic and Neefus 1996, Jung *et al*. 1999, Kalcounis *et al.* 1999). Other bat calls were identified to species. We considered one site in 2010 an outlier and excluded it from analysis because of the unusually high number of files, occurrence of feeding buzzes, and large size of files recorded over three nights. We describe the outlier site separately.

Habitat and survey data recorded at each site included the forest cover type (deciduous, coniferous, or mixed-wood), microphone direction and microphone height, topography, and detector tree characteristics. We used the Minnesota Climatology Working Group (MCWG) website to obtain daily temperature and precipitation data for each sampling period (MCWG 2010). Wind speed for survey sites was recorded from the nearest weather station to each bat detector site and accessed from the Weather Underground website (WUPWS 2010). We obtained the local sunset time from the U.S. Naval Observatory website (USNO 2010).

We randomly chose 10 bat call files from each of the 79 three-night surveys and counted files containing feeding buzzes to estimate foraging activity in aquatic, linear corridor, and interior forest microsites in 2009 and 2010. We sorted sites in order from southwest to northeast using UTM coordinates and plotted the number of files of each species at each site with the Lake Superior shoreline as the x-axis to determine if species were present throughout the north-south gradient of the study area. We also estimated vegetation volume at the understory (0-3 m), sub-canopy (3-6 m) and canopy (> 6 m) levels at each site (Jung *et al.* 1999). Percentages at each of three levels were scored “1” for volumes ≤ 33%, “2” for volumes > 33% and ≤ 66% and “3” for volumes > 66%. Scores for each forest level were summed for a total vegetation density score for aquatic sites, linear corridors, and interior forest sites.

We constructed ultra-violet insect light traps with three baffles made of 13 cm x 41 cm clear plastic surrounding a black light fluorescent bulb (Model # 2805, BioQuip Products, Rancho Dominguez, CA). Insects flying toward the light would hit the baffles and fall into a funnel and jar from which they could not escape. We trapped insects during one of three nights at each corridor and aquatic site beginning in July 2009. We did not sample insects at forest sites because bat activity is low even when insect activity is high in interior forest (Ober and Hayes 2008, Adams *et al.* 2009). Bat activity was significantly higher at an array of black lights than bat activity at an unlit site 20-60 m away (Adams *et al.* 2005). Therefore, we placed light traps >60 m from bat detectors to reduce the potential bias. Light traps were turned on around 7:00 pm and ran for approximately 10-12 hours during the night. We stored insects in 70% ethanol after field collection, then we oven-dried the insects at 150^{o} F for 2 days. We identified captured insects to orders preyed upon by bats (Anthony and Kunz 1977, Barclay 1991, Brigham 1990, Whitaker 2004). We used the dry weight of the insect samples as an index of relative insect abundance.

We used the local sunset and sunrise times to calculate the minutes since sunset and minutes until sunrise for each acoustic bat file. We created frequency distributions of the number of files recorded in 60-minute bins from 0 to 300 minutes since sunset at aquatic, linear corridor, and interior forest sites to analyze whether bat files were recorded earlier at interior forest sites than aquatic or linear corridor sites. We also created frequency distributions of the number of files recorded in 60-minute bins from 0 to 300 minutes since sunset and 300 to 0 minutes until sunrise to determine temporal patterns of activity by species and by month.

We used three different methods to evaluate acoustical bat activity data: the number of files saved (NFS), the acoustic activity index (AAI), and the file size index (FSI) (Britzke *et al.* 1999, Miller 2001, Broders 2003). We tested for consistency in habitat use conclusions drawn from the results of the NFS, AAI, and FSI. First we calculated the NFS after excluding any non-bat and fragmented bat call files by counting the number of files recorded in a three-night survey. We calculated the AAI as the count of one minute time intervals that each bat species was detected in a three-night survey (Miller 2001). If greater than one file of a given species is recorded in one minute, the other files are excluded from analysis when calculating the AAI. Lastly, we calculated the FSI by summing the size of Anabat files identified to species for each three-night survey.

We further examined the activity indices to identify reasons that the AAI and FSI would differ from the NFS. First we calculated the number of files recorded per minute (files min^{-1}) of species detected during each survey in order to test the AAI and to determine the frequency with which species are recorded within one minute. We then randomly chose 30 files of each species to test the FSI. For this test, calls of the *Myotis* genus were identified to species. We calculated the average kilobytes per second (*kBS*) to test for differences in *kBS* among bat species that would affect the FSI. We used *kBS* of each species to develop a correction factor,

$$CF = \frac{kBS_L}{kBS_i} \quad \text{Eq. 1,}$$

where kBS_L is from the species with the lowest kBS and kBS_i is the average kilobytes per second of the *i*th species. The *CF* was applied to the sample of files of each species to standardize the average file size of species with high *kBS*.

We analyzed bat activity for the most common species, *Myotis* species in 2009 and 2010, *L. noctivagans* in 2009 and *L. borealis* in 2010 using the NFS, AAI, and FSI. We tested bat activity data for normality using Wilk-Shapiro’s W statistic. Data was not normally distributed even after transformation, so we used the Kruskal-Wallis one-way ANOVA (K-W ANOVA) to test the effects of forest cover type and microsite type on the bat activity ranks for each species. Pair-wise comparisons were performed for each significant result. We used regression to test for a relationship between bat activity and vegetation density in each microsite type and cover type. We used a Welch's ANOVA for unequal variance to test the effect of microsite type on vegetation density. We also used regression to test for a relationship between insect density and bat activity. To test the effects of forest cover type and microsite type on relative insect density, we used the K-W ANOVA. Finally, we used chi-squared analysis to determine the differences in temporal patterns of bat activity and presence of feeding buzzes in call files between aquatic, linear corridor, and interior forest sites.

Software we used included ArcView 3.3, ArcMap 9.2, and ArcGIS 10.0 (Environmental Systems Research Institute, Inc. [ESRI], Redlands, CA) for Geographic Information System analysis. We also used CFCRead software v. 0.4.2.1 to download data and AnalookW software v. 0.3.3.17 to visualize bat call data (Chris Corben, Titley Scientific, Australia). We used Microsoft Access and Excel for data management. We used the Rand() function in Microsoft Excel to generate random numbers for the feeding buzz analysis and for measuring the *kBS* of calls of each species. We used Statistix v. 9.0.4.0 (Analytical Software, Tallahassee, FL) for all statistical analyses.

Results

We detected all seven species of bats throughout the study area, from the southwestern-most to the northeastern-most site along the Lake Superior shoreline (Figure 3). We recorded 7,666 identifiable bat calls and 5,710 unidentifiable or non-bat signals during 1,440 detector hours in 2009. In 2010 we recorded 8,554 bat calls and 3,184 unidentifiable or non-bat signals during 930 detector hours. We recorded *Myotis* species five times more often than any other species (Table 1). After *Myotis, Lasionycteris noctivagans* was the most common species recorded in 2009 with 14% as many files recorded as *Myotis* species. *Lasiurus borealis* was the most common species recorded after *Myotis* in 2010, with 8% as many files recorded as *Myotis* species. *Perimyotis subflavus* was the least commonly recorded species during the study. *L. cinereus, Eptesicus fuscus*, and *Perimyotis subflavus* were present in 2-3% of files in 2009 and in 1-2% of files in 2010. *L. noctivagans* and *L. borealis* were infrequently detected in 2010 and 2009, respectively, so we analyzed habitat use only for the *Myotis* species in 2009 and 2010, *L. noctivagans* in 2009, and *L. borealis* in 2010.

Table 1. Minnesota bat species and relative abundances during 2009 and 2010 in northeastern Minnesota. Percent of files per survey is based on the number of files recorded per survey (n_{2009} = 7,666; n_{2010} = 8,554). Percent of surveys detected is based on the number of surveys in which each species was detected.

		Percent of files per survey		Percent of surveys detected	
Common Name	**Latin Name**	**2009**	**2010**	**2009**	**2010**
Little Brown & Northern Long-eared Myotis	*Myotis lucifugus & Myotis septentrionalis*	81	86	100	90
Silver-haired Bat	*Lasionycteris noctivagans*	11	3	60	70
Eastern Red Bat	*Lasiurus borealis*	1	7	21	53
Hoary Bat	*Lasiurus cinereus*	3	2	35	53
Big Brown Bat	*Eptesicus fuscus*	2	1	42	63
Eastern Pipistrelle	*Perimyotis subflavus*	2	1	31	40

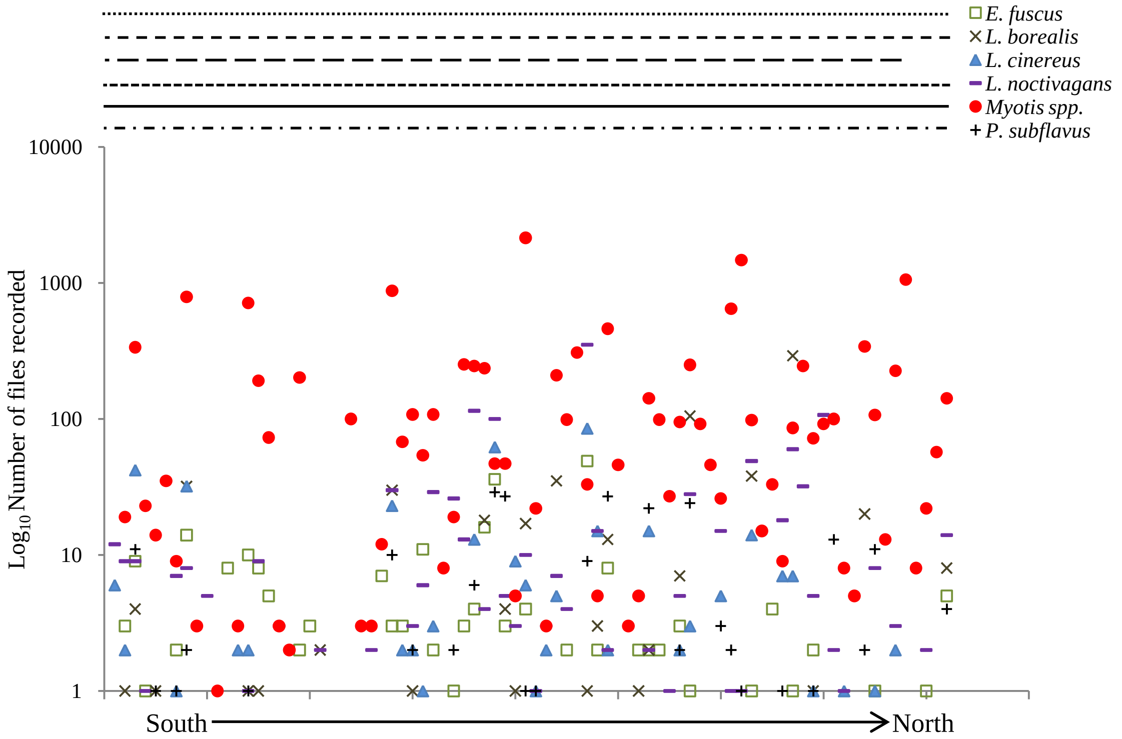


Figure 3. Spatial distribution of bat species at survey sites along the North Shore of Lake Superior. The number of files recorded for each species was log$_{10}$ transformed for visual clarity. Each site was ordered from the southwestern-most to the northeastern-most site using UTM coordinates. Horizontal lines next to species symbols indicate the extent that each species were detected along the shoreline.

Bat activity measured from each of the common species, *Myotis* species in 2009 (Figure 4a), *Lasionycteris noctivagans* in 2009 (Figure 5), and *L. borealis* in 2010 (Figure 6) was not different in deciduous, mixed-wood, and coniferous forest, with similar results for all indices (Table 2). In 2010 only, *Myotis* species were more active in deciduous than coniferous forest (Table 2), but bat activity in either deciduous or coniferous forest was not different from bat activity in mixed-wood forest (Figure 4b).

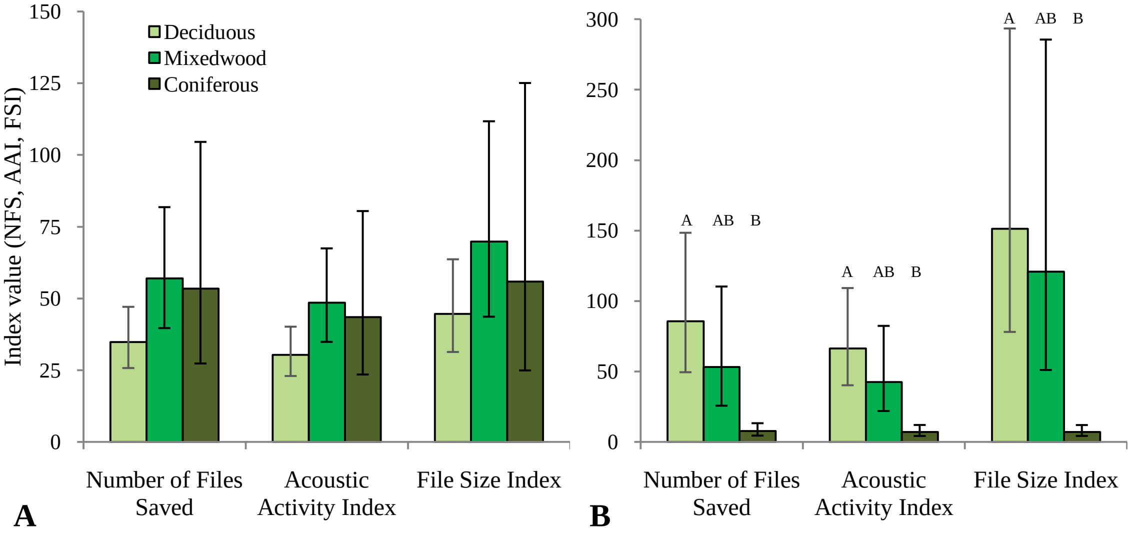


Figure 4. Mean (±SE) bat activity index values for *Myotis* species in deciduous, mixed-wood, and coniferous forest cover types in A) 2009 and B) 2010. NFS is the mean number of files saved per survey, AAI is the average number of minutes bats were active per survey, and FSI is the average of the file size (Kb) sums per survey. All means are the geometric means for each forest cover type. Brackets with letters indicate significant difference between groups for all three activity indices. Note the scale on the y-axis.

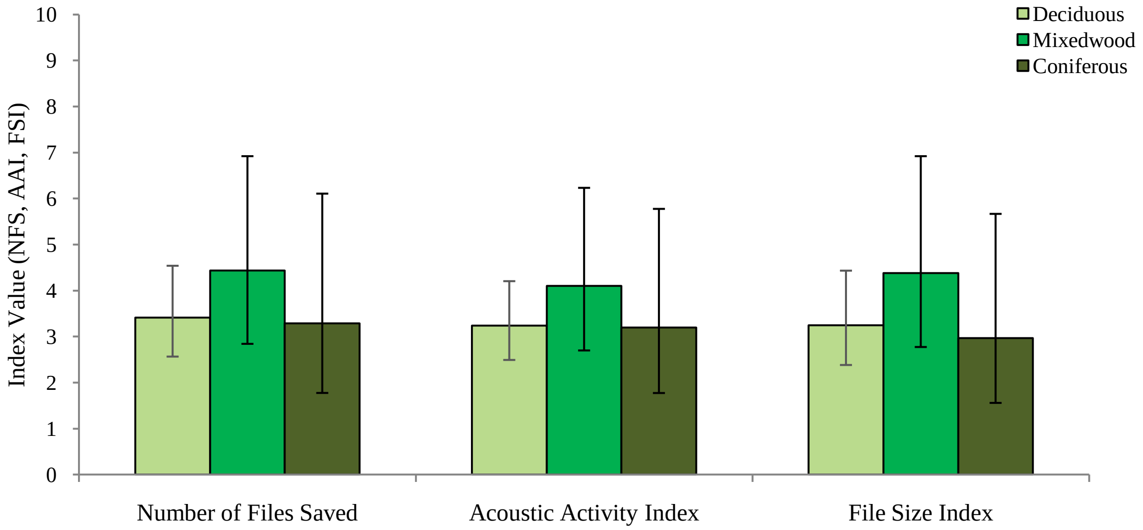


Figure 5. Mean (±SE) bat activity index values for *L. noctivagans* in deciduous, mixed-wood, and coniferous forest cover types in 2009. *L. noctivagans* was not detected at a high enough rate in 2010 for analysis. NFS is the mean number of files saved per survey, AAI is the average number of minutes bats were active per survey, and FSI is the average of the file size (Kb) sums per survey. All means are the geometric means for each forest cover type.

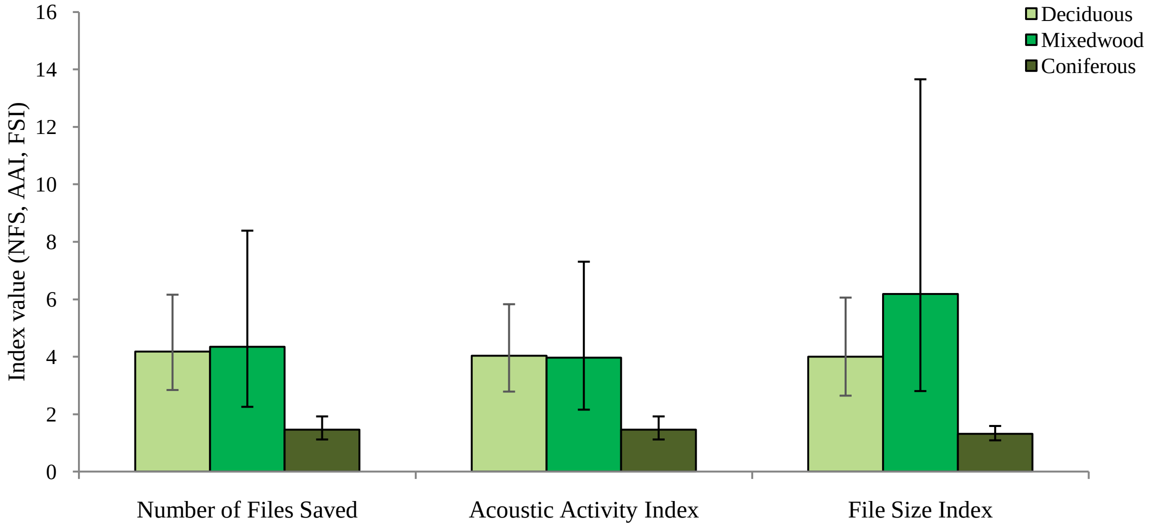


Figure 6. Mean (±SE) bat activity index values for *L. borealis* in deciduous, mixed-wood, and coniferous forest cover types in 2010. *L. borealis* was not detected at a high enough rate in 2009 for analysis. NFS is the mean number of files saved per survey, AAI is the average number of minutes bats were active per survey, and FSI is the average of the file size (Kb) sums per survey. All means are the geometric means for each forest cover type.

Table 2. Significance levels for activity of *Myotis* species, *L. noctivagans*, and *L. borealis* in deciduous, mixed-wood, and coniferous forest cover types sites using the number of files saved (NFS), acoustic activity index (AAI), and file size index (FSI) in 2009 and 2010. The Kruskal-Wallis ANOVA was used for analysis.

Year	**Index**	***Myotis* species**		***L. noctivagans***		***L. borealis***	
		$F_{2,45}$	P	$F_{2,45}$	P		
2009	Number of Files Saved	0.50	0.62	0.11	0.90		
	Acoustic Activity Index	0.60	0.57	0.11	0.90		
	File Size Index	0.30	0.74	0.24	0.79		
		$F_{2,28}$	P			$F_{2,28}$	P
2010	Number of Files Saved	3.40	0.05			1.10	0.36
	Acoustic Activity Index	3.50	0.04			1.10	0.36
	File Size Index	3.40	0.05			1.10	0.36

Bat activity of the common species, *Myotis* species in 2009 and 2010 (Figure 7), *Lasionycteris noctivagans* in 2009 (Figure 8), and *L. borealis* in 2010 (Figure 9) was significantly different at aquatic, linear corridor, and interior forest sites, with similar results for all indices (Table 3). Bat activity using the NFS, AAI, and FSI was always higher at aquatic sites than at interior forest sites. *Myotis* spp. activity at linear corridor sites was also higher than activity at interior forest sites.

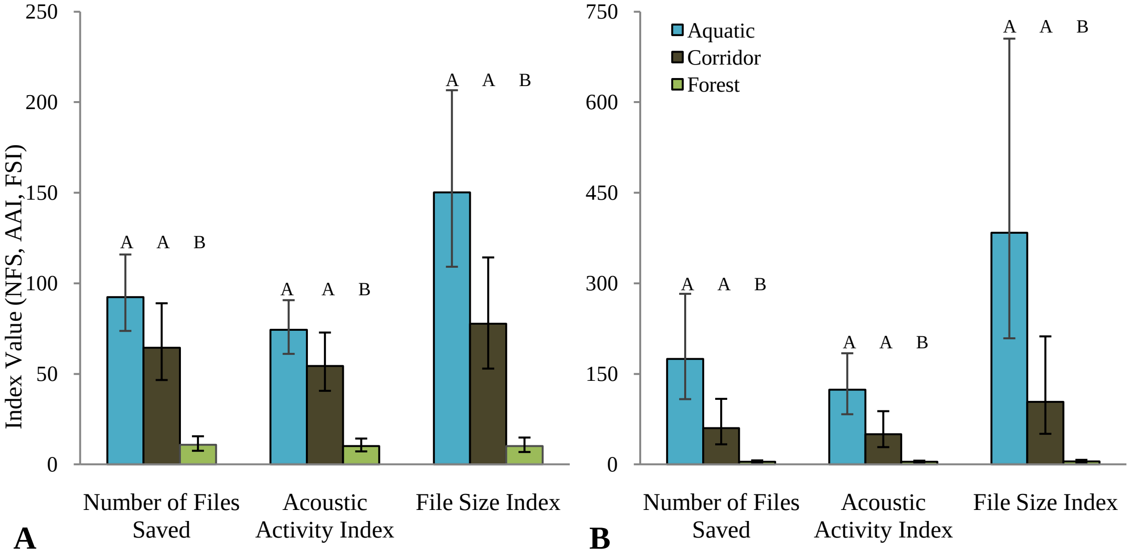


Figure 7. Mean (±SE) bat activity index values for *Myotis* species at aquatic, linear corridor, and interior forest sites in A) 2009 and B) 2010. NFS is the mean number of files saved per survey, AAI is the average number of minutes bats were active per survey, and FSI is the average of the file size (Kb) sums per survey. All means are the geometric means for each microsite type. Brackets with letters indicate significant difference between groups for all three activity indices. Note the difference in scale on the y-axis in 2009 and 2010.

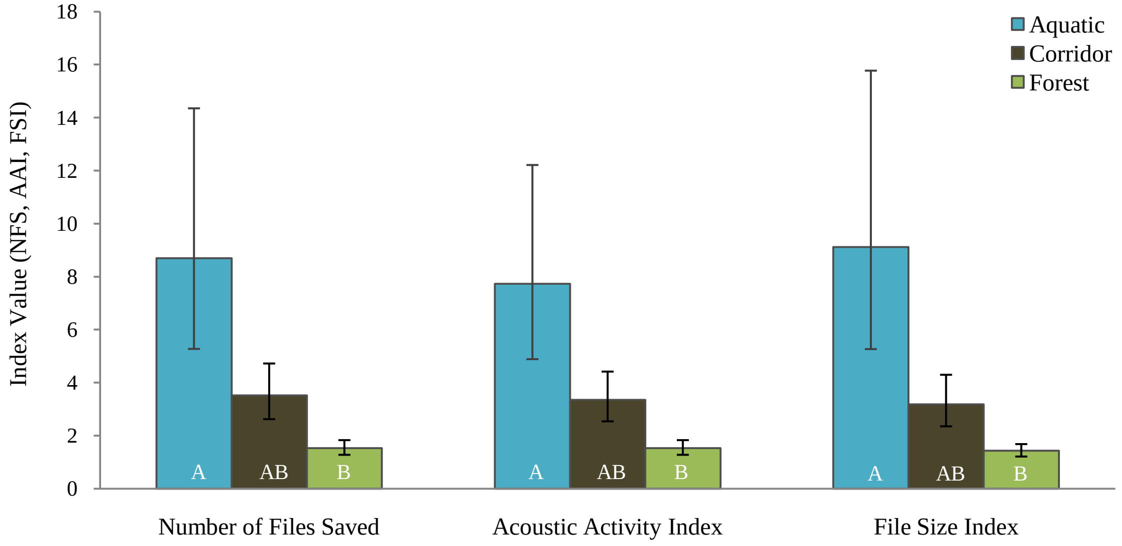


Figure 8. Mean (±SE) bat activity index values for *L. noctivagans* at aquatic, linear corridor, and interior forest sites in 2009. NFS is the mean number of files saved per survey, AAI is the average number of minutes bats were active per survey, and FSI is the average of the file size (Kb) sums per survey. All means are the geometric means for each microsite type. Brackets with letters indicate significant difference between groups for all three activity indices.

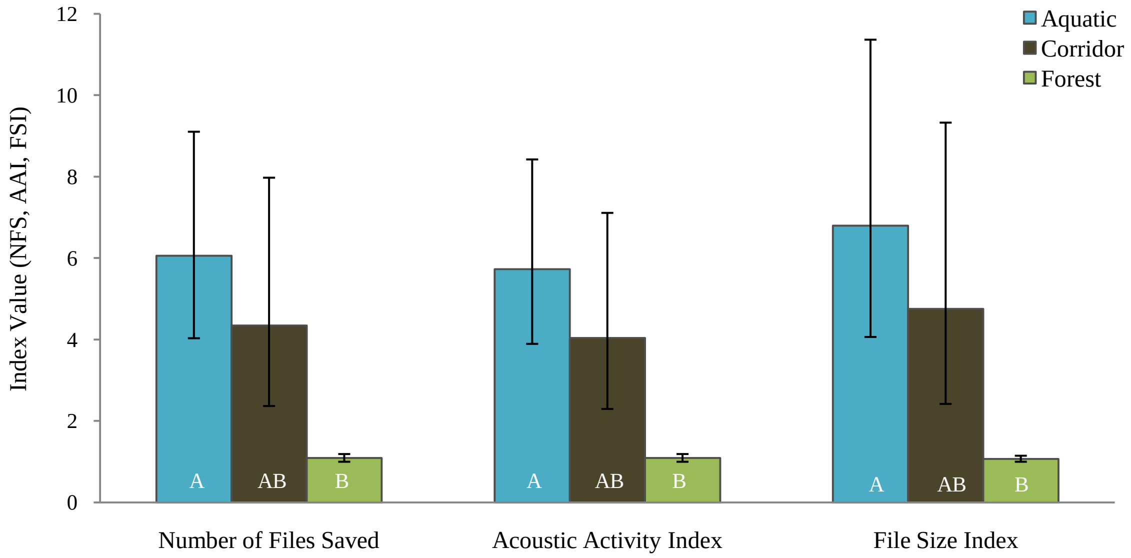


Figure 9. Mean (±SE) bat activity index values for *L. borealis* at aquatic, linear corridor, and interior forest sites in 2010. Sample size was too small for statistical analysis of *L. borealis* habitat use in 2009. NFS is the mean number of files saved per survey, AAI is the average number of minutes bats were active per survey, and FSI is the average of the file size (Kb) sums per survey. All means are the geometric means for each microsite type. Brackets with letters indicate significant difference between groups for all three activity indices.

Table 3. Significance levels for activity of *Myotis* species, *L. noctivagans*, and *L. borealis* at aquatic sites, linear corridors and interior forest sites using the number of files saved (NFS), acoustic activity index (AAI), and file size index (FSI) in 2009 and 2010. The Kruskal-Wallis ANOVA was used for analysis.

Year	**Index**	***Myotis* species**		***L. noctivagans***		***L. borealis***	
		$F_{2,45}$	P	$F_{2,45}$	P		
2009	Number of Files Saved	12.8	<0.001	5.0	0.01		
	Acoustic Activity Index	12.5	<0.001	5.0	0.01		
	File Size Index	13.9	<0.001	5.2	0.01		
		$F_{2,28}$	P			$F_{2,28}$	P
2010	Number of Files Saved	11.6	<0.001			4.90	0.01
	Acoustic Activity Index	11.2	<0.001			4.90	0.01
	File Size Index	10.5	<0.001			4.80	0.02

Vegetation density was significantly higher in interior forest microsites than either aquatic or linear corridor microsites (Welch's ANOVA, $F_{2,35} = 15.4$, $P < 0.001$). Bat activity and vegetation density were weakly negatively correlated at all sites (NFS: $R^2 = 0.11$, $P = 0.01$; AAI: $R^2 = 0.10$, $P = 0.01$; FSI: $R^2 = 0.12$, $P = 0.004$; Figure 10).

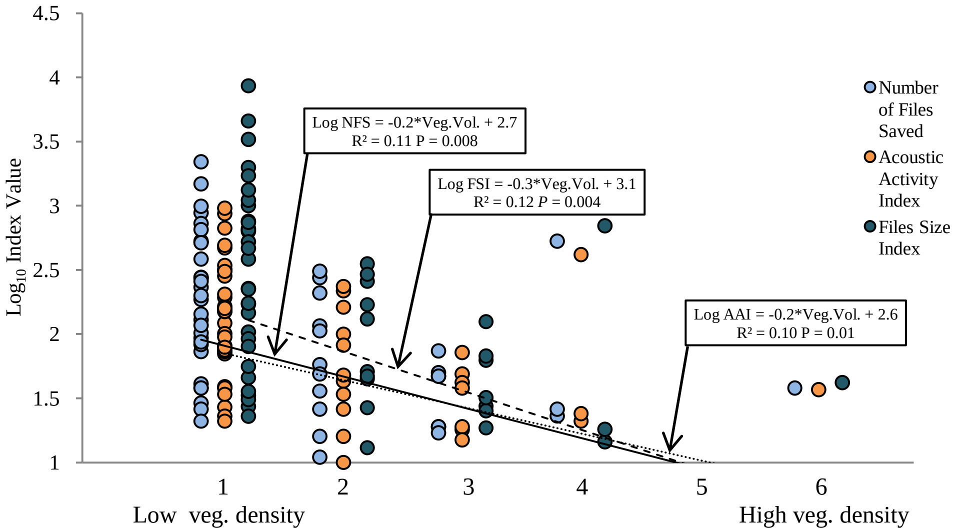


Figure 10. Bat activity with varying levels of vegetation density using NFS, AAI, and FSI. NFS is the mean number of files saved per survey, AAI is the average number of minutes bats were active per survey, and FSI is the average of the file size (Kb) sums per survey. Bat activity index values are $\log_{10}$ transformed. Numbers on the x-axis correspond to the score assigned for vegetation density, with increasing density as numbers increase from 1-6.

We trapped insects at 10 aquatic and 9 linear corridor sites. All identifiable insects trapped were in the orders consumed by bats and included Lepidoptera, Trichoptera, Diptera, Coleoptera, and Neuroptera. Lepidoptera was trapped at 79% of sites. Trichoptera, Diptera, and Coleoptera were trapped at 42%, 32%, and 11% of sites, respectively. Neuroptera was the least common order trapped at 5% of sites. Bat activity was weakly positively correlated with dry weight of insects, with similar results for the NFS, AAI, and FSI (NFS: $R^2 = 0.24$, $P = 0.04$; AAI: $R^2 = 0.23$, $P = 0.04$; FSI: $R^2 = 0.21$, $P = 0.02$; Figure 11).

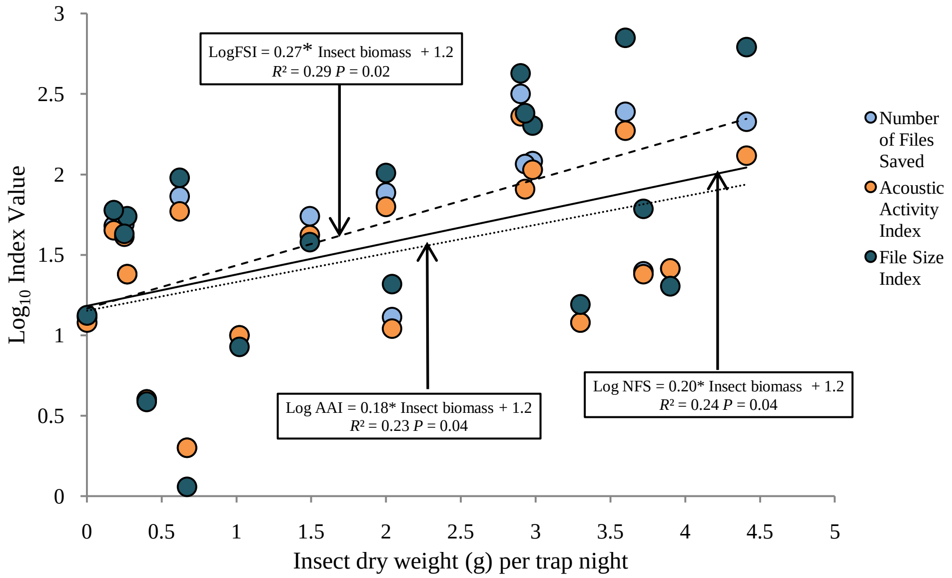


Figure 11. Linear regressions of insect density (dry g/night) and bat activity using $\log_{10}$ transformed NFS, AAI, and FSI. NFS is the mean number of files saved per survey, AAI is the average number of minutes bats were active per survey, and FSI is the average of the file size (kB) sums per survey.

Samples of bat call files containing feeding buzzes had proportionately similar distributions at aquatic, linear corridor, and interior forest sites in 2009 (K-W ANOVA, $F_{2,38} = 2.7$, $P = 0.08$) and 2010 ($F_{2,22} = 1.3$, $P = 0.29$; Figure 12). The sample size for *L. noctivagans*, *L. borealis*, *L. cinereus*, *E. fuscus*, and *P. subflavus* call files containing feeding buzzes was too small for statistical analysis so only the foraging activity from a sample of *Myotis* species files is presented here (Figure 13). The frequency of *Myotis* species feeding buzzes in files was not different at aquatic, linear corridor, and interior forest sites (K-W ANOVA, $F_{2,48} = 0.8$, $P = 0.5$).

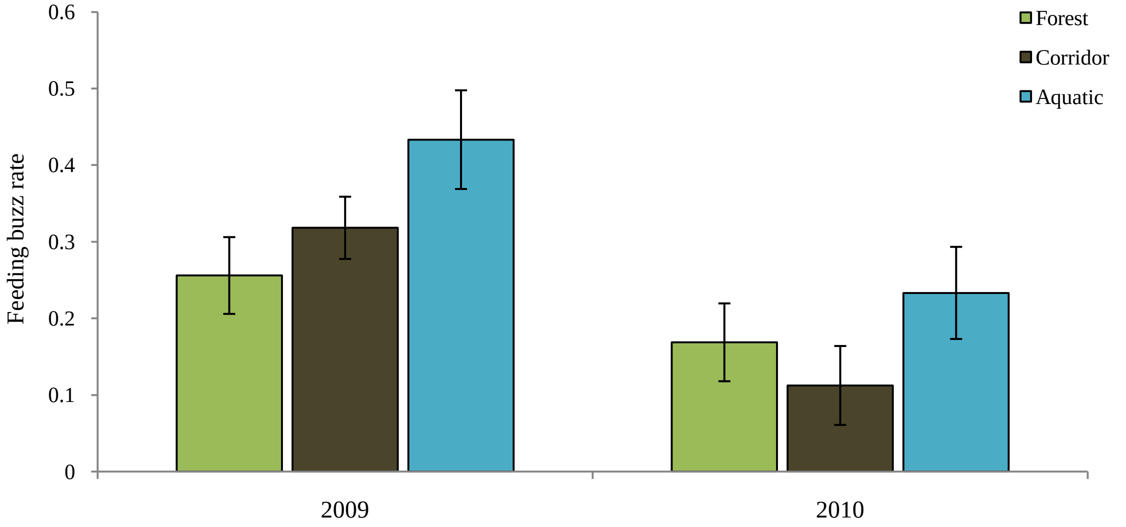


Figure 12. Average (±SE) rate of occurrence of files containing feeding buzzes at aquatic, linear corridor, and interior forest sites from random samples (n = 10) of bat call files from each survey in 2009 and 2010.

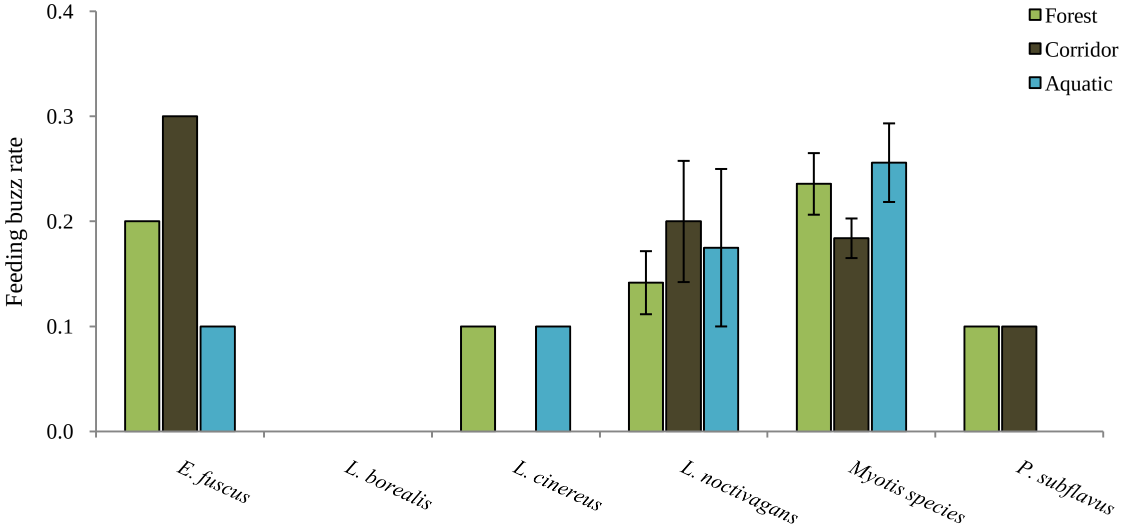


Figure 13. Average (±SE) rate of occurrence of files containing feeding buzzes from each species in random samples (n = 10) of bat call files from each survey in 2009 and 2010.

We expected differences between indices but our interpretation of bat activity was similar regardless of the activity index we used. There were no differences among bat activity indices even though 36% of *Myotis* spp. files were discarded and 27% of *L.*

noctivagans files were discarded when we computed the AAI. Files were discarded because of the higher frequency of occurrence during a one-minute period in surveys. When detected, *Myotis* species were recorded at significantly higher rates (files min^{-1}) than *E. fuscus, L. borealis*, *L. cinereus, P. subflavus,* and *E. fuscus* (K-W ANOVA, $F_{5,244} = 12.9$, $P < 0.001$; Table 4).

Table 4. The mean (±SE) files per minute (files min^{-1}) during acoustic bat surveys in northeastern Minnesota from the acoustic activity index analysis. Different superscript letters indicate significant difference between mean files min^{-1} of each genus or species in the acoustic activity index analysis ($\alpha = 0.05$). Percent omitted is based on the difference between NFS and AAI for each genus or species during 2009 and 2010. Any file from a given species is omitted from analysis if it is recorded within one minute of another file from the same species when calculating the AAI from the NFS.

Acoustic activity index (AAI)		
Species	**files min^{-1} ± SE**	**% omitted**
Myotis species	2.86 ± 0.50^{a}	39%
Lasiurus borealis	1.42 ± 0.16^{b}	29%
Lasionycteris noctivagans	1.32 ± 0.12^{b}	27%
Lasiurus cinereus	1.17 ± 0.06^{b}	19%
Eptesicus fuscus	1.14 ± 0.04^{b}	15%
Perimyotis subflavus	1.12 ± 0.04^{b}	9%

Small-bodied bats produced more kilobytes per second (*kBS*) in call files than large-bodied bats (ANOVA, $F_{5,204} = 20.6$ $P < 0.001$). *L. borealis* had the highest *kBS* and *L. cinereus* had the lowest *kBS* (Table 5). Without the correction factor (*CF*) FSI overrepresented the activity of *Myotis* species by a factor of 2.6 relative to *L. cinereus* because of higher *kBS* in files. Because of the difference in the *kBS* between small- and large-bodied bats, we applied the *CF* based on the ratio of *kBS* between *L. cinereus* and each of the four other species and the *Myotis* species. We applied the *CF* to the random sample of data to standardize the average file size of bat species when using the FSI (Figure 14). The *CF* did not alter the significance level for species habitat use since we used the Kruskal-Wallis ANOVA by ranks, however comparisons between species were standardized.

Table 5. The mean (±SE) kilobytes per second (*kBS*) of a random sample of recorded files for each species in Northeastern Minnesota (n = 30) from the file size index analysis. Small-bodied bat species are: *L. borealis*, *P. subflavus*, *M. lucifugus*, and *M. septentrionalis* (Shump and Shump 1982*a*, Fujita and Kunz 1984, Norberg and Rayner 1987, Caceres 2000). Large-bodied bat species are: *L. noctivagans*, *L. cinereus*, and *E. fuscus* (Kunz 1982, Shump and Shump 1982*b*, Kurta and Baker 1990). *CF* is the correction factor based on the ratio of *kBS* of *L. cinereus* and each species. Different superscript letters indicate significant difference between mean *kBS* of each species in the file size index analysis (α = 0.05).

File size index			
Species	***kBS* ± SE**	***CF***	**Size**
Myotis lucifugus	0.77 ± 0.08^{a}	0.39	Small
Myotis septentrionalis	0.81 ± 0.09^{a}	0.37	Small
Lasiurus borealis	0.91 ± 0.09^{a}	0.33	Small
Lasionycteris noctivagans	0.34 ± 0.03^{b}	0.89	Large
Lasiurus cinereus	0.30 ± 0.04^{b}	1.00	Large
Eptesicus fuscus	0.34 ± 0.04^{b}	0.90	Large
Perimyotis subflavus	0.74 ± 0.09^{a}	0.40	Small

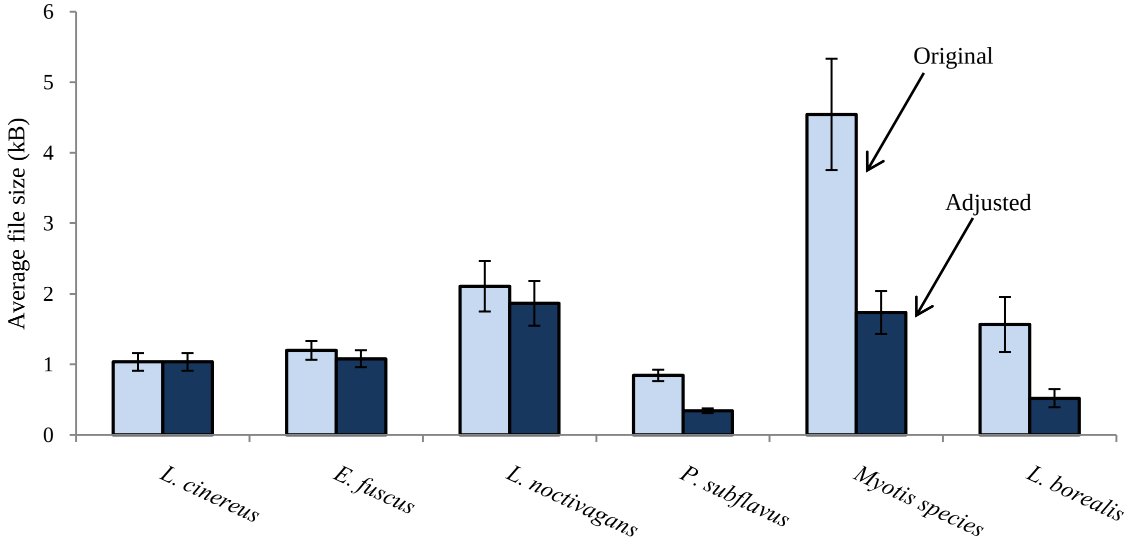
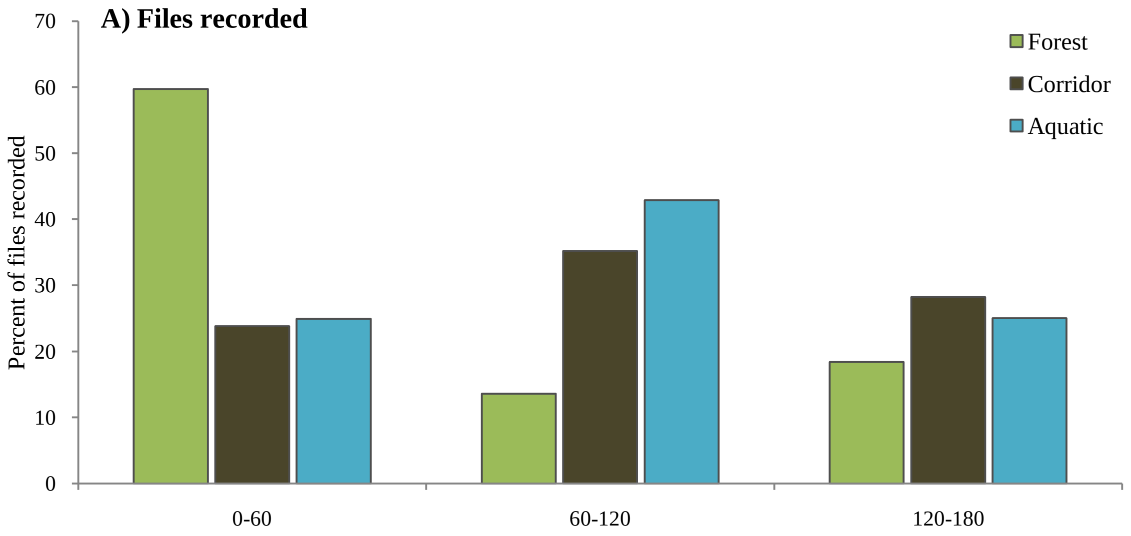


Figure 14. Mean (±SE) file size of a random sample of files (n = 30) from each species. The correction factor (*CF*) is a ratio based on kBS_L, from the species with the lowest *kBS* (*L. cinereus)* and kBS_i, the average kilobytes per second of the *i*th species to standardize the *kBS*. The original file size was calculated before the *CF* was applied, and the adjusted file size was calculated after the *CF* was applied.

Bats in interior forest microsites were active earlier after sunset than bats at aquatic or linear corridor microsites ($x_4^2 = 45$, $P < 0.001$). The factor contributing most to the chi-squared value is the earlier occurrence of bat activity at interior forest microsites from the expected distribution (Figure 15a). There was no significant difference in the time until sunrise of files recorded at aquatic, linear corridor, or interior forest sites. Feeding buzzes were also present in call files earlier in interior forest microsites than aquatic or linear corridor microsites ($x_4^2 = 69$, $P < 0.001$). The factor contributing most to the chi-squared value is the earlier occurrence of feeding buzzes at interior forest microsites from the expected distribution (Figure 15b).



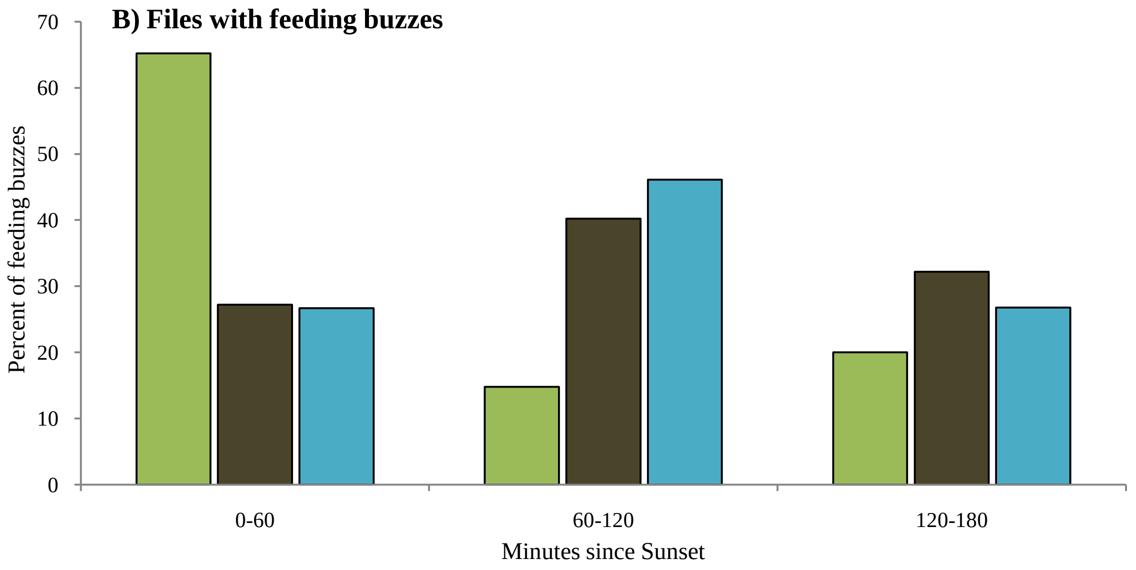


Figure 15. Frequency distribution of the time since sunset (60 minute bins) of A) acoustic bat files recorded before midnight and B) feeding buzzes recorded before midnight at aquatic, linear corridor, and interior forest sites.

The temporal activity of *E. fuscus*, *Myotis* species, *L. noctivagans*, *L. borealis,* and *P. subflavus* was bimodal, with the first activity peak within the first two hours after sunset, and the second peak just before sunrise (Figure 16). *L. cinereus* activity was high just after sunset, but there also were three other peaks in activity throughout the night.

Bat activity in the months of May, June, and September are bimodal with peaks just after sunset and before sunrise. Bat activity in July and August occurred at all times of the night, with slight increases in activity just after sunset and before sunrise (Figure 17).

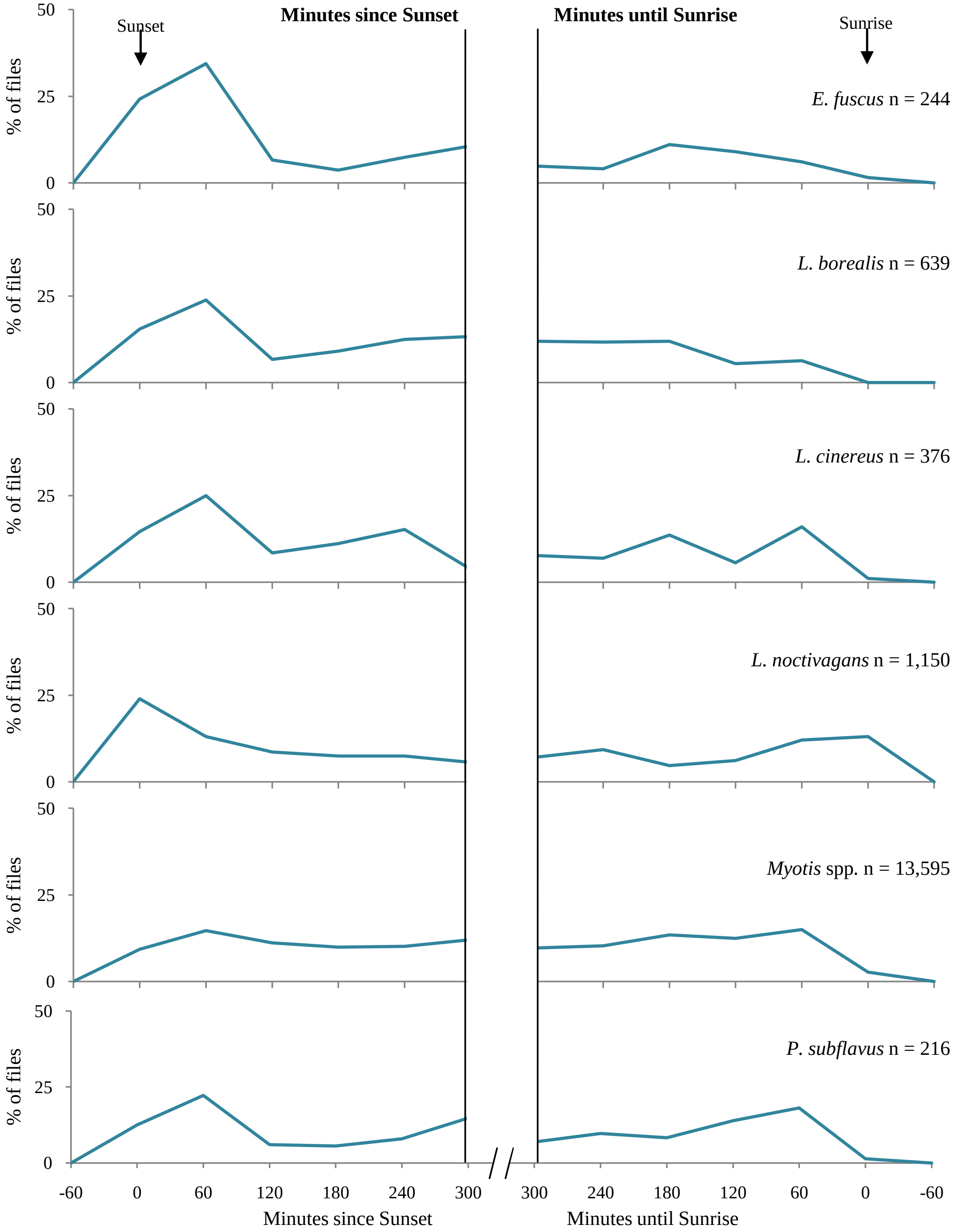


Figure 16. Frequency distribution with 60 minute bins showing the temporal activity of northeastern Minnesota during the 2009 and 2010 study. The time of each file was converted to minutes since sunset and minutes until sunrise. Black arrows indicate the start and end of the night. The dotted line indicates the switch between minutes since sunset and minutes until sunrise.

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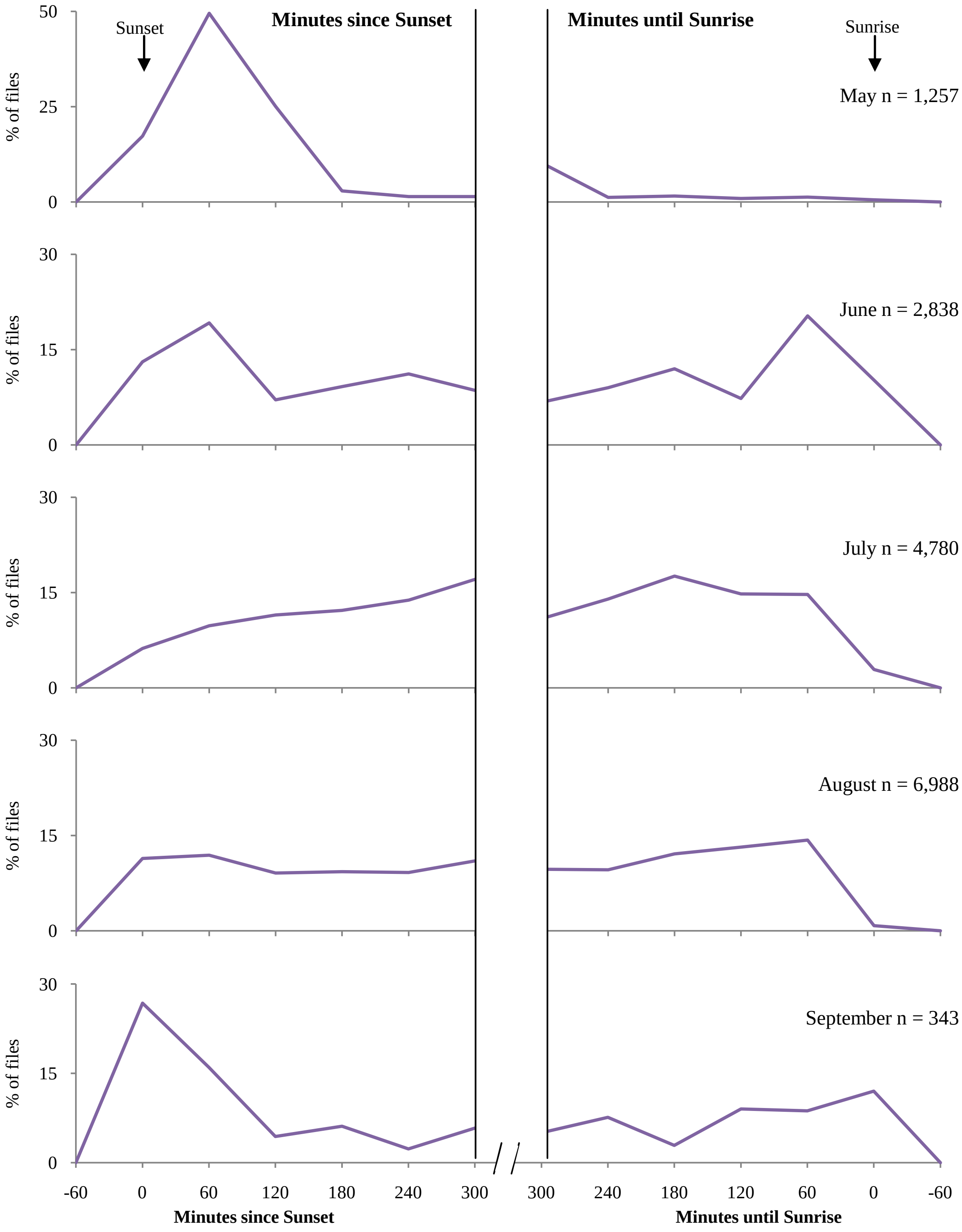

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Figure 17. Frequency distribution with 60 minute bins showing the temporal activity by month of northeastern Minnesota bats combined in 2009 and 2010. The time of each file was converted to minutes since sunset and minutes until sunrise. Black arrows indicate the start and end of the night. The dotted line indicates the switch between minutes since sunset and minutes until sunrise.

We excluded one linear corridor site as an outlier in 2010 because of its unusual characteristics. 6,140 acoustic files were recorded over three nights, which was 40% of all files recorded in 2010. 98% of files were *Myotis* spp. and 2% were *L. noctivagans* and *L. borealis*. 4.4 ± 0.03 files were recorded per minute at this site and bat activity was consistently high during the entire night for three nights. 77% of a sample of files from this site contained feeding buzzes whereas only 28 ± 2% of files from other sites contained feeding buzzes.

Discussion

Using bat detectors along the North Shore of Lake Superior in Minnesota, we recorded all seven resident bat species (Hazard 1982, Caceres 2000). *Myotis lucifugus, M. septentrionalis, Lasiurus cinereus, L. borealis, Lasionycteris noctivagans*, and *Eptesicus fuscus* were all within the extent of their range, of which Minnesota is in the northern portion. *Perimyotis subflavus* is at the northern-most extent of its range in Minnesota but our records of *P. subflavus* extended 161 km further northeast along the North Shore than previous records in Minnesota (Hazard 1982, Nordquist 2006). Even though we detected all seven species, 84% were *Myotis* species. The overwhelming presence of the *Myotis* genus is consistent with a recent study conducted in northeastern Minnesota (Kruger and Peterson 2008, Miller 2010). *E. fuscus* make up a significant portion of the species composition during the spring and fall on the North Shore (Nordquist 2006), but our results from the summer months did not reflect this.

We placed bat detectors in deciduous, mixed-wood, and coniferous forests, but we found bats at aquatic and linear corridor sites regardless of forest type. Bats are active in all forest cover types to some degree (Walsh and Harris 1996, Kalcounis *et al.* 1999, Patriquin and Barclay 2003, Broders *et al.* 2006). Linear corridors and aquatic features within forested habitats are important for bats in northeastern Minnesota. Even though bats may have been using corridors to commute to aquatic habitats, which are thought to have more insects (Krusic *et al.* 1996, Grindal *et al.* 1999), feeding buzzes indicate that bats were also encountering prey in linear corridors. The confounding effect of aquatic and linear corridor features present in all forest types may explain the inconsistent conclusions of forest type use and preference in bat literature. North Shore streams were always present historically but roads and trails were not always at their current density, nonetheless bats are currently benefiting from both. Stream corridors will continue to be maintained with current forest management efforts, but road and trail density may change with shifting management goals.

Aquatic and linear corridor sites had 5-10 times more bat activity than interior forest sites even though interior forest sites were only 100 m from the forest edge in all forest types. Additionally, bat activity began earlier at interior forest sites than at aquatic or linear corridor sites. Bats use the interior forest for roosting during the day and leave shortly after sunset to commute to foraging habitats (Thomas 1988, Grindal and Brigham 1999, Kalcounis *et al.* 1999, Hayes and Gruver 2000), but we found evidence that bats also forage as they commute through the interior forest. Light intensity, among other factors, is important in determining insect (Lewis and Taylor 1964, Brittain 1982, McGeachie 1989) and bat activity (Jones and Rydell 1994, Lang *et al*. 2006). The lower light level in interior forest at dusk enables nocturnal flying insects to become active earlier than in open habitats and bats respond accordingly. However, significantly less bat activity 50, 100, and 150 m from the forest edge (Krusic *et al.* 1996) implies that although bats do forage in interior forest early in the evening, bats concentrate their foraging effort at forested aquatic and linear corridor habitats for the remainder of the foraging period. An implication to improve bat survey efforts in temperate forested areas is the early period of bat activity in interior forest and the later concentration of bat activity at aquatic and corridor features.

The rather flat relationship between relative insect abundance and bat activity suggests that food is not a limiting resource in northeastern Minnesota. Adult aquatic insects emerge from the abundant water bodies throughout the summer because of different timing and length of emergence periods of different insect species (Judd 1962). Even though food may not be a limiting factor, bats still respond to insect swarms (Jones and Rydell 2003). Further evidence for this is the survey we treated as an outlier in 2010, with a disproportionately high rate of both bat activity and occurrence of feeding buzzes. The patchy distribution of aquatic insects in northeastern Minnesota may be a source of variability too large for insect light trapping alone to reveal a stronger relationship between bat activity and relative insect abundance.

There was high variation in bat activity among nights, surveys, and months during the summer. Similar levels of variation in bat activity have been found in Oregon (Hayes and Adam 1996, Hayes 1997), New Brunswick, Canada (Broders 2003), and Germany

(Kusch and Idelberger 2005) over one season. Bat distribution varies spatially and temporally due to the differences in distributions of insect prey (Kusch and Idelberger 2005), among other factors (Ciechanowski *et al.* 2007). The variation in our bat activity data may be due to the spatial and temporal shifts in distribution of bats in their response to patchy insect distributions. Our sampling effort was enough to identify bat habitat use, but not to capture patterns in population-level variability. Surveying sites for multiple years or singly with multiple stationary bat detector sites over the entire season would have allowed us to address this issue further.

The acoustic activity index (AAI) was developed to address the bias of individual bats repeatedly passing bat detector microphones. The benefit of the AAI is the removal of call files from those bats repeatedly passing the detector (Miller 2001). The cost of the AAI is that data is being discarded, for example the loss of 1/3 of our entire dataset seems excessive. *Myotis* species files were nearly three times more likely to be discarded because more calls per minute were recorded compared to other species. Bats in the genus *Myotis* are morphologically adapted for slow but maneuverable flight. Open-adapted bats are unable to maneuver in tight spaces (Norberg and Rayner 1987) and the same individual would be less likely to be recorded more than once per minute. Clutter-adapted and open-adapted bats are differentially affected by the AAI because of their use of different flight strategies.

The file size index (FSI) was developed to account for the lengths of bat call sequences in acoustic files (Broders 2003). Implicit in the FSI is the assumption that kilobytes per second (*kBS*) of calls are the same among bat species, but we found that the *kBS* varied among species. Small-bodied bats in Minnesota had higher *kBS* than large-bodied bats. Insectivorous bats couple echolocation with wing beat frequency to produce one or fewer calls per wing beat (Jones 1994, Holdereid and von Helversen 2003). Because wing beat frequency is inversely related to body mass (Jones 1994), small-bodied bats emit calls more frequently and produce more *kBS* in acoustic files. Because of the difference in *kBS* among bats of different sizes, the FSI as originally defined would over represent small-bodied bats. Prior to using the FSI in future studies, the *kBS* of each species can be measured and if needed, a correction factor (*CF*) should be applied to standardize the *kBS* when relative abundance of species is being compared.

Conclusions of habitat use in this study are based on the most commonly recorded species in the study area, *Myotis lucifugus* and *M. septentrionalis* collectively, and *L. noctivagans* and *L. borealis*. Bats preferentially used aquatic and linear corridor features for commuting and foraging regardless of forest type. Conclusions from the statistical tests were consistent for all three bat activity indices even though 1/3 of our data from the *Myotis* species, *L. noctivagans*, and *L. borealis* was discarded. Using the AAI elsewhere with different bat species composition could cause indices to provide different results. The NFS and FSI are the preferred methods to show true relative habitat use because potentially useful habitat selection data is discarded when calculating the AAI. The correction factor standardized the larger *kBS* and reduced the overrepresentation of small-bodied bats in northeastern Minnesota. Although non-parametric methods of analysis prevented any change in statistical conclusions here, in regions where bat species are more evenly distributed or if parametric statistics are possible, *kBS* levels that are not standardized prior to using the FSI may result in different statistical conclusions than the NFS or AAI. All three indices are easily applied to an acoustic dataset, and in areas of high bat diversity, the use of multiple activity indices would be the most complete way to evaluate bat activity and habitat use when using bat detectors.

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Appendices

Appendix A. Mean index values for bat species in northeastern Minnesota during 2009 and 2010. Adjusted FSI is the mean sum of files sizes for each survey after we applied the correction factor (*CF*) to the dataset.

		NFS	**AAI**	**FSI**	**Adjusted FSI**
Year	**Species**	**Mean number of files saved (files)**	**Mean minutes present per survey (min)**	**Mean sum of file size per survey (kB)**	**Mean sum of adjusted file size per survey**
2009	*E. fuscus*	3.1 ± 1.3	2.6 ± 1.0	4.2 ± 1.9	3.7 ± 1.7
	L. borealis	1.5 ± 0.8	1.0 ± 0.5	1.6 ± 0.9	0.5 ± 0.3
	L. cinereus	4.2 ± 2.2	3.1 ± 1.4	4.2 ± 2.4	4.2 ± 2.4
	L. noctivagans	17.9 ± 8.1	11.8 ± 4.3	27.3 ± 16.3	24.2 ± 14.4
	Myotis species	119.2 ± 33.2	86.9 ± 21.8	220.6 ± 72.6	84.2 ± 27.7
	P. subflavus	2.7 ± 1.0	2.4 ± 0.9	3.0 ± 1.2	1.2 ± 0.5
2010	*E. fuscus*	4.5 ± 1.5	4.0 ± 1.3	8.1 ± 3.4	7.2 ± 3.1
	L. borealis	18.2 ± 10.0	13.2 ± 6.6	30.8 ± 15.4	10.2 ± 5.1
	L. cinereus	5.7 ± 1.8	5.2 ± 1.6	5.7 ± 2.0	5.7 ± 2.0
	L. noctivagans	10.0 ± 2.6	9.2 ± 2.3	22.2 ± 8.5	19.6 ± 7.5
	Myotis species	238.5 ± 78.7	138.3 ± 35.6	756.8 ± 307.3	289.0 ± 117.3
	P. subflavus	2.8 ± 1.2	2.6 ± 1.1	2.4 ± 1.0	1.0 ± 0.4